Photosynthesis, Morphology, Yield, and Phytochemical Accumulation in Basil Plants Influenced by Substituting Green Light for Partial Red and/or Blue Light

Haijie Dou

Department of Horticultural Sciences, Texas A&M University, College Station, TX 77843

Genhua Niu

Department of Horticultural Sciences, Texas A&M AgriLife Research Center at El Paso, Texas A&M University System, 1380 A&M Circle, El Paso, TX 79927

Mengmeng Gu

Department of Horticultural Sciences, Texas A&M AgriLife Extension Service, College Station, TX 77843

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Abstract. Green light penetrates deeper into the plant canopy because of its high transmittance and reflectance, and may potentially increase light interception and whole-canopy photosynthesis, whereas red and blue light is absorbed primarily by upper leaves. Moreover, green light induces shade avoidance responses and regulates secondary metabolism in plants. In this study, we investigated the effects of substituting partial red and/or blue light with green light on plant growth and development in basil (*Ocimum basilicum*) ‘Improved Genovese Compact’ (green) and ‘Red Rubin’ (purple) plants. There were four treatments: one combined red and blue (R&B) light treatment, R₇₆B₂₄ [the proportion of red (R) and blue (B) light was 76% and 24%, respectively]; and three green (G) light treatments—R₄₄B₂₄G₃₂, R₇₄B₁₆G₁₀, and R₄₂B₁₃G₄₅—with green light proportions of 32%, 10%, and 45%, respectively. The experiment was conducted in a growth room and the photosynthetic photon flux density (PPFD) of all treatments was set at 220 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with a 16-h photoperiod. Plants were subirrigated as needed using a nutrient solution with an electrical conductivity (EC) of 2.0 $\text{dS}\cdot\text{m}^{-1}$ and a pH of 6.0. The net photosynthetic rate (P_n) in lower leaves was unaffected by green light treatments in green basil plants, whereas in purple basil plants it increased by 59% and 45% under treatments R₄₄B₂₄G₃₂ and R₇₄B₁₆G₁₀, respectively, compared with the combined R&B light. In green basil plants, treatments R₄₄B₂₄G₃₂ and R₄₂B₁₃G₄₅ induced stem elongation, but green light treatments showed no effects on petiole elongation, leaf expansion, leaf thickness, or plant yield. In purple basil plants, treatments R₄₄B₂₄G₃₂ and R₄₂B₁₃G₄₅ induced stem elongation and decreased leaf thickness and plant yield, but only the R₄₂B₁₃G₄₅ treatment induced petiole elongation, and green light treatments showed no effects on leaf expansion. Concentrations of anthocyanin, phenolics, and flavonoids, and antioxidant capacity in green basil leaves showed no differences between treatments R₇₆B₂₄ and R₄₄B₂₄G₃₂, but decreased under treatments R₇₄B₁₆G₁₀ and R₄₂B₁₃G₄₅. Concentrations of phenolics and flavonoids, and antioxidant capacity in purple basil leaves showed no differences between treatments R₇₆B₂₄ and R₇₄B₁₆G₁₀, but decreased under treatments R₄₄B₂₄G₃₂ and R₄₂B₁₃G₄₅. Combining plant yield, nutritional values, and the working environment for growers, a white light with low green light proportion ($\approx 10\%$) is recommended for basil production in a controlled environment.

Plants sense and respond to a broad range of light spectra from ultraviolet to far-red regions, whereas photosynthetically active radiation [including blue (400–499 nm), green (500–599 nm), and red (600–700 nm) lights] significantly affects plant photosynthesis, morphology, and secondary metabolism (Amaki et al., 2011; Brazaityte et al., 2016). The development of light-emitting diode (LED) technology provided researchers opportunities to regulate plant

yield and nutritional quality using different light wavelengths, which has proved to be a good tool for plant production under controlled environment (Bantis et al., 2018; Dou et al., 2017; Piovene et al., 2015).

Among all light spectra, red and blue lights have the most important wavelengths for plant biomass accumulation by affecting plant photosynthesis and photomorphogenesis (McCree, 1972). It was reported that dominant red light with supplemental blue

light achieved greater shoot fresh weight (FW) and dry weight (DW) in a range of plant species such as lettuce (*Lactuca sativa*) (Martineau et al., 2012; Tamulaitis et al., 2005), radish (*Raphanus sativus*) (Tamulaitis et al., 2005), strawberry (*Fragaria xananassa*) (Nhut et al., 2003), and lily (*Lilium*, ‘Pesaro’) (Lian et al., 2002), compared with monochromatic red or blue light. Leaf area, shoot FW, and shoot DW in spinach (*Spinacia oleracea*) and nonheading Chinese cabbage (*Brassica campestris* ‘Te Ai Qing’) increased under combined R&B light compared with monochromatic red or blue light (Fan et al., 2013; Ohashi-Kaneko et al., 2007). Similarly, leaf area and shoot FW in Chinese cabbage (*Brassica alboglabra*) grown under combined R&B light increased by 36% to 121% and 34% to 119% compared with plants grown under monochromatic blue light, respectively (He et al., 2015).

Compared to red and blue lights, green light is less studied because of its low absorptivity coefficient in the absorption spectra of chlorophylls compared with red or blue light. However, green light penetrates deep into the mesophyll layers at a single-leaf level and the lower leaves at a canopy level, therefore driving photosynthesis, whereas red and blue wavelengths are absorbed mostly by the upper leaves (Meng et al., 2019; Tera-shima et al., 2009; Wang and Folta, 2013). It was reported that the absorption of brief flashes of 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ monochromatic blue, red, and green light from the adaxial to abaxial surface of spinach leaves was at depths of 50, 100, and 150 μm , respectively (Vogelmann and Han, 2000). In a living leaf or whole-plant canopy, the relative quantum efficiency of green light is 0.87, which is slightly less than red light (0.91), but greater than blue light (0.73) (Sager et al., 1988). Theoretically, quantum yield of a dense plant canopy should be more equalized under green light as a result of increased light interception by lower leaves, which could potentially increase whole-canopy photosynthesis and, subsequently, increase plant yield. In fact, Paradiso et al. (2011) validated that canopy quantum efficiency of green light was not much less than that of red light in ‘Akito’ rose (*Rosa*). Kim et al. (2004) also reported that substituting partial red light with green light increased leaf area and shoot FW and DW in ‘Waldmann’s Green’ lettuce by 31%, 45%, and 47%, respectively, compared with plants grown under combined R&B light.

Green light also contributes to plant growth, which can induce shade avoidance responses (i.e., stem elongation, leaf expansion, and petiole elongation) and alter secondary metabolism in plants (Meng et al., 2019). It was reported that known photoreceptors such as phytochromes and cryptochromes can respond to green light as a result of their broad-band absorption spectrum that tails into the green light wavelength (Smith et al., 2017). Consistently, plant responses to green light showed a tendency to counteract blue or red light-induced responses, such as inhibition of stem elongation, stomatal opening,

and anthocyanin accumulation (Talbot et al., 2006; Zhang and Folta, 2012). It is postulated that shade avoidance responses induced by green light could increase light interception by a larger plant canopy, subsequently increasing whole-plant photosynthesis and resulting in a greater plant yield. For example, leaf length and width of 'Rex' and 'Rouxai' lettuce and 'Siberian' kale plants, and shoot FW of 'Siberian' kale plants all increased under green light compared with combined R&B light (Meng et al., 2019). Stomatal opening stimulated by blue light was reversed by green light in a range of plant species such as *Arabidopsis thaliana*, broadbean (*Vicia faba*), pea (*Pisum sativum*), dayflower (*Commelina communis*), and two tobacco species (*Nicotiana tabacum* and *N. glauca*) (Frechilla et al., 2000; Talbot et al., 2002). Furthermore, increasing green light proportions significantly decreased anthocyanin concentration in *Arabidopsis* and 'Red Sails' lettuce plants (Zhang and Folta, 2012; Zhang et al., 2011).

Inclusion of green light in growth light sources has also been shown to be beneficial for human-based diagnostics of plant health. Combined R&B light produces a purple light that causes plants to look gray/black, making visualization of plant health status difficult for growers, whereas inclusion of green light gives plants a green appearance and makes diagnostics of pests, disease, or nutrient deficiency much easier (Smith et al., 2017). In addition, the inclusion of green light showed other beneficial effects on plant growth. For example, Bian et al. (2016, 2018) reported that the photosynthetic capacity (photosynthetic rate, maximum photosynthetic efficiency in dark-adapted and light-adapted leaves, and photochemical quenching) in 'Butterhead' lettuce plants decreased under continuous R&B light as a result of photoinhibition, but increased in plants grown under continuous white (supplemental green light to combined R&B light) light. This indicates that inclusion of green light could alleviate photoinhibition and maintain high photosynthetic capacity in plants grown under continuous R&B light. Inclusion of green light also induced disease resistance to anthracnose (*Glomerella cingulata*) in 'Sachinoka' strawberry plants grown in the field (Kudo et al., 2011).

Previous studies raise the hypothesis that substituting green light for red and/or blue light may increase plant photosynthesis and yield, as well as alter plant secondary metab-

olites accumulation. Therefore, in our study, we chose basil (*Ocimum basilicum*) as a model plant and substituted partial red and/or blue light with green light at different green light proportions to investigate the effects of green light on plant photosynthesis, morphology, growth, and secondary metabolism.

Materials and Methods

Plant material and growing conditions

The experiment was conducted in a walk-in growth room with vertical grow racks in the Texas A&M AgriLife Research Center at El Paso, TX, using green basil 'Improved Genovese Compact' and purple basil 'Red Rubin' plants (Johnny's Selected Seeds, Winslow, ME). For both cultivars, one seed per cell was sown in 72 square cell trays (cell size: length, 3.86 cm; height, 5.72 cm; volume, 59 cm³) with Metro-Mix 360 (peat-moss 41%, vermiculite 34%, pine bark 25%; Sun Gro® Horticulture, Bellevue, WA). All trays were put under mist in a greenhouse for germination. Seedlings were moved out from beneath the mist after germination and were grown in a greenhouse for 2 weeks. Seedlings were then transplanted to 4-inch² pots (length, 9.52 cm; height, 8.26 cm; volume, 574 cm³) with Metro-Mix 360 when roots were visible on the outside of the plug root ball. Uniform plants were selected and moved to the walk-in growth room for different treatments. A vertical grow rack with four shelves was used, and each shelf was designated with one treatment.

All plants were subirrigated manually with a nutrient solution containing 1.88 g·L⁻¹ (277.5 ppm N) 15N-2.2P-12.5K (Peters 15-5-15 Ca-Mg Special; The Scotts Company, Marysville, OH) as needed. The nutrient solution was mixed and stored in a 100-gallon tank with a lid, and EC and pH were adjusted to 2.01 ± 0.06 dS·m⁻¹ and 5.98 ± 0.03, respectively, using an EC/pH meter (Model B-173; Horiba, Ltd., Kyoto, Japan). Planting density of both basil cultivars was 79 plants/m². Plant canopy temperature of each treatment was recorded every 30 min using a type T thermocouple connected to a data logger (CR1000; Campbell Scientific, Logan, UT). The average plant canopy temperature of four treatments throughout the experiment period was 24.0 ± 0.15/21.6 ± 0.18 °C day/night. The carbon dioxide (CO₂) concentration in the growth room

was recorded (LI-830; LI-COR, Lincoln, NE) every 5 min, and the average CO₂ concentration throughout the experiment was 418 ± 8 μmol·mol⁻¹. Mechanical mini fans (LS1225A-X; AC Infinity, City of Industry, CA) were used for air circulation to achieve uniform temperatures across treatments. All plants were harvested when plant height reached about 25 cm, which was 21 and 28 d after treatment (42 and 53 d after sowing) for green and purple basil plants, respectively. There were 12 plants per treatment for each experiment.

Green light treatments

There were four different light-quality treatments: the combined R&B light treatment as the control, R₇₆B₂₄ (the proportion of red and blue light was 76% and 24%, respectively; model GEHL48HPPB, Hort Americas, Bedford, TX), substituting partial red light with green light; R₄₄B₂₄G₃₂, reducing the red light proportion from 76% to 44% with the addition of 32% green light (ESW X6; Illumitex, Austin, TX), substituting partial blue light with green light; R₇₄B₁₆G₁₀, reducing the blue light proportion from 24% to 16%, with the addition of 10% green light (ESW F3; Illumitex), and substituting partial red and blue lights with green light; R₄₂B₁₃G₄₅, reducing both red and blue light proportions with the addition of 45% green light (model GEHL48HWTB; Hort Americas, Bedford, TX) (Table 1, Fig. 1). *PPFD* of each treatment was set at the same level of 220 ± 10 μmol·m⁻²·s⁻¹ with a 16-h photoperiod, and *PPFD* was measured 15 cm underneath the light sources at nine spots for each treatment using a PS-100 spectroradiometer (Apogee Instruments, Logan, UT). To minimize light distribution being disproportionate within each treatment, all plants were rearranged systematically every 3 d.

Measurements

Gas exchange rates. A portable gas exchange analyzer (CI-RAS-3; PP Systems International, Amesbury, MA) was used to measure the photosynthetic capacity of basil leaves at harvest, including comparative P_n, the transpiration rate (E), and stomatal conductance (g_s). A PLC3 leaf cuvette (PP System International, Amesbury, MA) with LED light unit (white light, in which the proportion of red, blue, and green light was 38%, 25%, and 37%, respectively) was used, and *PPFD*, relative air humidity, and CO₂

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G.N. is the corresponding author. E-mail: gniu@ag.tamu.edu.

Table 1. Light spectral distribution of different light-quality treatments: R₇₆B₂₄, R₇₄B₁₆G₁₀, R₄₄B₂₄G₃₂, and R₄₂B₁₃G₄₅.

Wavelength	Single-band photon flux density (μmol·m ⁻² ·s ⁻¹)			
	R ₇₆ B ₂₄	R ₄₄ B ₂₄ G ₃₂	R ₇₄ B ₁₆ G ₁₀	R ₄₂ B ₁₃ G ₄₅
Blue	53	54	36	28
Green	—	70	22	98
Red	169	97	165	93
<i>PPFD</i> ²	222	221	223	219

²Photosynthetic photon flux density (*PPFD*, 400–700 nm) was measured using a PS-100 spectroradiometer (Apogee Instruments, Logan, UT).

Subscript numbers indicate the proportions of red (R, 600–699 nm), blue (B, 400–499 nm), and green (G, 500–599 nm) light in the total light intensity.

Fig. 1. Light spectral distribution of four light-quality treatments: R₇₆B₂₄ [subscript numbers indicate the proportions of red (R, 600–699 nm), blue (B, 400–499 nm), and green (G, 500–599 nm) light in the total light intensity], R₇₆B₁₆G₁₀, R₄₄B₂₄G₃₂, and R₄₂B₁₃G₄₅. Photosynthetic photon flux density (PPFD; 400–700 nm) and light spectral distribution were measured using a PS-100 spectroradiometer (Apogee Instruments, Logan, UT).

concentration inside the leaf chamber were kept constant at 800 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 50%, and 390 $\mu\text{mol}\cdot\text{mol}^{-1}$, respectively. The third and fifth pair of leaves from the top were used for measuring the upper and lower leaves gas exchange rate, respectively, in both green and purple basil plants. Measurements were taken when P_n reached a steady state.

Relative chlorophyll content. The soil-plant analysis development (SPAD) index of basil leaves was measured at harvest to quantify relative chlorophyll content in basil leaves using a chlorophyll meter SPAD-502 (Konica-Minolta Co., Ltd., Osaka, Japan). The third pair of leaves from the top were used for measurement. Three measurements were taken for each plant and the average was recorded for data analysis.

Growth characteristics. Growth characteristics such as plant height, plant width (average of the widest point of plant canopy and its perpendicular width), and number of internodes were recorded at harvest. Five plants per treatment were selected randomly for measurement. Leaf area was measured using a leaf area meter (LI-3100; LI-COR), and shoot FW was recorded at harvest. Specific leaf area was calculated (leaf area per unit leaf DW) and used as an indicator of leaf thickness. Shoot tissues were dried at 80 °C in a drying oven (Grieve, Round Lake, IL) for 3 d to determine the shoot DW and root DW.

Secondary metabolites. Five plants were selected randomly at harvest for the measurement of secondary metabolites in basil leaves, including concentrations of anthocyanin, phenolics, and flavonoids, and antioxidant capacity. Fresh basil leaves were collected in a cooler and stored immediately in a deep freezer (IU1786A; Thermo Fisher Scientific, Marietta, OH) at –80 °C until phytochemical analysis.

Extraction. About 2 g fresh basil leaves were ground in liquid nitrogen and extracted with 15 mL 1% acidified methanol at 4 °C in darkness. After overnight extraction, the mixture was centrifuged (Sorvall RC 6 Plus

Centrifuge; Thermo Fisher Scientific, Madison, WI) at 13,200 rpm (26,669 g_n) for 15 min, and the supernatant was collected for phytochemical analysis (Xu and Mou, 2016).

Anthocyanin analysis. Absorbance of the extract collected from extraction was measured at 530 nm vs. an acidified methanol (1%) blank, using a spectrophotometer (Genesys 10S ultraviolet/ Vis; Thermo Fisher Scientific, Madison, WI). Because the extracts were prepared from leaf tissues maintained at –80 °C and did not undergo extensive processing or significant browning, a pH differential method for anthocyanin content was considered unnecessary (Connor et al., 2002). Anthocyanin concentration was expressed as milligrams cyanidin-3-glucoside equivalent per 100 g FW of basil leaves using a molar extinction coefficient of 29,600, which was stated as the following (Connor et al., 2002):

$$\text{Anthocyanin concentration (mg}\cdot\text{100 g}^{-1}\text{ FW)} = \frac{V \times n \times M \times A \times 100}{\epsilon \times m},$$

where V is the volume of extracted liquid (measured in milliliters), n is the dilution factor, M is the molecular weight of cyaniding-3-glucoside (449.2), A is the absorbance at 530 nm, ϵ is the molar extinction coefficient (29,600), and m is the weight of the sample

Phenolics analysis. Total phenolics concentration of basil leaves was determined using the modified Folin-Ciocalteu reagent method (Xu and Mou, 2016) as follows: A 100- μL extraction sample was added to a mixture of 150 μL distilled water and 750 μL 1/10 dilution Folin-Ciocalteu reagent. After a 6-min reaction, 600 μL 7.5% Na_2CO_3 was added and the mixture was incubated at 45 °C in a water bath for 10 min. When the mixture temperature cooled to room temperature, its absorbance was measured at 725 nm using a microplate reader (ELx800; BioTek, Winooski, VT). Results are expressed as milligrams of gallic acid equivalent per gram FW of basil leaves.

Flavonoids analysis. Total flavonoid concentration of basil leaves was determined (Dou et al., 2018) as follows: A 20- μL extraction sample was added to a mixture of 85 μL distilled water and 5 μL 5% NaNO_2 . After a 6-min reaction, 10 μL of 10% $\text{AlCl}_3\cdot 6\text{H}_2\text{O}$ was added to the mixture. After another 5-min reaction, 35 μL of 1M NaOH and 20 μL distilled water were added to the mixture, and its absorbance was measured at 520 nm using the aforementioned microplate reader. Results are expressed as milligrams of (+)-catechin hydrate equivalent per gram FW of basil leaves.

Antioxidant capacity analysis. Antioxidant capacity of plant leaves was measured using the 2,2'-azino-bis (3-ethylbenzothiazoline-6-sulfonic acid) (ABTS) method (Arnao et al., 2001) as follows: A mixture of 150-mL basil leaf extracts was added to 2.85 mL ABTS⁺ solution and was incubated at room temperature for 10 min. Absorbance of the mixture was measured at 734 nm using the aforementioned spectrophotometer. Antioxidant capacity of basil leaves is expressed as milligrams of Trolox equivalent antioxidant capacity per 100 grams FW of basil leaves.

Statistical analysis

One-way analysis of variance was conducted to analyze the effects of light-quality treatments on all measured parameters. Mean comparison among treatments was conducted using Student's t test ($P < 0.05$). All statistical analyses were performed using JMP software (version 13; SAS Institute Inc., Cary, NC).

Results

Photosynthetic capacity and chlorophyll content. In green basil plants, comparative P_n of the upper leaves was the greatest under the combined R&B light treatment—namely, R₇₆B₂₄—and it showed no differences among treatments in the lower leaves (Fig. 2A). Green light treatments showed no effects on comparative E and g_s in green basil plants regardless of leaf position (Fig. 2B and C). In purple basil plants, comparative P_n , E , and g_s of the upper leaves showed a similar trend, which was greater under treatments without green light and under treatments with less green light proportions—namely, R₇₆B₂₄, R₄₄B₂₄G₃₂, and R₇₄B₁₆G₁₀—and less with the greatest green light proportion (R₄₂B₁₃G₄₅) (Fig. 2A–C). In contrast, comparative P_n of the lower leaves in purple basil plants increased under treatments R₄₄B₂₄G₃₂ and R₇₄B₁₆G₁₀ compared with plants grown under treatments R₇₆B₂₄ or R₄₂B₁₃G₄₅ (Fig. 2A), whereas comparative E and g_s was the greatest under R₄₄B₂₄G₃₂, followed by R₇₄B₁₆G₁₀ and R₇₆B₂₄, and the least under R₄₂B₁₃G₄₅ (Fig. 2B and C). Green light treatments showed no effects on SPAD reading in green basil plants, whereas in purple basil plants the SPAD reading was the greatest under R₇₆B₂₄, followed by R₄₄B₂₄G₃₂ and R₇₄B₁₆G₁₀, and the least under R₄₂B₁₃G₄₅ (Fig. 3).

Fig. 2. Net photosynthetic rate (P_n) (A), transpiration rate (E) (B), and stomatal conductance (g_s) (C) of green basil 'Improved Genovese Compact' and purple basil 'Red Rubin' plants grown under different light-quality treatments: including R₇₆B₂₄, R₄₄B₂₄G₃₂, R₇₄B₁₆G₁₀, and R₄₂B₁₃G₄₅. Means followed by the same lower- and uppercase letters are not significantly different for green and purple basil plants, respectively, according to Student's t mean comparison ($P < 0.05$). Bars represent SE.

Fig. 3. Soil-plant analysis development (SPAD) of green basil 'Improved Genovese Compact' and purple basil 'Red Rubin' plants grown under different light-quality treatments: R₇₆B₂₄, R₄₄B₂₄G₃₂, R₇₄B₁₆G₁₀, and R₄₂B₁₃G₄₅. Means followed by the same lower- and uppercase letters are not significantly different for green and purple basil plants, respectively, according to Student's t mean comparison ($P < 0.05$). Bars represent SE.

Plant growth and yield. Plant height in green and purple basil plants both increased under treatments with greater green light proportions (namely, R₄₄B₂₄G₃₂ and R₄₂B₁₃G₄₅) compared with R₇₆B₂₄ and R₇₄B₁₆G₁₀ (Fig. 4A). Plant width (Fig. 4B), leaf area (Fig. 4C), and leaf thickness (Fig. 4D) showed no differences among treatments in green basil plants. In purple basil plants, plant width increased by 15% to 18% under R₄₂B₁₃G₄₅ compared with the other treatments (Fig. 4B). Leaf area in purple basil plants showed no

differences among treatments (Fig. 4C), whereas leaf thickness decreased with increasing green light proportions, with the greatest under R₇₆B₂₄, followed by R₇₄B₁₆G₁₀, and the least under R₄₄B₂₄G₃₂ and R₄₂B₁₃G₄₅ (Fig. 4C). The number of internodes in green and purple basil plants were five and seven, respectively (data not shown).

Shoot FW and DW in green basil plants showed no differences among treatments (Fig. 5A). In purple basil plants, shoot FW and DW showed a similar trend, which was

greater under treatments without green light or with the least green light proportion: R₇₆B₂₄ and R₇₄B₁₆G₁₀ compared with R₄₄B₂₄G₃₂ and R₄₂B₁₃G₄₅ (Fig. 5B). Specifically, shoot FW in purple basil plants under R₇₆B₂₄ and R₇₄B₁₆G₁₀ was 32% and 30% greater, respectively, compared with plants grown under R₄₂B₁₃G₄₅.

Accumulation of secondary metabolites.

In green basil plants, concentrations of phenolics and flavonoids, and antioxidant capacity decreased under R₇₄B₁₆G₁₀ and R₄₂B₁₃G₄₅ compared with R₇₆B₂₄ and R₄₄B₂₄G₃₂, whereas anthocyanin concentration decreased under R₄₂B₁₃G₄₅ (Table 2). Specifically, concentrations of anthocyanin, phenolics, and flavonoids, and antioxidant capacity in green basil plants grown under R₇₆B₂₄ was 17%, 18%, 15%, and 20% greater, respectively, compared with plants grown under R₄₂B₁₃G₄₅. In purple basil plants, concentrations of phenolics and flavonoids, and antioxidant capacity decreased under R₄₄B₂₄G₃₂ and R₄₂B₁₃G₄₅, respectively, compared with R₇₆B₂₄ and R₇₄B₁₆G₁₀, whereas anthocyanin concentration was not influenced by green light treatments (Table 2).

The total amount of phytochemicals per plant in green basil plants decreased by 17% to 21% under green light treatments (Table 3). In purple basil plants, total amounts of anthocyanin, phenolics, and flavonoids per plant decreased with increasing green light proportions, which were the greatest under R₇₆B₂₄ and R₇₄B₁₆G₁₀, followed by R₄₄B₂₄G₃₂, and the least under R₄₂B₁₃G₄₅ (Table 3). The total amount of antioxidant capacity per plant in purple basil plants was the greatest under R₇₄B₁₆G₁₀, which was 5%, 41%, and 63% greater compared with plants grown under R₇₆B₂₄, R₄₄B₂₄G₃₂, and R₄₂B₁₃G₄₅, respectively (Table 3).

Discussion

Substituting green light for red or blue light increased photosynthesis in the lower level plant canopy. Red and blue lights are strongly absorbed in upper leaves, whereas green light, which is hard for chloroplasts to absorb, penetrates and is absorbed by the chloroplasts in lower leaves (Terashima et al., 2009). In an open field, just $\leq 0.5\%$ of blue and $\leq 2.1\%$ of red light from above the canopy penetrated through to the bottom leaves, whereas up to 6.5% of green light reached leaves at the bottom (Kasperbauer, 1971). This resulted in increased PPFD in the lower level plant canopy under light sources with green light compared with red and/or blue light; and, accordingly, resulted in different patterns in comparative P_n between the upper and lower leaves. Under green light treatments, contrary to decreased P_n in the upper leaves, P_n in the lower leaves was equal to or greater than plants grown under combined R&B light in both basil cultivars (Fig. 2A). In the upper leaves, decreased P_n by green light contributed to, at least in part, green light reversing blue light-induced stomatal opening and chloroplast synthesis, which has been found in a diversity of plant

Fig. 4. Plant height (A), plant width (B), leaf area (C), and specific leaf area (SLA) (D) of green basil 'Improved Genovese Compact' and purple basil 'Red Rubin' plants grown under different light-quality treatments: R₇₆B₂₄, R₄₄B₂₄G₃₂, R₇₄B₁₆G₁₀, and R₄₂B₁₃G₄₅. Means followed by the same lower- and uppercase letters are not significantly different for green and purple basil plants, respectively, according to Student's *t* mean comparison ($P < 0.05$). Bars represent SE.

species (Talbot et al., 2002, 2006), and was also confirmed in purple basil plants in our study (Figs. 2C and 3). In particular, the flavin chromophore of cryptochrome is driven to a biologically active semireduced form by blue light; this semireduced form is shifted to a deactivated reduced state by the absorption of green light (Banerjee et al., 2007; Bouly et al., 2007). The deactivation of cryptochrome by green light removes the signal for suppression of abscisic acid pro-

duction in guard cells and results in decreased stomatal aperture and stomatal opening (Sun et al., 1998). In contrast, increased PPFD in the lower level plant canopy by high green light transmission resulted in unaffected or increased P_n in lower leaves (Fig. 2A). Similarly, P_n in 'Waldmann's Green' lettuce grown under a green light treatment (R₆₁B₁₅G₂₄) showed no difference from plants grown under combined R&B light (Kim et al., 2004). Sun et al. (1998) reported that CO₂

fixation in the upper layer of spinach leaves (upper epidermal layer and palisade mesophyll) decreased under green light compared with red or blue light, but increased in deeper layers of the leaf. The transmission of green light deeper into the plant canopy could allow carbon fixation to continue, whereas upper leaf photosynthesis is suppressed as a result of photoinhibition under greater PPFD levels or continuous light (Bian et al., 2016, 2018). Specifically, under greater PPFDs, nonphotochemical quenching could be engaged in upper leaves, whereas in lower leaves, penetrating green light could drive photosynthesis efficiently. Such coactions of nonphotochemical quenching and photosynthesis driven by green light allow carbon fixation to continue efficiently even under strong light (Sun et al., 1998).

Plant photosynthetic responses to green light varied between green and purple basil plants. In upper leaves, comparative P_n in purple basil plants was less negatively affected by green light than in green basil plants; in lower leaves, comparative P_n in purple basil plants increased under treatments with mild green light proportions (10% and 32%), but was unaffected in green basil plants (Fig. 2A). One hypothesis regarding the differences between two cultivars is a result of the lower quantum efficiency of blue light in purple basil plants compared with green basil plants. In purple basil plants, the relatively high concentration of flavonoids absorbs more blue light, which decreases the absorption of blue light by chloroplasts and subsequently decreases the photochemical energy transferred to reaction centers (Sun et al., 1998). This weakened the effects of blue light during photosynthesis in purple basil plants and resulted in unaffected P_n in upper leaves under treatments with mild green light proportions (10% and 32%). The other hypothesis is a result of the different plant canopy density between green and purple basil plants. Under a denser plant canopy, lower leaves in plants have a greater capacity to absorb and use transmitted green light via the process of photoacclimation to shade, which causes increased synthesis of chlorophyll b (Nishio, 2000; Sun et al., 1998). Chlorophyll b has a CHO group instead of the CH₃ group in chlorophyll a, and this small change in chemical structure shifts the absorption peak in the blue light wavelength to a weak absorption of green light, which aids in the acquisition of green light deeper in the plant canopy (Nishio, 2000). In our study, purple basil plants had a denser plant canopy, with seven pairs of leaves at harvest, compared with the five pairs of leaves in green basil plants, which strengthened the effects of green light in purple basil plants and led to increased P_n in lower leaves. However, none of the previous studies—nor ours—evaluated the relationship between effects of green light and plant canopy density, which should be paid attention to in future studies.

Substituting green for red and/or blue light induced shade avoidance responses. It

Fig. 5. Shoot fresh weight (FW) and dry weight (DW) of green basil ‘Improved Genovese Compact’ plants (A) and purple basil ‘Red Rubin’ plants (B) grown under different light-quality treatments: R₇₆B₂₄, R₄₄B₂₄G₃₂, R₇₄B₁₆G₁₀, and R₄₂B₁₃G₄₅. Means followed by the same lower- and uppercase letters are not significantly different for shoot FW and DW, respectively, according to Student’s *t* mean comparison ($P < 0.05$). Bars represent se.

Table 2. Anthocyanin, phenolics, and flavonoids concentrations (conc.), and antioxidant capacity of green basil ‘Improved Genovese Compact’ and purple basil ‘Red Rubin’ plants grown under different light-quality treatments: including R₇₆B₂₄, R₄₄B₂₄G₃₂, R₇₄B₁₆G₁₀, and R₄₂B₁₃G₄₅.

Cultivar	Treatment	Anthocyanin conc. (mg·100 g ⁻¹)	Phenolics conc. (mg·g ⁻¹)	Flavonoids conc. (mg·g ⁻¹)	Antioxidant capacity (mg·100 g ⁻¹)
Green basil	R ₇₆ B ₂₄	8.11 a ^z	2.06 a	1.77 ab	366 a
	R ₄₄ B ₂₄ G ₃₂	8.23 a	1.89 ab	1.84 a	353 a
	R ₇₄ B ₁₆ G ₁₀	7.58 ab	1.75 b	1.67 bc	319 b
	R ₄₂ B ₁₃ G ₄₅	6.95 b	1.75 b	1.54 c	306 b
Purple basil	R ₇₆ B ₂₄	13.36 A	3.71 A	2.29 AB	1,293 A
	R ₄₄ B ₂₄ G ₃₂	14.15 A	3.46 B	2.16 B	1,174 B
	R ₇₄ B ₁₆ G ₁₀	13.33 A	3.81 A	2.34 A	1,367 A
	R ₄₂ B ₁₃ G ₄₅	12.92 A	2.94 C	1.82 C	1,101 B

^zMeans followed by the same lower- and uppercase letters are not significantly different for green and purple basil plants, respectively, according to Student’s *t* mean comparison ($P < 0.05$). Subscript numbers indicate the proportions of red (R, 600–699 nm), blue (B, 400–499 nm), and green (G, 500–599 nm) light in the total light intensity.

Table 3. Total amounts of anthocyanin, phenolics, flavonoids, and antioxidant capacity per plant of green basil ‘Improved Genovese Compact’ and purple basil ‘Red Rubin’ plants grown under different light-quality treatments: including R₇₆B₂₄, R₄₄B₂₄G₃₂, R₇₄B₁₆G₁₀, and R₄₂B₁₃G₄₅.

Cultivar	Treatment	Total amount of phytochemicals (mg/plant)			
		Anthocyanin	Phenolics	Flavonoids	Antioxidant capacity
Green basil	R ₇₆ B ₂₄	1.63 a ^z	41 a	35 a	73 a
	R ₄₄ B ₂₄ G ₃₂	1.54 a	35 b	34 a	66 b
	R ₇₄ B ₁₆ G ₁₀	1.51 a	35 b	33 a	64 b
	R ₄₂ B ₁₃ G ₄₅	1.32 b	33 b	29 b	58 c
Purple basil	R ₇₆ B ₂₄	1.90 A	53 A	33 A	184 B
	R ₄₄ B ₂₄ G ₃₂	1.66 B	41 B	25 B	138 C
	R ₇₄ B ₁₆ G ₁₀	1.90 A	54 A	33 A	19 A
	R ₄₂ B ₁₃ G ₄₅	1.40 C	32 C	20 C	119 D

^zMeans followed by the same lower- and uppercase letters are not significantly different for green and purple basil plants, respectively, according to Student’s *t* mean comparison ($P < 0.05$). Subscript numbers indicate the proportions of red (R, 600–699 nm), blue (B, 400–499 nm), and green (G, 500–599 nm) light in the total light intensity.

has been widely reported that green light could induce shade avoidance responses, including promotion of stem and petiole elongation and hyponasty in arabidopsis (Folta

and Maruhnich, 2007; Zhang et al., 2011). This was evidenced in our study: Treatments with greater green light proportions (32% and 45%) resulted in increased stem and petiole

elongation and decreased leaf thickness (Fig. 5). Similarly, Meng et al. (2019) reported that substituting blue light with green light increased petiole length in kale (*Brassica oleracea*). Shade avoidance responses induced by green light are likely mediated in two categories: cryptochrome-dependent and cryptochrome-independent pathways (Folta, 2004; Wang and Folta, 2013). Increased green light proportions significantly promoted hypocotyl elongation both in wild-type and *phyA phyB* seedlings, suggesting that green light-induced hypocotyl elongation occurs via a cryptochrome-mediated pathway instead of a phytochrome one (Sellaro et al., 2010). In addition to hypocotyl elongation, there are a number of blue and green light reversible effects regulated by a cryptochrome-dependent pathway, such as green light reversal of blue light-mediated stomatal opening (Frechilla et al., 2000; Kim et al., 2004; Talbott et al., 2006), inhibition of blue light-induced flowering induction (Banerjee et al., 2007), and blue light-stimulated anthocyanin synthesis (Banerjee et al., 2007; Zhang and Folta, 2012). On the other hand, some responses to green light persist in *cry* knockout mutant backgrounds, such as green light-regulated leaf architecture changes and plant adaptation, suggesting an unknown green light receptor through a novel mechanism (Sellaro et al., 2010; Zhang et al., 2011).

In our study, shoot FW and DW in purple basil plants decreased under treatments with greater green light proportions (32% and 45%), which was different from the results reported by Meng et al. (2019) and Kim et al. (2004), in which inclusion of green light resulted in greater shoot FW in kale and lettuce. One hypothesis of the difference might be a result of the different plant canopy architecture or canopy density (e.g., leaf area index) among lettuce, kale, and basil plants. Lettuce and kale plants are almost stemless and have rosette-like ground leaves or a folded-leaf structure during the vegetative stage, whereas basil plants have stems with much lower plant canopy density/compactness. The denser plant canopy of lettuce and kale plants would strengthen the effects of green light, resulting in increased light interception and photosynthesis of the entire plant canopy, and would lead to greater biomass accumulation. With regard to a less dense plant canopy, the detrimental effects caused by reduced red and/or blue light density may be equal to or may override the beneficial effects of green light and lead to unaffected or decreased biomass accumulation. For instance, green light treatment showed no effects on the growth of ‘Cumlaude’ cucumber (*Cucumis sativus*) seedlings (Hernandez et al., 2016), which also has a much lower plant canopy density/compactness than lettuce or kale plants. The other hypothesis causing the difference might be a result of the different compositions of green light (green light peak wavelength or ratios of short to long green light wavelength) used in studies. Research has shown that plant responses to short-wavelength green light

(500–550 nm) and long-wavelength green light (580–600 nm, also defined as yellow light) are different (Dougher and Bugbee, 2001). The biomass accumulation of ‘Red Fire’ lettuce was the greatest under a G510 treatment (green light peak wavelength, 510 nm) compared with treatments of G520 and G530 (green light peak wavelength, 524 and 532 nm, respectively) at a PPFD of 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Johkan et al., 2012). It was also reported that an increased proportion of long-wavelength green light (580–600 nm, also defined as yellow light) decreased lettuce yield, perhaps as a result of suppression of chloroplast or chlorophyll formation (Bouly et al., 2007). Therefore, a broad-band green light source may result in different plant responses according to its peak wavelength or ratios of short to long green light wavelength.

Substituting green for red and/or blue light decreased secondary metabolite accumulation. Although mechanisms of how light quality affects plant secondary metabolism is still unclear, shared facts evidence that blue, green, and red lights are all involved in phytochemical accumulation through photoreceptor pathways (Dou et al., 2017; Zhang and Foltá, 2012). The expression of key enzymes in the synthesis of phytochemicals, such as phenylalanine ammonia-lyase, chalcone synthase, dihydroflavonol 4-reductase, and polyphenol oxidase are reported to be regulated by blue and red lights (Li, 2010; Meng et al., 2004). However, little information is known on the regulation of phytochemicals by green light, in addition to green light reversal of blue light-induced anthocyanin accumulation (Bouly et al., 2007; Zhang et al., 2011). Similar results were observed in our study: Concentrations of phenolics and flavonoids in green and purple basil plants were both decreased by green light radiation (Table 2). Consistently, Zhang and Foltá (2012) reported that as green light intensity increased, the amount of anthocyanin in arabidopsis decreased to half the level present in plants grown under combined R&B light. Also, Pennisi et al. (2019) reported that substituting green light for red light significantly decreased antioxidant capacity and flavonoid concentration in basil plants. It was postulated that the decreased phytochemical concentration under green light treatments is caused by the coactions of decreased red and/or blue light proportions and an increasing reversal of blue light-induced effects by green light.

Furthermore, regulation of phytochemical accumulation by light radiation was in species-dependent and phytochemical-dependent manners. For example, blue light is more effective on accumulation of phytochemicals such as phenolics, flavonoids, and anthocyanins in Chinese foxglove (*Rehmannia glutinosa*) and perilla (*Perilla frutescens*) (Lee et al., 2014; Manivannan et al., 2015), whereas red light is more effective on accumulation of rosmarinic acid in basil plants (Shiga et al., 2009). In our study, phytochemical concentration in green basil plants showed no difference between treatments with a similar blue light proportion

(R₇₆B₂₄ and R₄₄B₂₄G₃₂), whereas in purple basil plants it showed no difference between treatments with a similar red light proportion (R₇₆B₂₄ and R₇₄B₁₆G₁₀) (Table 2). This indicates that the phytochemical accumulations in green and purple basil plants were predominated by blue and red light, respectively, regardless of the inclusion of green light. Moreover, the proportions of blue and red light played a major role in regulating phytochemical accumulation in basil plants, instead of the absolute red or blue light intensity.

Conclusion

Inclusion of green light in growth light sources increased the P_n in lower leaves in purple basil plants, but showed no effects on green basil plants as a result of different phytochemical composition and plant canopy density. Green light induced shade avoidance responses such as stem and petiole elongation, decreased leaf thickness, and reduced chlorophyll concentration in both basil cultivars. However, greater green light proportions decreased the shoot FW and DW in purple basil plants, whereas the inclusion of green light showed no effects on the shoot FW and DW in green basil plants. In addition, treatments with greater green light proportions decreased the phytochemical concentration such as phenolics, flavonoids, and anthocyanin in basil plants. These results suggest that the inclusion of a small proportion of green light in growth light sources could produce a pleasant environment for growers and plants without reducing the yield and phytochemical contents in basil plants. Further studies are needed to determine the optimal green light proportions for plant production with different canopy densities and phytochemical compositions, and more tests are needed with different green light peak wavelengths or ratios of short to long green light wavelengths.

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