Growth and Acclimation of Impatiens, Salvia, Petunia, and Tomato Seedlings to Blue and Red Light

Heidi M. Wollaeger1,2 and Erik S. Runkle3,4

Department of Horticulture, Michigan State University, 1066 Bogue Street, East Lansing, MI 48824

Abstract. Plant growth is plastic and adaptive to the light environment; characteristics such as extension growth, architecture, and leaf morphology change, depending on the light spectrum. Although blue (B; 400–500 nm) and red (R; 600–700 nm) light are generally considered the most efficient wavelengths for eliciting photosynthesis, both are often required for relatively normal growth. Our objective was to quantify how the B:R influenced plant seedling growth and morphology and understand how plants acclimated to these light environments. We grew seedlings of three ornamental annuals and tomato under six sole-source light-emitting diode (LED) lighting treatments or one cool-white fluorescent treatment that each delivered a photosynthetic photon flux (PPF) of 160 μmol·m⁻²·s⁻¹. The following treatments were provided with B (peak = 446 nm) and R (peaks = 634 and 664 nm) LEDs: B160 (160 μmol·m⁻²·s⁻¹ of B light only), B80®R80, B30®R120, B150®R140, B160®R150, and R160. Seedlings of impatiens (Impatiens walleriana), salvia (Salvia splendens), petunia (Petunia ×hybrida), and tomato (Solanum lycopersicum) were grown for 31 to 37 days at a constant 20 °C. Plants with as little as 10 μmol·m⁻²·s⁻¹ of B light were 23% to 50% shorter and had 17% to 50% smaller leaves than plants under only R light. Impatiens and salvia had 53% to 98% greater fresh shoot weight under treatments without B light than with 280 μmol·m⁻²·s⁻¹ of B light. Plants grown under fluorescent lamps had the greatest chlorophyll content but also had among the thinnest leaves of treatments. Blue-rich light increased flowering in impatiens and reduced incidence of intumescences on tomato. As little as 10 μmol·m⁻²·s⁻¹ of B light in an R-dominant background can elicit desirable growth responses for the production of young plants and for other situations in which compact growth is desired.

Blue (B; 400–500 nm) and red (R; 600–700 nm) light are generally considered the most efficient wavelengths for eliciting photosynthesis in plants (McCree, 1972; Sager et al., 1988). Therefore, B and R LEDs with peak light emission that coincides with peaks of the relative quantum efficiency curve (McCree, 1972) make a logical choice for sole-source commercial plant production (Mitchell et al., 2012). Previous results with tomato (Solanum lycopersicum), salvia (Salvia splendens), impatiens (Impatiens walleriana), and petunia (Petunia ×hybrida) (Wollaeger and Runkle, 2014) and those for lettuce (Lactuca sativa) (Johkan et al., 2010), cherry tomato (Solanum lycopersicum var. cerasiforme) (Liu et al., 2011b), rice (Oryza sativa) (Ohashi-Kaneko et al., 2006), and strawberry (Fragaria ×ananassa) (Nhut et al., 2003) showed that plants grown under a combination of wavebands, particularly including B light, have growth characteristics more similar to those grown under sunlight than those grown under a single waveband of light. However, the addition of B to R light can decrease shoot biomass, such as in lettuce, which had 25% or 17% less fresh shoot biomass when grown under B light alone compared with R or R+B light, respectively (Johkan et al., 2010). Similarly, salvia, petunia, and tomato seedlings grown under 50% green (G; 500–600 nm) + 50% R light from LEDs or those with ≥25% B light at the same PPF had 35% to 57% less fresh shoot weight than plants under only R light (Wollaeger and Runkle, 2014).

 Marketable characteristics of young ornamental plants include, but are not limited to, compact growth, presence of a well-developed root system, and adequate branching. Plant growth retardants and limited watering and fertility are methods commercial growers use to suppress extension growth (Hendriks and Uebcr, 1995). Extension growth can also be inhibited by modifying the light spectrum, especially by B light and the R:far-red (FR; 700–800 nm) light ratio (Liu et al., 2011a; Smith, 2000). Blue-light-stimulated cryptochrome receptors suppress gibberellic acid biosynthesis, which in turn inhibits cell elongation and stem extension of plants (Ahmad et al., 2002; Cashmore et al., 1999; Liu et al., 2011a; Sellaro et al., 2010). For example, sweetpotato (Ipomoea batatas) stems were 17% shorter when the B:R was 1:10 compared with that of plants grown under a B:R of 1:1 at a PPF of 330 μmol·m⁻²·s⁻¹ (Yang et al., 2011). In a separate study, cherry tomato plants grown under B or R+B LEDs were 33% or 49% shorter than those grown under only R LEDs at a PPF of 320 μmol·m⁻²·s⁻¹ (Liu et al., 2011b). Phytocromes, with absorption peaks at 660 and 735 nm, are a family of photoreceptors that mediate stem elongation, as well as leaf expansion, chloroplast development, and flowering (Folta and Childers, 2008; Horwitz et al., 1988; Parks et al., 2001; Valverde et al., 2004).

In addition to extension growth, plants acclimate to a high B:R by increasing chlorophyll concentration (Lichtenthaler et al., 1981). Blue light stimulates cryptochrome (CRY1), which upregulates the transcription of genes for chlorophyll synthesis (Li et al., 2009). High chlorophyll content in plants, which causes a dark green coloration of leaves, is also desirable in commercial production of young plants such as microgreens, herbs, and ornamental propagules. Growing plants under sole-source solid-state lighting that includes B light in an R-dominant background can yield this characteristic (Goins et al., 1997; Li et al., 2011; Ohashi-Kaneko et al., 2006; Salebo et al., 1995; Tennessen et al., 1994). For example, lettuce grown under B or R+B (1:1) LEDs had ≥11% greater chlorophyll per unit of dry mass than plants grown under R LEDs at the same intensity (Johkan et al., 2010). In a separate study, cucumber (Cucumis sativus) had increased chlorophyll content per unit leaf area with increasing ratios of B:R light at the same intensity (Hogewoning et al., 2010).

Plants also acclimate to a low R:FR or B-deficient environment by increasing leaf thickness (Fan et al., 2013; Fukuda et al., 2008; Schuerger et al., 1997). Thicker leaves have not been directly attributed to cryptochrome or phototropin photoreceptors (Ohashi-Kaneko et al., 2006). However, the CRY1 cryptochrome receptor downregulates gibberellin biosynthesis and therefore suppresses leaf expansion, which in turn results in thicker leaves (Ahmad et al., 2002; Liu et al., 2011a; Sellaro et al., 2010). Therefore, plants grown under solely R light typically have larger, thinner leaves than those of plants grown under light that includes B. For example, pepper plants (Capsicum annuum) grown at a PPF of 330 μmol·m⁻²·s⁻¹ had 24%, 37%, or 29% greater overall leaf thickness, palisade parenchyma, or spongy parenchyma layers, respectively, under R LEDs and B fluorescent light.
lamps than plants grown under R LEDs alone (Schuerger et al., 1997). Similarly, geranium (Pelargonium zonale) irradiated with 100 μmol·m⁻²·s⁻¹ of B LED light had ≥16% thicker leaves compared with plants under R LED light at the same intensity (Fukuda et al., 2008).

Our objective was to quantify how plants acclimate to light environments with different B:R ratios, but the same PPF to facilitate the commercial production of young plants with desirable morphological characteristics. We postulated that as the proportion of B light increased, extension growth would decrease, whereas chlorophyll concentration and leaf thickness would increase.

Materials and Methods

Plant materials. Seeds of tomato ‘Early Girl’, salvia ‘Vista Red’, impatiens ‘SuperEllin XP Red’, and petunia ‘Wave Pink’ were sown in 128-cell (2.7 × 2.7 cm; 12.0-mL volume) seedling trays by a commercial young plant producer (C. Baker and Sons, Inc., Litchfield, MI). Trays were moved to Michigan State University (East Lansing, MI) within 2 d, and all the seedling trays were then cut into sections that each contained ≥20 seedlings, thinned to one plant per cell, and immediately placed in the lighting treatments.

Light treatments and environment. Six modules that were described by Wollaeger and Runkle (2013) contained dimmable B (peak = 446 nm) and R (peaks = 634 and 664 nm) LEDs. The intensities of these three LED types were adjusted to create six light-quality treatments based on an average of six measurements from a spectroradiometer (PS-200; Apogee Instruments, Inc., Logan, UT) made at seedling-tray level at different horizontal positions inside each module. Each module delivered a PPF of 160 μmol·m⁻²·s⁻¹ that consisted of the following light treatments: B₁₆₀ (160 μmol·m⁻²·s⁻¹ of B and no R light; 100% R), B₄₀₊R₁₂₀ (50% B, 50% R), B₈₀₊R₁₀₀ (25% B, 75% R), B₂₀₊R₁₄₀ (12.5% B, 87.5% R), B₄₀₊R₁₂₀ (6.2% B, 93.8% R), and R₁₆₀ (100% R) (Fig. 1). All treatments that delivered R light were delivered equally by the two types of R LEDs. The LED modules were placed in a refrigerated growth chamber and the experiment was performed three times. In a separate growth chamber, plants were grown under cool-white fluorescent lamps (F96T12; Philips, Amsterdam, Netherlands) with the same PPF and temperature set points, which served as a control. The flux of photons in the B, R, and FR wavebands was calculated for the fluorescent lamps and was 33, 43, and 3 μmol·m⁻²·s⁻¹, respectively. Plants were grown under an 18-h photoperiod (0500 to 2300 h) as controlled by a data logger (CR10; Campbell Scientific, Logan, UT). The growth chambers were set at a constant (day/night) 20 °C to minimize any potentially confounding effect of a diurnal temperature difference on extension growth. In each treatment, air and plant canopy temperature and light intensity were continuously measured as described by Wollaeger and Runkle (2014), and means are presented in Table 1. Plants were irrigated as needed by subsurface irrigation with a water-soluble fertilizer as described by Wollaeger and Runkle (2014).

Data collection. Ten random plants of each species and treatment were harvested per replication the following number of days after seed sow (rep. 1, 2, 3): tomato (32, 31, 33), impatiens (33, 33, 34), petunia (34, 35, 35), and salvia (36, 34, 37). The variability in harvest time among experimental replications was due to availability of labor. The following data were collected at harvest: leaf (at node) number; total leaf area [measured with a leaf area meter (LI-3000; LI-COR, Lincoln, NE)]; fresh shoot, leaf (without petiole), and petiole weight; shoot dry weight (after plants were dried at ≥66 °C for ≥5 d), and macroscopic flower bud number. A visible leaf that was ≥25% unfolded was counted in leaf number. Stem length was measured by a ruler (from the medium surface to the apical meristem) on all plants except for petunia, which grew as a rosette. The number of leaflets with intumescences was counted on tomato; the physiological disorder did not occur on the other plants. Tomato was also subjectively evaluated for chlorosis by assigning a score from 1 (no chlorosis, 100% green) to 5 (severe chlorosis, 100% yellow). Chlorophyll concentration was determined as reported by Wollaeger and Runkle (2013) on the following days after seed sow (rep 1, 2, 3): 29, 31, and 30.

Leaf thickness of tomato and salvia was measured from each treatment on the two largest leaves of each plant on the harvest dates. Three leaflets of each plant were placed in separate plastic bags with deionized water to prevent desiccation until they were sectioned. The leaves were layered, rolled, and inserted into a handheld microtome (MT.5503; Euromex Microscopes Holland, Arnhem, the Netherlands). Nine to eleven cross sections per sampled plant of each species and treatment were sliced and placed with deionized water on a single-frosted precleaved microscope slide (75 × 25 mm; Corning Glass Works, Corning, NY) with a 28 g coverslip (VWR Scientific Inc., San

<table>
<thead>
<tr>
<th>Light quality treatment</th>
<th>Replication 1</th>
<th>Replication 2</th>
<th>Replication 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>B₁₆₀</td>
<td>21.2</td>
<td>20.6</td>
<td>21.2</td>
</tr>
<tr>
<td>B₄₀₊R₁₂₀</td>
<td>20.8</td>
<td>21.1</td>
<td>20.8</td>
</tr>
<tr>
<td>B₂₀₊R₁₄₀</td>
<td>20.6</td>
<td>20.4</td>
<td>20.9</td>
</tr>
<tr>
<td>B₄₀₊R₁₂₀</td>
<td>21.4</td>
<td>20.6</td>
<td>20.4</td>
</tr>
<tr>
<td>B₂₀₊R₁₄₀</td>
<td>21.4</td>
<td>20.6</td>
<td>20.4</td>
</tr>
<tr>
<td>B₄₀₊R₁₂₀</td>
<td>21.0</td>
<td>20.5</td>
<td>20.6</td>
</tr>
<tr>
<td>R₁₆₀</td>
<td>20.7</td>
<td>20.4</td>
<td>20.4</td>
</tr>
<tr>
<td>Fluorescent</td>
<td>21.7</td>
<td>21.9</td>
<td>21.9</td>
</tr>
</tbody>
</table>

Table 1. Actual air and canopy temperatures (°C) as measured by thermocouples and IR sensors for LED-lighting treatments (B: blue, R: red) and one fluorescent lighting treatment. The value after each waveband represents its intensity (in micromole per square meter per second).

Fig. 1. The spectral distribution of seven light quality treatments delivered by blue (B; 400–500 nm) and red (R; 600–700 nm) LEDs or cool-white fluorescent lamps, each delivering a photosynthetic photon flux of 160 μmol·m⁻²·s⁻¹. The value after each waveband represents its intensity (in micromole per square meter per second).
Francisco, CA). Wet-mounted fresh sections were examined under 64× magnification on an Olympus Stereo microscope (SZH-ILLD; Olympus American Inc., Center Valley, PA). The thickness of the leaf, away from a vein or a midrib, was measured using the ocular micrometer in the viewfinder for each sample while the same magnification was maintained. A conversion factor was determined between the viewfinder reticule in the microscope and a stage micrometer.

**Results**

**Leaf number and relative leaf area.** In all species, the mean leaf number was similar among treatments and was 10.9, 9.8, 5.6, and 11.6 for impatiens, salvia, tomato, and petunia, respectively (Fig. 2). Leaf area was greatest in impatiens and petunia under the fluorescent lamps (27.2 and 29.0 cm², respectively), under the R₄₆₀ treatment in salvia (34.1 cm²), and under the B₂₀/R₁₄₀ in tomato (39.9 cm²). Leaf area of plants grown under fluorescent lamps was set to 100% and leaf area for all LED treatments is presented relative to these values. Leaf area of all plant species under treatment R₄₆₀ was similar to that of plants under fluorescent lamps. Leaf area of impatiens and salvia under treatment R₄₆₀ was about twice that of plants grown with 80 µmol·m⁻²·s⁻¹ of B light. Petunia leaf area under treatment R₄₆₀ was 80% to 116% greater than plants under treatments B₁₀⁺R₁₅₀ or B₈₀⁺R₈₀, respectively. In tomato, there was no significant effect of light quality on leaf area and there was a significant (P ≤ 0.001) interaction between light quality and replication (data not shown).

**Seedling height.** Mean height of salvia and tomato grown under the fluorescent lamps was 51 and 80 mm, respectively, and were similar to those under the R₄₆₀ treatment. Impatiens was 58% taller under the R₄₆₀ treatment than under fluorescent lamps, which were 28 mm in height. Impatiens, salvia, and tomato with ≥10 µmol·m⁻²·s⁻¹ of B light were 37% to 48%, 29% to 50%, or 23% to 49% shorter than plants under the R₄₆₀ treatment, respectively. Stem height of impatiens was similar for all other treatments. Salvia grown under treatment B₈₀⁺R₈₀ was 22% to 36% shorter than plants grown under treatment B₁₀⁺R₁₅₀ or under fluorescent lamps. Similarly, tomato plants under treatment B₈₀⁺R₈₀ were 24% to 26% shorter than those irradiated with 10 or 20 µmol·m⁻²·s⁻¹ of B light or those grown under fluorescent lamps.

**Fresh shoot weight.** The fresh weight of impatiens, salvia, tomato and petunia grown under fluorescent lamps (1.34, 0.86, 1.00, and 1.39 g, respectively) were similar to those grown under R₄₆₀ for all species. Fresh shoot weight under all LED treatments was calculated relative to those grown under fluorescent lamps (Fig. 3).
Impatiens fresh shoot weight was 53% to 78% greater for plants grown under treatment R 160 than for those grown under ≥80 μmol·m⁻²·s⁻¹ of B light or under treatment B₁₀+R₁₅₀. Fresh shoot weight of salvia under R₁₆₀ was 65% to 98% greater for plants grown under ≥40 μmol·m⁻²·s⁻¹ of B light. Petunia under treatment R₁₆₀ had 84% greater fresh weight than plants under treatment B₈₀+R₈₀. The fresh shoot weight of tomato was similar among plants under all treatments, and there was a significant (P ≤ 0.001) interaction between light quality and replication (data not shown).

**Dry weight.** Dry weight of impatiens, salvia, tomato, and petunia (73, 66, 105, and 144 mg, respectively) grown under fluorescent lamps were among the least when compared with all LED treatments. Dry weight under all LED treatments was calculated relative to those grown under fluorescent lamps. Dry weight was greatest for salvia and petunia under the R₁₆₀ treatment (221 and 133 mg, respectively), for impatiens under treatment B₁₀+R₁₅₀ (167 mg), and for tomato under treatment B₂₀+R₁₄₀ (304 mg). Dry weight of impatiens was essentially the same under treatments that delivered 0 to 40 μmol·m⁻²·s⁻¹ of B light, and all of those were more than twice that of plants grown under fluorescent lamps. Salvia showed a trend for dry weight that was similar to but stronger than that for fresh shoot weight. Plants grown under treatment R₁₆₀ had 70% to 133% greater dry weight than plants grown with ≥40 μmol·m⁻²·s⁻¹ of B light or plants grown under fluorescent lamps. Tomato grown under B₂₀+R₁₄₀ had 112% greater dry weight than plants grown under fluorescent lamps. Tomato grown under B₂₀+R₁₄₀ had 112% greater dry weight than plants grown under fluorescent lamps, but it was similar among the other treatments. Dry weight of petunia under treatment R₁₆₀ was 33% to 91% greater than that of plants under ≥20 μmol·m⁻²·s⁻¹ of B light.

**Leaf:stem fresh weight.** Salvia and tomato had a decreasing leaf:stem fresh weight ratio with increasing percentage of R light. Plants of both species had a relatively high leaf:stem fresh weight ratio under treatments with ≥80 μmol·m⁻²·s⁻¹ of B light but a relatively low ratio in treatment R₁₆₀. The leaf:stem fresh weight of impatiens was similar among treatments except for plants grown under fluorescent lighting, which had a 58% to 85% greater leaf:stem weight ratio.

### Chlorophyll concentration

Salvia, tomato, and petunia had the greatest chlorophyll concentration under the fluorescent lamps (183, 142, and 138 mg Chl/g fresh tissue, respectively) (Fig. 4). Impatiens grown under treatment R₁₆₀ (87.9 mg Chl/g fresh tissue) had a similar chlorophyll concentration to those grown under fluorescent lamps. Chlorophyll concentration under all LED treatments was calculated relative to values for those grown under fluorescent lamps. Impatiens, salvia, tomato, and petunia had 33% to 44%, 28% to 46%, 51% to 131%, and 47% to 145% greater concentration of chlorophyll under fluorescent lamps, respectively, than plants under all other treatments except impatiens under treatment R₁₆₀.

#### Leaf thickness

Leaves of salvia and tomato were among the thinnest (0.18 and 0.17 mm, respectively) when plants were grown under fluorescent lamps. Leaf thickness of all LED treatments was calculated relative to that of plants grown under fluorescent lamps. Salvia leaves were thickest under the B₁₆₀ treatment (0.33 mm), whereas tomato leaf thickness was the greatest under treatment B₄₀+R₁₂₀ (0.31 mm). Leaves of salvia were
Impatiens | Salvia | Tomato | Petunia
---|---|---|---
[Graph showing relative chlorophyll content for four seedling crops]  
**Discussion**

Plants can acclimate to and thus exploit a particular light quality environment by modifying leaf size and shape (anatomical changes), chlorophyll density (physiological changes), and/or photosynthesis reactions [biochemical changes, e.g., biosynthesis of ribulose bisphosphate carboxylase/oxygenase (Rubisco)] (Senger and Bauer, 1987). Our objective was to quantify how plant morphology changes in response to light environments with different B:R ratios. Plants acclimate to being grown under only R light, in the absence of B and FR light, by increasing leaf expansion and developing characters analogous with the shade-avoidance response, including increased chlorophyll content and stem length and decreased leaf thickness (Blackman and Wilson, 1951; Eskins, 1992; Franklin and Whiteman, 2005; Grime and Jeffrey, 1965; Jarvis, 1964). In our study, leaf area of impatiens, salvia, and petunia grown without B light was much greater than that of plants grown with B light. Similarly, leaf area was 47% to 130% greater in tomato, impatiens, petunia, and salvia grown under only R light compared with the same PPF that included ≥25% B light (Wollaeger and Runkle, 2014). Interestingly, in this study, leaf area of all species under only R light was similar to that of plants under fluorescent lamps even though the fluorescent lamps emitted 33 μmol·m⁻²·s⁻¹ of B light, which was more than that of the B₂₀⁺R₄₀ treatment. Similarly, lettuce grown at a PPF of 300 μmol·m⁻²·s⁻¹ had a 44% greater leaf area under R fluorescent light than under B fluorescent light, whereas it was similar under R, R+B, or white fluorescent light (Ohashi-Kaneko et al., 2007). In contrast, leaf area of cotton (*Gossypium hirsutum*) was similar between plants grown under 100% B or R LEDs (peaks of 460 or 660 nm), whereas both were greater than that of plants under B+R (1:3) at the same PPF of 50 μmol·m⁻²·s⁻¹ (Li et al., 2010). These contrasting results with cotton could at least partially be attributed to the low PPF, which was less than half of that in our study.

Plants grown in environments with B light can have less biomass accumulation and thicker stems than those under only R light, but responses have varied among species studied (Johkan et al., 2010; Schuerger et al., 1997; Wollaeger and Runkle, 2014). In this study, fresh shoot weight of impatiens, petunia, and salvia was 53% to 98% greater under treatments without B LED light than with ≥50% B light. Biomass allocation between leaves and stems was similar among all treatments except those of plants grown under fluorescent lighting for the shade-tolerant impatiens, whereas leaf biomass of the shade-intolerant salvia and tomato was proportionately greater under light with lower B:R ratios. Although fresh shoot weight was similar among treatments grown under only R light or fluorescent lamps, plants grown under only R light had 33% to 133% greater dry weight than plants grown under fluorescent lamps. Thus, plants grown under only R light fixed more carbon than those under fluorescent light, and apparently had a higher water content. Contrasting results have been reported in lettuce and komatsuna; lettuce had 28% greater shoot dry weight under white than R fluorescent light, whereas komatsuna had 43% greater dry weight under R light than white light (Ohashi-Kaneko et al., 2006). In strawberry, fresh shoot weight was 42% greater under only R (peak = 660 nm) than only B (peak = 450 nm) LED light at a PPF of 45 μmol·m⁻²·s⁻¹ (Nhuil et al., 2003).

In protected climates, the shade-avoidance response can be prevented by low-density spacing of plants to avoid mutual shading.
and by delivering B light or light with a high R:FR. Phytochrome and cryptochrome photoreceptors perceive R and FR light or B light and ultraviolet-A (320–390 nm) radiation, respectively, and mediate extension growth (Liu et al., 2011a; Smith, 2000; Stapleton, respectively, and mediate extension growth and ultraviolet-A (320–390 nm) radiation, receptors perceive R and FR light or B light or fluorescent lamps at the same photosynthetic photon flux. Chlorosis score: 1 = least chlorotic, 5 = most chlorotic. The photosynthetic photon flux. Chlorosis score: 1 = least chlorotic, 5 = most chlorotic. The value after each waveband represents its intensity in micromoles per square meter per second. Means sharing a letter are not statistically different by Tukey’s honestly significant difference at $P \leq 0.05$. Error bars indicate SE.

and by delivering B light or light with a high R:FR. Phytochrome and cryptochrome photoreceptors perceive R and FR light or B light and ultraviolet-A (320–390 nm) radiation, respectively, and mediate extension growth (Liu et al., 2011a; Smith, 2000; Stapleton, respectively, and mediate extension growth and ultraviolet-A (320–390 nm) radiation, receptors perceive R and FR light or B light or fluorescent lamps at the same photosynthetic photon flux. Chlorosis score: 1 = least chlorotic, 5 = most chlorotic. The value after each waveband represents its intensity in micromoles per square meter per second. Means sharing a letter are not statistically different by Tukey’s honestly significant difference at $P \leq 0.05$. Error bars indicate SE.

and by delivering B light or light with a high R:FR. Phytochrome and cryptochrome photoreceptors perceive R and FR light or B light and ultraviolet-A (320–390 nm) radiation, respectively, and mediate extension growth (Liu et al., 2011a; Smith, 2000; Stapleton, respectively, and mediate extension growth and ultraviolet-A (320–390 nm) radiation, receptors perceive R and FR light or B light or fluorescent lamps at the same photosynthetic photon flux. Chlorosis score: 1 = least chlorotic, 5 = most chlorotic. The value after each waveband represents its intensity in micromoles per square meter per second. Means sharing a letter are not statistically different by Tukey’s honestly significant difference at $P \leq 0.05$. Error bars indicate SE.

and by delivering B light or light with a high R:FR. Phytochrome and cryptochrome photoreceptors perceive R and FR light or B light and ultraviolet-A (320–390 nm) radiation, respectively, and mediate extension growth (Liu et al., 2011a; Smith, 2000; Stapleton, respectively, and mediate extension growth and ultraviolet-A (320–390 nm) radiation, receptors perceive R and FR light or B light or fluorescent lamps at the same photosynthetic photon flux. Chlorosis score: 1 = least chlorotic, 5 = most chlorotic. The value after each waveband represents its intensity in micromoles per square meter per second. Means sharing a letter are not statistically different by Tukey’s honestly significant difference at $P \leq 0.05$. Error bars indicate SE.

and by delivering B light or light with a high R:FR. Phytochrome and cryptochrome photoreceptors perceive R and FR light or B light and ultraviolet-A (320–390 nm) radiation, respectively, and mediate extension growth (Liu et al., 2011a; Smith, 2000; Stapleton, respectively, and mediate extension growth and ultraviolet-A (320–390 nm) radiation, receptors perceive R and FR light or B light or fluorescent lamps at the same photosynthetic photon flux. Chlorosis score: 1 = least chlorotic, 5 = most chlorotic. The value after each waveband represents its intensity in micromoles per square meter per second. Means sharing a letter are not statistically different by Tukey’s honestly significant difference at $P \leq 0.05$. Error bars indicate SE.
environmental factors such as diurnal temperature fluctuations (Massa et al., 2008). Thus, intumescence development may have been especially severe because a constant day/night temperature was delivered in this research.

Early flowering can be induced in some species by B light. Impatients under only B light developed significantly more flower buds with \( \pm 20 \text{ \mu mol m}^{-2} \text{s}^{-1} \) of B light. CR2 cryptochrome receptors can stimulate flowering by promoting downstream flowering genes, including CO and FT (Chaves et al., 2011; El-Assal et al., 2003). This suggests that increasing stimulation of CR2 by increasing B light caused impatients to flower earlier than do treatments with little or no B light. Increased flower number in light that contains B, compared with that without B, has been reported in other ornamental annual plants. For example, marigold and salvia produced 43% or 100% more flower buds, respectively, under B-R (peaks = 440 and 650 nm, respectively) LED light compared with those grown under fluorescent light at the same intensity (Heo et al., 2006). In contrast, marigold and salvia grown under B or R LEDs (peaks = 440 and 650 nm, respectively) at a PPF of 90 \( \text{\mu mol m}^{-2} \text{s}^{-1} \) developed a similar number of flower buds, whereas plants under either treatment had 77% to 86% fewer flower buds than those under fluorescent lamps (Heo et al., 2002). Similarly, impatients grown under 100% B light had 71 times more flower buds than those grown under only R light (Wollager and Runkle, 2014). We ended experiments before salvia, tomato, or petunia had visible flower buds, so we do not know whether B light would have had effects on flowering similar to that in impatients.

We conclude that plants acclimate to only R light by increasing leaf expansion and stem elongation, whereas plant responses to B light include inhibited extension growth and, in some cases, greater leaf thickness and chlorophyll concentration. Subsequently, plants under only R light accumulated more biomass than those of other treatments in part because of the increased leaf surface area for light capture. About 6% to 13% B light was apparently sufficient to stimulate (presumably cryptochrome) photoreceptors that inhibited extension growth, thereby reducing leaf size and biomass accumulation. Therefore, including as little as 10 \( \text{\mu mol m}^{-2} \text{s}^{-1} \) of B light in an R-dominant background can elicit desirable growth responses for the production of propagules, herbs, and microgreens, and for other situations in which compact growth is desired.

**Literature Cited**


