Morphology and Flowering Responses of Four Bedding Plant Species to a Range of Red to Far Red Ratios

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Abstract. In greenhouse ornamental crop production, bedding plants grown below high densities of hanging baskets (HBs) tend to be of lower quality. Hanging basket crops can decrease the red to far red ratio (R:FR) of the growing environment below; however, the extent to which decreased R:FR affects plant morphology and flowering of the lower-level crops is unknown. The present study examined effects of R:FR on morphology and flowering of marigold ‘Antigua Orange’ (*Tagetes erecta*), petunia ‘Duvet Red’ (*Petunia* × *hybrida*), calibrachoa ‘Kabloom Deep Blue’ (*Calibrachoa* × *hybrida*), and geranium ‘Pinto Premium Salmon’ (*Pelargonium* × *hortorum*). Five R:FR light treatments were provided ranging from R:FR 1.1 (representing unfiltered sunlight) to R:FR 0.7 (representing shaded conditions under HBs) using light-emitting diodes (LEDs) in growth chambers, each with identical photosynthetically active radiation (PAR) (400–700 nm) and FR added to achieve the target R:FR ratio. Two experiments using the same R:FR treatments were conducted with day/night temperature regimes of 20 °C/18 °C and 25 °C/21 °C, respectively. In the second experiment, a fluorescent light treatment was included. The results of the second experiment were more dramatic than the first, where reducing R:FR from 1.1 to 0.7 increased height by 11%, 22%, and 32% in marigold, petunia, and calibrachoa, respectively, and increased petiole length in geranium by 10%. Compared with R:FR 1.1, the R:FR 0.7 shortened the time to the appearance of first flower bud by 2 days in marigold, whereas flowering was minimally affected in other species. Compared with pooled data from the LED treatments, fluorescent light increased relative chlorophyll content for all species, reduced height in marigold, petunia, calibrachoa, and geranium by 26%, 67%, 60%, and 48%, and reduced stem dry weight by 28%, 39%, 21%, and 31%, respectively. The differences in morphology observed under fluorescent light compared with LED R:FR treatments indicate that light quality manipulation is a potential alternative to chemical growth regulators in controlled environments such as greenhouses and growth chambers.

In greenhouse production, it has been observed that bedding plants tend to be of lower quality when grown below a dense canopy of HBs, characterized by elongated stems and reduced branching (Hamrick, 2003). Although it has been demonstrated that HBs alter both light quantity and quality (Faust et al., 2014; Llewellyn et al., 2013), the extent to which altered light quality beneath HBs contributes to changes in plant morphology is unknown. Research into the factors of the light environment which contribute to ‘leggy’ plants may also provide insight toward the use of light as a nonchemical plant growth regulator, which has been of growing interest in ornamental horticulture (Folta and Childers, 2008).

Bedding plants, especially flowering annuals, are produced in high quantities in the winter and early spring in preparation for the gardening season in North America (Brown, 2014; Kessler, 2004). To maximize production space, some growers install rows of HBs above bench- or floor-level crops. Our group (Llewellyn et al., 2013) surveyed the light environment in some Southern Ontario greenhouses to quantify reductions in light intensity and characterize alterations to the red (R, 600–700 nm) to far red (FR, 700–800 nm) photon flux ratio (R:FR) at lower crop level because of the presence and growth of HBs. The photosynthetic photon flux (PPF, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ between 400 and 700 nm), measured inside the greenhouses just above the HB level, were reduced by 40% to 53% relative to outdoors. The PPF was reduced by an additional 15% to 55% at lower crop levels, relative to measurements above HBs, with greater reductions as HB plants grew larger. These results were corroborated by Faust et al. (2014) in North Carolina, who found that the greenhouse structures intercepted 48% of outdoor PPF, and HBs intercepted up to 45% of the transmitted light,

with greatest PPF interception resulting from the highest density of HBs, darkest pot color, and presence of plants. The reductions in PPF at the lower crop-level because of high density HB production may result in a daily light integral (DLI) at or below the minimum requirement for ‘good quality’ bedding plants, which is considered to be 10–12 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for greenhouse ornamental crops including *Pelargonium hortorum*, *Tagetes* spp., and *Petunia* spp. (Faust, 2003; Llewellyn et al., 2013).

Llewellyn et al. (2013) also reported reductions in R:FR under HBs. Reductions in R:FR are commonly observed below foliage canopies, as green leaves absorb light strongly within the range of PAR (400–700 nm), including R, whereas higher proportions of wavelengths longer than 700 nm are either reflected or transmitted to the surrounding environment (Gates et al., 1965; Holmes and Smith, 1977a). Accordingly, Llewellyn et al. (2013) reported a decrease in R:FR over the season (April to mid-May) as the light reaching the lower crop passed through an increasingly large canopy of HB foliage. At the lower crop level, the lowest R:FR measurement was 0.86, whereas the average R:FR above HB level was 1.11. The average R:FR above HBs was similar to other reported values for unfiltered sunlight, generally ranging between 1.0 and 1.3 (Holmes and Smith, 1977b; Kittas et al., 1999). However, care should be taken when comparing values using other methods for calculating R:FR, which sometimes include the common narrow-waveband R:FR ($R:FR_{\text{narrow}}$, 660 ± 5 nm : 730 ± 5 nm) (Holmes and Smith, 1977b; Meng and Runkle, 2014). The R:FR of sunlight at the Earth’s surface is generally stable throughout the day when the solar elevation is greater than 15° (Holmes and Smith, 1977b), although R:FR is known to vary with geographic location (Goldberg and Klein, 1977).

Plant responses to R:FR have been extensively documented (Casal and Smith, 1989; Chen and Chory, 2011; Demotes-Mainard et al., 2016). Plants respond to R:FR via phytochrome, a class of pigments which interconvert between red-absorbing and far-red-absorbing forms (P_r and P_{fr} , respectively) based on the proportion of R and FR photons illuminating the plant (Smith and Holmes, 1977). The proportion of these two forms within the plant, represented by the phytochrome photoequilibrium (P_{fr}/P_r), initiates a cascade of metabolic events ultimately influencing germination, flowering, and morphology (Blom et al., 1995; Chory et al., 1996). The R:FR is a reliable signal for plants indicating competition for light from nearby or overhead vegetation (Gates et al., 1965; Holmes and Smith, 1975). In many plant species, reduced R:FR contributes to ‘shade avoidance’ responses such as stem elongation and apical dominance as means to compete for available light (Casal, 2012; Casal and Smith, 1989; Chen and Chory, 2011; Smith and Whitelam, 1997). The ultimate phenotypic expression to low R:FR is species-specific and is codependent on other interacting factors,

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including temperature (Qaderi et al., 2015; Xiong et al., 2002) and absolute intensity of R and FR (Lund et al., 2007). There are limited studies of R:FR effects on bedding plants, including petunia (*Petunia* sp.), impatiens (*Impatiens* sp.), and marigold (*Tagetes* sp.) (Bachman and McMahon, 2006; Craig and Runkle, 2012; Fletcher et al., 2005). However, these studies vary widely in the range of R:FR investigated, as well as intensities and timing of R:FR treatment applications.

The objective of the present study was to quantify the effects of R:FR ranging from 0.7 to 1.1 on bedding plant morphology and flowering. This range captures the R:FR measured above and below HBs as measured by Llewellyn et al. (2013).

Materials and Methods

Two experiments (Expts. 1 and 2) were conducted sequentially in walk-in growth chambers at the University of Guelph, ON, Canada, from 2 May to 22 Sept. 2016. Environmental conditions were consistent across the two experiments except for temperature and relative humidity.

Seedling propagation. Seeds of petunia 'Duvet Red' (*Petunia ×hybrida*) (Ball Horticultural Co., West Chicago, IL), marigold 'Antigua Orange' (*T. erecta*) (Syngenta Flowers, Gilroy, CA), geranium 'Pinto Premium Salmon' (*Pelargonium ×hortorum*) (Express Seed Company, Oberlin, OH) and calibrachoa 'Kabloom Deep Blue' (*Calibrachoa ×hybrida*) (PanAmerican Seed Co., West Chicago, IL) were sowed in 288-cell (10 mL) plug trays containing a commercial growth medium (Sunshine LP5 Plug Mix; Sun Gro Horticulture Distribution, Agawam, MA). Plug trays were placed in a walk-in growth chamber (floor area: 29.2 m²) under a panel of Sylvania 4200K cool-white fluorescent lamps (F96T12/CW/WHO; LEDVANCE, Wilmington, MA). The light panel height was adjusted weekly to maintain a constant canopy-level *PPF* of 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, measured with a LI-190 quantum sensor (LI-COR, Inc., Lincoln, NE) calibrated to a spectrometer. The chamber photoperiod was set to 16-h. Air temperature and relative humidity were set at constant 20 °C and 60%, respectively, for Expt. 1 and day/night temperatures were set at 25 °C/22 °C for Expt. 2. The CO₂ concentration for both experiments was $\approx$ 440 ppm.

Seedlings were top-irrigated as needed with tap water until cotyledons were visible on 50% of the plugs. Thereafter, groundwater supplemented with water-soluble fertilizer (20N–3.4P–16.6K All Purpose High Nitrate; Master Plant-Prod, Inc., Brampton, ON, Canada) was used for irrigation, providing (in mg·L⁻¹) 250 N, 42 P, 207 K, 1.8 Mg, 1.2 Fe, 0.62 Mn, Zn, and Cu, 0.25 B, and 0.18 Mo. Two separate fertilizer solution tanks were adjusted to pH 5.5 (for petunia and calibrachoa) and pH 6.0 (for geranium and marigold) using aqueous phosphoric acid. Uniform-sized seedlings were transplanted into 8.89-cm-tall black plastic pots (458 mL)

containing an all-purpose soilless substrate (Sunshine Mix #1; Sun Gro Horticulture Distribution) when the roots could hold the shape of the substrate when gently pulled (22–42 d for Expt. 1, 17–28 d for Expt. 2). The growth chamber was divided into six treatment zones, separated by white vinyl curtains to prevent light contamination between treatments while allowing sufficient air flow to maintain air temperature and relative humidity. Each treatment area, or plot, was divided into four subplots (2 × 2 grid). Each species was randomly assigned to one subplot and five uniformly sized sample plants of a given species were placed in its respective subplot. Border plants were placed around the outer edges of the plot. Over time, plants were spread further apart to prevent mutual shading, while keeping sample plants within the characterized light treatment plot area. Plants were rearranged within the subplots or the subplots were rotated within the plot at least every 3 d to reduce effects of nonuniform light distribution.

Plants were top-irrigated as needed by hand until minimal drainage was observed. Tap water was used for the first two irrigations after transplant. Thereafter, fertilizer solutions of either pH 6.0 or 5.5 were used as previously described for seedlings before transplanting.

The day/night air temperatures (mean $\pm$ SD), excluding 30 min after each day/night transition, were 20.4 $\pm$ 0.6 °C/18.3 $\pm$ 0.5 °C in Expt. 1 and 25.1 $\pm$ 0.9 °C/21.4 $\pm$ 0.3 °C (excluding fluorescent light treatment) in Expt. 2. When the lights were on, the fluorescent treatment plot was 1.5 °C higher than the average temperature of the LED treatment plots, but when the lights were off, all treatment plots had homogeneous temperatures. Average RH was 75% $\pm$ 7% in Expt. 1 and 69% $\pm$ 7% in Expt. 2.

Light treatments. In five of the six treatment zones, pairs of programmable LED lights (LX602C; Heliospectra AB, Gothenburg, Sweden) were suspended side by side (centers 38 cm apart), 60 cm above pot level. Each fixture had a rectangular array of 240 LEDs (27.6 cm × 16.8 cm) comprised of blue (450 nm), white (5700 K), red (660 nm), and far red (735 nm) LEDs, as described by the manufacturer. In the second experiment, the fluorescent light panels used for plug development provided a sixth light treatment.

LED lamps were programmed using System Assistant Version 1.3.0 software (Heliospectra AB). The photoperiod was 16-h from 0900 to 0100 HR. The red and white LEDs provided the same pot-level *PPF* and spectral distribution in all LED treatments. The blue channel was not used as the white LEDs provided sufficient blue light to give a B:R ratio of almost 2:5. Far red settings were adjusted to target R:FR of 0.70, 0.80, 0.90, 1.00, and 1.10 for the treatments. The light treatments were rerandomized among the five LED plots for the second experiment. The fluorescent lights in Expt. 2 were programmed to the same photoperiod, and panel height was adjusted to provide the same canopy-level *PPF* as the LED treatments.

Light spectra were measured with a USB2000 + spectrometer equipped with a 1.5-m long, 3900- μm diameter ultraviolet-VIS optical fiber with a CC-3 cosine corrector (OceanOptics, Dunedin, FL). The spectrometer was calibrated for absolute irradiance on 16 Mar. 2016 between 300 and 1050 nm using an LS-1 calibrating light source (OceanOptics). The average spectral distribution under each treatment was obtained from 25 points, measured at pot height on an equally spaced 5-by-5 square grid covering a 56 cm × 56 cm plot.

The peak wavelengths of the LED colors (mean $\pm$ SD), averaged from all 25 points under each treatment, were 445.7 $\pm$ 1.1 nm (blue peak of white channel), 659.5 $\pm$ 0.7 nm (red), and 736.2 $\pm$ 0.5 nm (far red) with full width at half maxima of 21 $\pm$ 2.2 nm, 17 $\pm$ 0.5 nm, and 22 $\pm$ 0.5 nm, respectively, at treatment intensities.

The spectral irradiance data were converted from $\mu\text{W}\cdot\text{cm}^{-2}\cdot\text{nm}^{-1}$ to $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{nm}^{-1}$, then multiplied by corresponding spectrometer pixel wave bandwidths and summed over the following ranges to calculate photon flux of blue (B, 400–500 nm), green (G, 500–600 nm), R, and PAR, with B:G:R presented as percent of total PAR in Table 1. The R:FR photon flux ratio of each treatment was measured and described using wide (R:FR) and narrow (R:FR_{narrow}) wavebands, and P_{fr}/P was estimated for each treatment following Sager et al. (1988) and Sager and McFarlane (1997), also presented in Table 1. The wide-bandwidth R:FR was preferred over R:FR_{narrow} for analysis because a slight shift in LED peak wavelength could lead to a large percentage of the peak being truncated in a R:FR_{narrow} calculation. This may skew the R:FR_{narrow} data substantially without a corresponding physiological response.

Because the fluorescent panel was initially positioned higher than the LED panels, over time, the canopy-level *PPF* under LEDs increased at a faster rate as plants grew. The relationship between height and average *PPF* under LED treatments was determined before transplant with spectrometer measurements at five heights. After treatments commenced, average canopy-level *PPF* under the LED treatments was calculated from canopy height measurements and the fluorescent panel height was adjusted weekly using a LI-190 quantum sensor calibrated to the spectrometer to match the canopy-level *PPF* under LED treatments.

Mean *PPF* at pot level was 210.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Expts. 1 and 2), corresponding to a DLI of 12.1 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. As the plants grew closer to the light fixtures, canopy-level *PPF* increased to 266 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (calculated based on canopy height), corresponding to a DLI of 15.3 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at harvest.

Data collection. Harvest dates were determined based on the development of reproductive structures, with one harvest date for each species. The harvest dates were chosen to be late enough to provide data relevant to generative tissue development whereas early enough to avoid excessive

Table 1. Summary of light treatments in Expts. 1 and 2.^z

Light treatment	R:FR ^y	R:FR _{narrow}	Estimated P_{fr}/P	PPF			B:G:R (%) ^x
				Max	Avg	Min	
Expt. 1							
LED R:FR 0.7	0.71 ± 0.04	0.73 ± 0.07	0.63	239.9	206.8 ± 19.3	174.5	19:31:50
LED R:FR 0.8	0.79 ± 0.04	0.78 ± 0.06	0.65	251.3	213.1 ± 22.4	171.4	19:31:50
LED R:FR 0.9	0.90 ± 0.04	0.91 ± 0.06	0.67	243.0	209.5 ± 20.2	167.6	19:30:51
LED R:FR 1.0	1.00 ± 0.05	1.00 ± 0.07	0.69	252.3	213.1 ± 22.7	174.5	19:31:50
LED R:FR 1.1	1.09 ± 0.05	1.04 ± 0.05	0.70	246.3	209.9 ± 21.4	168.9	19:31:50
Expt. 2							
LED R:FR 0.7	0.70 ± 0.03	0.73 ± 0.02	0.63	243.6	210.6 ± 20.2	168.3	19:30:51
LED R:FR 0.8	0.80 ± 0.04	0.80 ± 0.03	0.65	247.0	210.3 ± 22.5	164.9	19:31:50
LED R:FR 0.9	0.89 ± 0.04	0.87 ± 0.02	0.67	252.6	213.5 ± 23.2	171.2	19:31:50
LED R:FR 1.0	1.00 ± 0.05	0.98 ± 0.10	0.69	238.7	205.9 ± 19.2	173.5	19:31:50
LED R:FR 1.1	1.09 ± 0.05	1.08 ± 0.06	0.70	253.3	212.8 ± 22.4	174.7	19:31:50
WFL ^w	14.9 ± 0.5	9.6 ± 0.6	0.86	216.4	212.7 ± 2.6	206.3	18:55:27

^zMeasurements were taken at 25 locations per treatment at pot height. All LED treatments used the same lamp settings for white, blue, and red channels with the far red channel adjusted to produce the target R:FR.

^yThe R:FR (600–700 nm : 700–800 nm), R:FR_{narrow} (655–665 nm : 725–735 nm), estimated P_{fr}/P , and average PPF (400–700 nm) are reported as mean ± SD ($n = 25$) with all calculations based on photon flux (PF, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

^xPhoton flux ratios of blue (B, 400–500 nm), green (G, 500–600 nm), and red (R, 600–700) are reported as percentage of total PPF.

^wWhite fluorescent lamps (WFL) had PF for ultraviolet-A (320–400 nm) and ultraviolet-B (300–320 nm) of $1.60 \pm 0.06 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $0.08 \pm 0.01 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively.

R:FR = red to far red ratio; PPF = photosynthetic photon flux.

mutual shading between plants. Marigolds were harvested before flowering, when the average apical flower stem length (all treatments combined) was more than 2.5 cm. Petunia and calibrachoa were harvested when all plants in all treatments had at least one flower, and geraniums were harvested when flower buds were visible on more than 50% of all plants.

Plants were checked at least every 2 d for presence of generative tissues. Date of first bud and date of first flower were recorded on the first instance of a bud or open flower on each plant. A bud was counted for petunia and calibrachoa when developing petals were visible from any angle; for marigold, buds were counted when the white of the bud was visible; for geranium, buds were counted when any amount of flower stem was visible between the bud cluster and primary shoot. For calibrachoa, the number of nodes below the first bud was also recorded.

At harvest, all measurements for a species were recorded within a 24-h period except for dry weight. Nondestructive measurements common to all species were height, stem diameter, number of buds/inflorescences and flowers, and relative leaf chlorophyll content (SPAD units). Plant height was defined as length of the primary stem from substrate surface to shoot tip. If a terminal bud was present, as in marigolds, height was measured up to the last node where the flower stem emerged. For marigold, flower stem length (from the last node on primary stem to base of the flower bud) was also recorded. Stem diameter was measured immediately above the hypocotyl using a vernier caliper. The relative chlorophyll content for each plant was the average of three measurements from randomly selected newly fully expanded leaves using a SPAD-502Plus chlorophyll meter (Konica Minolta, Inc., Tokyo, Japan). Number of side branches was counted for

petunia in Expt. 1, and for both petunia and calibrachoa in Expt. 2. Nodes on the primary stem were counted for all species except geranium, for which leaves were counted instead. For geranium, the length of the longest petiole on each plant was measured.

The destructive measurements included leaf area, leaf dry weight, and stem dry weight. Stems were severed at the substrate surface. Then, leaves were cut from stems at the leaf axil except for geraniums, for which leaves were cut below the leaf blade. Larger marigold leaves were dissected following a ‘2-mm rule’: any part of the central vein wider than 2 mm was excised and placed in the stem category to prevent skew of the specific leaf area measurement (SLA; leaf area per unit leaf dry weight). All biomass above the substrate surface other than leaves were placed in the ‘stem’ category. Leaf area was measured with a leaf area meter (LI-3100; LI-COR, Inc.). Leaves and stems were oven-dried separately at 65 °C for at least 5 d (until weight was constant) and weighed. Total dry weight (total DW; leaf dry weight + stem dry weight) was also calculated.

Statistical analysis. Statistical analysis was performed in RStudio (RStudio Team, 2016) using “R” software version 3.3.1 (R Core Team, 2016). Significance for all analyses was defined at $P \leq 0.05$. Each measured variable was individually analyzed for linear and quadratic regression over the range of R:FR using the linear model function followed by analysis of variance, using sequential sums of squares. Only the best fit model equations are presented for variables with significant regressions, whereas overall means (pooled data from all LED treatments) are presented when there were no treatment effects for descriptive purposes. Packages used were “dplyr” (Wickham and Francois, 2016) for summary statistics and “agricolae” (de Mendiburu, 2016) for Tukey’s honestly

significant difference post hoc test to check for differences between the fluorescent and pooled LED treatment data.

Results

Expt. 1

There were no treatment effects on final height or dry weight (Table 2) for all four species.

Calibrachoa. There were no treatment effects for any variable measured.

Petunia. Low R:FR resulted in greater number of nodes and earlier appearance of first bud (compared with higher R:FR) although there was no subsequent difference in days to first flower.

Geranium. Decreasing R:FR was associated with fewer leaves and reduced bud count.

Marigold. Stem diameter, leaf area, and SLA responded to R:FR quadratically. Stem diameter followed a positive parabolic function, with minimum at R:FR of 0.94, whereas leaf area and SLA followed negative parabolic functions with maxima at R:FR of 0.89 and 0.91, respectively.

During the experiment, an interesting observation was made. A few excess plants were kept in the unused chamber zone under fluorescent lights (initially used to produce the seedlings). These plants had noticeably darker green leaves and markedly shorter stems and internodes than the plants under any of the LED treatments. Hence, a fluorescent treatment was included in Expt. 2 to compare morphology between plants grown under fluorescent and LED treatments.

Expt. 2

A greater number of treatment effects were observed in Expt. 2 compared with Expt. 1. Some measures of height were affected in all species, as decreased R:FR increased the height (primary stem length) of marigold, petunia, and calibrachoa, and increased petiole length in geranium (Table 2).

Marigold. Plants treated with R:FR 0.7 had 11% greater height than those treated with R:FR 1.1 (i.e., 17.0 cm vs. 15.3 cm). Lower R:FR (0.7) was also associated with earlier date of first flower bud by ≈ 2 d, longer terminal flower bud stems, and greater stem and total dry weight than higher R:FR (1.1).

Petunia. Plants treated with R:FR 0.7 had 22% greater height than those treated with R:FR 1.1 (i.e., 12.5 cm vs. 10.2 cm). Petunia leaf area and leaf dry weight both followed positive quadratic trends, with minima at R:FR 0.89 and 0.90, respectively.

Calibrachoa. Plants treated with R:FR 0.7 had 32% greater height than those treated with R:FR 1.1 (i.e., 40.7 cm vs. 30.7 cm).

Geranium. Plants treated with R:FR 0.7, length of the longest petiole was 10% greater than those treated with R:FR 1.1 (i.e., 10.9 cm vs. 9.9 cm).

Table 2. Effects of R:FR (0.7–1.1) on growth and flowering of marigold, petunia, calibrachoa, and geranium in Expts. 1 and 2.

Measurement	Expt. 1		Expt. 2	
	Regression equation or avg ^a	r ²	Regression equation or avg	r ²
Marigold				
Height (cm)	10.4 ± 0.2		y = 19.9 – 4.2x	0.18
Flower stem length (cm)	2.9 ± 0.1		y = 6.4 – 4.1x	0.25
Nodes (no.)	6.9 ± 0.1		11.6 ± 0.2	
Stem diameter (mm)	y = 19.3 – 24.5x + 13.0x ²	0.28	9.4 ± 0.1	
Leaf area (cm ²)	y = –859 + 3,574x – 2,006x ²	0.26	1,312 ± 13	
Leaf dry weight (g)	2.41 ± 0.04		4.19 ± 0.04	
Stem dry weight (g)	1.22 ± 0.04		y = 5.3 – 1.7x	0.44
Total dry weight (g)	3.63 ± 0.07		y = 9.1 – 1.2x	0.18
SLA (cm ² ·g ^{–1})	y = –270 + 1,262x – 696x ²	0.49	313 ± 3	
Bud count	9.8 ± 0.4		8.6 ± 0.4	
Days to first bud (DAT)	17.4 ± 0.4		y = 12.6 + 5.6x	0.19
Petunia				
Height (cm)	16.6 ± 0.4		y = 16.4 – 5.6x	0.16
Nodes (no.)	y = 10.0 – 3.1x	0.22	5.1 ± 0.1	
Stem diameter (mm)	4.6 ± 0.1		4.4 ± 0.1	
Branches (no.)	9.5 ± 0.3		10.4 ± 0.2	
Leaf area (cm ²)	711 ± 13		y = 1,868 – 3,028x + 1,698x ²	0.43
Leaf dry weight (g)	1.62 ± 0.04		y = 3.9 – 6.3x + 3.5x ²	0.35
Stem dry weight (g)	2.33 ± 0.08		1.25 ± 0.11	
Total dry weight (g)	3.95 ± 0.11		y = 8.1 – 12.6x + 7.0x ²	0.37
SLA (cm ² ·g ^{–1})	441 ± 6		445 ± 5	
Flower and bud count	34.4 ± 1.3		16.8 ± 0.3	
Days to first bud (DAT)	y = 4.6 + 4.8x	0.20	10.2 ± 0.2	
Days to first flower (DAT)	17.4 ± 0.5		16.3 ± 0.3	
Calibrachoa				
Height (cm)	32.3 ± 1.0		y = 58.1 – 24.9x	0.27
Nodes (no.)	26.1 ± 0.8		25.4 ± 0.5	
Stem diameter (mm)	3.2 ± 0.1		3.0 ± 0.1	
Branches (no.)	NA		21.5 ± 0.8	
Leaf area (cm ²)	600 ± 34		498 ± 23	
Leaf dry weight (g)	2.58 ± 0.14		1.38 ± 0.06	
Stem dry weight (g)	2.12 ± 0.11		1.51 ± 0.06	
Total dry weight (g)	4.70 ± 0.23		2.89 ± 0.12	
SLA (cm ² ·g ^{–1})	235 ± 7		360 ± 7	
Flower and bud count	41.0 ± 3.9		19.7 ± 1.4	
Days to first flower (DAT)	30.6 ± 0.4		20.4 ± 0.4	
Nodes below first bud (no.)	20.8 ± 0.5		20.6 ± 0.4	
Geranium				
Height (cm)	10.3 ± 0.3		9.5 ± 0.2	
Longest petiole (cm)	10.5 ± 0.16		y = 12.6 – 2.5x	0.22
Leaves (no.)	y = 8.8 + 2.0x	0.16	10.4 ± 0.1	
Stem diameter (mm)	9.1 ± 0.12		8.9 ± 0.1	
Leaf area (cm ²)	585 ± 22		526 ± 11	
Leaf dry weight (g)	3.35 ± 0.16		2.46 ± 0.07	
Stem dry weight (g)	1.34 ± 0.06		0.81 ± 0.02	
Total dry weight (g)	4.69 ± 0.22		3.27 ± 0.08	
SLA (cm ² ·g ^{–1})	179 ± 5		215 ± 4	
Bud count	y = –1.0 + 1.7x	0.22	0.6 ± 0.1	

^aVariables with significant ($P \leq 0.05$) linear or quadratic regressions over R:FR are presented as equations; for nonsignificant variables, mean ± SE ($n = 25$) is presented for descriptive purposes.

SLA = specific leaf area; DAT = days after transplant; NA = not applicable.

Fluorescent versus LED treatments in Expt. 2

Compared with the means of pooled data for LED treatments, all species under fluorescent light had reduced height, reduced stem dry weight, and increased relative chlorophyll content (SPAD) (Table 3). Overall, plants grown under fluorescent lights were visually more compact.

Height, dry weight, petiole length, and stem diameter. Under fluorescent light, marigolds, petunias, calibrachoa, and geraniums were 26%, 67%, 60%, and 48% shorter, and had 28%, 39%, 21%, and 31% lower stem dry weights, respectively.

Under fluorescent light, marigold leaf dry weight was reduced by 8%, and total dry weight was reduced in all species except for

calibrachoa. For geraniums, the length of the longest petiole under fluorescent light was 46% shorter than under the LED treatments. Although reduction in dry weight primarily occurred in the stems, stem diameter was unaffected in all species. It follows that the reductions in dry weight could be primarily accounted for by shorter stems, and also shorter petioles in geraniums.

Number of nodes and leaves, branching, and flowering. Marigold and petunia had 9% and 22% fewer nodes on the primary stem, respectively, under fluorescent light. Geraniums had 12% more leaves under fluorescent lights. There were no differences in branching in petunia and calibrachoa between fluorescent and LED treatments. The days to first bud and first flower were

unaffected for all species. The only treatment effect pertaining to flowering was the total number of buds and flowers in petunia, with 38% fewer buds and flowers under fluorescent lights than under LEDs.

Leaf area, SLA. The only treatment effect for leaf area was 13% reduction in that of marigold under fluorescent vs. LEDs. Specific leaf area, however, was reduced under fluorescent lights in both marigold and calibrachoa by 5% and 19%, respectively.

Leaf color and relative chlorophyll content. The relative chlorophyll content (SPAD) for all species was higher under fluorescent light (Table 3), where leaves were also observably darker green in color when viewed under a common light environment. Geranium leaves also had starker

Table 3. Growth and flowering of marigold, petunia, geranium, and calibrachoa under fluorescent light and LEDs^a in Expt. 2.

Measurement	Fluorescent	LED
Marigold		
Height (cm)	11.9 ± 0.4 b	16.1 ± 0.3 a
Flower stem length (cm)	2.6 ± 0.3 a	2.7 ± 0.2 a
Nodes (No.)	10.6 ± 0.4 b	11.6 ± 0.2 a
Stem diameter (mm)	9.5 ± 0.3 a	9.4 ± 0.1 a
Leaf area (cm ²)	1,147 ± 30 b	1,312 ± 12 a
Leaf dry weight (g)	3.87 ± 0.10 b	4.19 ± 0.04 a
Stem dry weight (g)	2.85 ± 0.14 b	3.84 ± 0.07 a
Total dry weight (g)	6.72 ± 0.22 b	8.02 ± 0.08 a
SLA (cm ² ·g ⁻¹)	297 ± 8 b	314 ± 3 a
Bud count	9.6 ± 0.7 a	8.6 ± 0.4 a
Days to first bud (DAT)	16.0 ± 0.0 a	17.6 ± 0.4 a
SPAD ^b	67.8 ± 1.2 a	53.5 ± 0.6 b
Petunia		
Height (cm)	3.7 ± 0.2 b	11.3 ± 0.4 a
Nodes (No.)	4.0 ± 0.0 b	5.1 ± 0.1 a
Stem diameter (mm)	4.7 ± 0.1 a	4.4 ± 0.1 a
Branches (No.)	10.2 ± 0.2 a	10.4 ± 0.2 a
Leaf area (cm ²)	524 ± 47 a	551 ± 8 a
Leaf dry weight (g)	1.19 ± 0.08 a	1.24 ± 0.02 a
Stem dry weight (g)	0.82 ± 0.04 b	1.34 ± 0.03 a
Total dry weight (g)	2.01 ± 0.09 b	2.58 ± 0.04 a
SLA (cm ² ·g ⁻¹)	438 ± 12 a	445 ± 5 a
Flower and bud count	10.4 ± 1.0 b	16.8 ± 0.3 a
Days to first bud (DAT)	10.0 ± 0.0 a	10.2 ± 0.2 a
Days to first flower (DAT)	16.4 ± 0.7 a	16.3 ± 0.3 a
SPAD	49.6 ± 1.0 a	43.3 ± 0.5 b
Geranium		
Height (cm)	4.9 ± 0.2 b	9.5 ± 0.2 a
Longest petiole (cm)	5.6 ± 0.0 b	10.3 ± 0.1 a
Leaves (No.)	11.6 ± 0.2 a	10.4 ± 0.1 b
Stem diameter (mm)	8.6 ± 0.3 a	8.9 ± 0.1 a
Leaf area (cm ²)	476 ± 21 a	526 ± 11 a
Leaf dry weight (g)	2.19 ± 0.15 a	2.46 ± 0.07 a
Stem dry weight (g)	0.56 ± 0.03 b	0.81 ± 0.02 a
Total dry weight (g)	2.74 ± 0.18 b	3.27 ± 0.08 a
SLA (cm ² ·g ⁻¹)	219 ± 6 a	215 ± 4 a
Bud count	0.6 ± 0.2 a	0.6 ± 0.1 a
SPAD	39.7 ± 1.1 a	35.0 ± 0.8 b
Calibrachoa		
Height (cm)	14.2 ± 1.6 b	35.9 ± 1.4 a
Nodes (No.)	24.8 ± 1.0 a	25.4 ± 0.5 a
Stem diameter (mm)	2.8 ± 0.1 a	3.0 ± 0.1 a
Branches (No.)	25.4 ± 2.0 a	21.5 ± 0.8 a
Leaf area (cm ²)	459 ± 36 a	498 ± 23 a
Leaf dry weight (g)	1.57 ± 0.12 a	1.38 ± 0.06 a
Stem dry weight (g)	1.19 ± 0.11 b	1.51 ± 0.06 a
Total dry weight (g)	2.76 ± 0.20 a	2.89 ± 0.12 a
SLA (cm ² ·g ⁻¹)	293 ± 14 b	360 ± 7 a
Flower and bud count	19.2 ± 1.9 a	19.7 ± 1.4 a
Days to first flower (DAT)	21.2 ± 0.6 a	20.4 ± 0.4 a
Node of first flower	20.8 ± 1.0 a	20.6 ± 0.4 a
SPAD	58.5 ± 1.7 a	39.6 ± 0.7 b

^aData for all LED treatments were pooled (mean ± SE; *n* = 25) and compared with the cool-white fluorescent (mean ± SE; *n* = 5) treatment using Tukey's honestly significant difference test. Data in the same row with different letters are significantly different (*P* < 0.05).

^bSPAD units represent relative chlorophyll content.

SLA = specific leaf area; DAT = days after transplant.

leaf variegation pattern under fluorescent lights.

Discussion

Effects of R:FR on growth and morphology of bedding plants. Plant growth and morphology were affected over the R:FR range of 0.7–1.1, which corresponds to the range measured under HBs in greenhouses in Southern Ontario, Canada, during early spring. Some metrics responded differently between experiments such as height, petiole

length, and dry weight only showed treatment effects in Expt. 2, whereas numbers of nodes and leaves, stem diameter, and SLA only showed treatment effects in Expt. 1.

The response trends across the four species were more consistent in Expt. 2, where lower R:FR produced longer stems in marigold, calibrachoa, and petunia and longer petioles in geranium (typical shade avoidance responses). These results are consistent with other studies which reported greater stem elongation or petiole elongation in response to lower R:FR during the day or at the

end-of-day in *Petunia ×hybrida* (Bachman and McMahon, 2006; Ilias and Rajapakse, 2005), zinnia, chrysanthemum, cosmos (Cerny et al., 2003), impatiens (Fletcher et al., 2005), squash rootstock (Yang et al., 2012), *Cucurbita pepo*, *Chenopodium album* (Holmes and Smith, 1977c), soybean (Kasperbauer, 1987), tobacco (Kasperbauer and Peaslee, 1973), and other dicotyledonous species (Demotes-Mainard et al., 2016). The different responses to R:FR between Expts. 1 and 2 might be related to temperature differences, as several studies have reported interactions between R:FR and day/night temperature differential (DIF) (Blom and Kerec, 2003; Kubota et al., 2000; Moe et al., 1991; Xiong et al., 2011) or with absolute temperature (higher or lower with the same DIF) (Qaderi et al., 2015) on the stem length of various species, where low R:FR combined with positive DIF or higher absolute temperatures result in longer stem length.

Reductions in *PAR* have also been implicated as an influential factor promoting stem elongation under HBs, as the DLI may fall below minimum requirements for “good quality” plants in greenhouse production (Faust, 2003; Llewellyn et al., 2013). However, interaction between R:FR and irradiance was not investigated and cannot be ruled out, as evidence suggests that phytochrome B (phyB), which is considered to be the main photoreceptor for shade-avoidance responses, has an integrated response to R:FR and irradiance on the subcellular level (Trupkin et al., 2014). More specifically, lowering irradiance (from 200 to 25 μmol·m⁻²·s⁻¹) in addition to lower R:FR (from 4.3 to 0.8) had compounding effects on the number and size of phyB nuclear bodies within *Arabidopsis* petiole cells (phyB in the nucleus is related to phytochrome activity, as phyB migrates from the cytosol to the cell nucleus only in the ‘active’ *P_{fr}* form).

Effects of R:FR on flowering. The R:FR had limited effects on flower development. For petunia in Expt. 1, lower R:FR was associated with earlier date of first bud, but there was subsequently no difference in the date of first flower. For geraniums, lower R:FR was associated with reduced bud count, which in this case may be interpreted as a delay in flowering; because plants had 0 or 1 bud, treatments with lower average bud numbers had a higher proportion of plants with no buds at the time of harvest. In Expt. 2, lower R:FR stimulated flowering in marigold, with R:FR 0.7 producing an earlier date of first bud by ≈2 d and longer terminal flower stems than R:FR 1.1. Although the effects on flowering were subtle, results for marigold and petunia agree with other studies which reported that a reduced R:FR can accelerate flower development (Ilias and Rajapakse, 2005), or conversely that an FR-deficient environment (increased R:FR) can delay flower initiation (Cerny et al., 2003; Runkle and Heins, 2001), especially in long-day plants.

Differences between LED and fluorescent treatments (Expt. 2). Some of the pooled data for plants grown under LED treatments were substantially different from the fluorescent treatment plants. Common effects across all four species were reduced height, reduced stem dry weight, and increased relative chlorophyll content under fluorescent light. There were no differences in flower development except for petunia, for which there were greater number of total buds and flowers at harvest in the fluorescent treatment.

There are many features of the fluorescent spectral distribution that may have affected morphological responses. For example, in comparison with the LED treatments, fluorescent light had higher R:FR (14.9 vs. ≤ 1.1), presence of ultraviolet-A and ultraviolet-B, higher G photon flux, lower R photon flux, and a correspondingly higher B:R (2:3 vs. ≈ 2.5) as the B photon flux and percent B of PPF were similar for all treatments (Table 1). A higher R:FR, higher blue (relative or absolute amount), and presence of ultraviolet have been implicated in the inhibition of stem elongation (Cope and Bugbee, 2013; Fletcher et al., 2005; Hernández and Kubota, 2016; Wargent, 2016).

Reductions in stem DW and higher relative chlorophyll content of fluorescent-grown plants could also be due to multiple factors including ultraviolet and high intensity green. In lettuce, the removal of ultraviolet in a greenhouse setting using selective filters was associated with increased dry weight (Tsormpatsidis et al., 2008). With regard to green light, Kim et al. (2004) found that higher intensities of green light (51% and 86% of PPF) provided in growth chambers resulted in lower dry weight of lettuce compared with lower intensity of green (24% of PPF) with the same total PPF. However, because the high-intensity green treatments in Kim et al. (2004) emitted more ultraviolet light than the lower-intensity green treatments, it is also possible that the effects of ultraviolet were conflated with elevated levels of green. Higher B:R has also been associated with reduced DW in lettuce (Son and Oh, 2013) but was attributed to a reduction in leaf area; a phenomenon which was not observed in our experiment except in marigold. It is also worth noting that Son and Oh (2013) achieved their different B:R by varying both B and R intensities, whereas in our study, fluorescent spectrum had a higher B:R because of a lower R intensity only, meaning the absolute amount of B was the same in both LED and fluorescent treatments.

Similar to the relative chlorophyll content results of the present study, Johkan et al. (2010) found that fluorescent light-induced higher chlorophyll content in sole source lettuce production than a combination of R and B LEDs. This indicates that lower R:FR may not be the only reason why plants grown with fluorescent light had higher relative chlorophyll contents than those grown under LEDs in this study. Still, it is possible that the lower R:FR provided by LED treatments may have had a further effect to reduce

chlorophyll and variegation patterns, similar to Li and Kubota (2009) who found that supplemental FR resulted in reduced chlorophyll and anthocyanins in lettuce. Other studies have reported reduced chlorophyll content in response to low R:FR in a variety of species (Heraut-Bron et al., 1999; Smith and Whitelam, 1997; Tucker, 1981). The presence of ultraviolet, which has been associated with elevated anthocyanin pigments in lettuce (Tsormpatsidis et al., 2008), baby leaf lettuce (Li and Kubota, 2009), and turnip hypocotyls (Zhou et al., 2007), may have also contributed to the increased leaf variegation in geranium grown under fluorescent lights as anthocyanins have been found to be abundant in zonal dark rings of *Pelargonium × hortorum* leaves (Liakopoulos and Spanorigas, 2012).

In summary, although the specific causes of morphological difference in the fluorescent treatment are uncertain, the results show the potential for light spectrum manipulations to induce changes to morphology and flowering.

There were three noteworthy differences between the growth chamber experiments and realistic greenhouse conditions which could affect the transferability of the results. Although the LED treatments provided wavelengths in blue, green, and red wavebands, solar spectral ratios were not replicated. The LED treatments had a B:G:R of 19:31:50 whereas solar radiation was measured to be $\approx 28:37:35$ (measured on a mostly clear day on 8 Feb. 2017 at lat. 42°N, data not shown). In addition, the PPF in the growth chamber was constant throughout the photoperiod, whereas PPF in a greenhouse follows a variable, diurnal pattern with instantaneous PPF being highly influenced by outdoor weather. Differences in temperature may also interact with R:FR to influence transferability of results to commercial production.

Conclusion

This study investigated the effects of R:FR on morphology and flowering of marigold, petunia, calibrachoa, and geranium under the range of R:FR (0.7–1.1) found in commercial greenhouse production scenarios where a canopy of HBs is grown above the bench level. Although light treatment effects were found, the crop responses were generally not considered commercially relevant because of similar appearances between plants grown under different treatments.

In terms of the potential of using light as a growth regulator, the fluorescent treatment provided evidence that spectral manipulation could be used to control growth, as plants grown under fluorescent lights showed noticeable differences in qualitative factors such as leaf coloration and stem elongation. Any of the distinct spectral parameters in fluorescent lights are candidates for further investigation toward using light as a growth regulator in a greenhouse setting, including increased R:FR, presence of ultraviolet-A or ultraviolet-B, or increased B:R. Further

research is needed to determine whether spectral manipulation can be used to create commercially relevant outcomes.

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