

# End-of-day Far-red Lighting with a Low Daily Light Integral Increases Stem Length But Does Not Promote Early Leaf Expansion for *Petunia* × *hybrida* Seedlings

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**Abstract.** Greenhouse production of high-quality young annual bedding plants (plugs) at northern latitudes often requires supplemental lighting to compensate for a low natural daily light integral (DLI), but radiation interception by plugs is limited by a low leaf area index. Some species show an increase in leaf area in response to growth under a low ratio of red to far-red radiation (R:FR), and an early increase in leaf area may allow for more effective radiation capture by seedlings and a reduction in wasted radiation. Thus, the objective of this study was to examine the effects of end-of-day far-red (EOD-FR) radiation treatments varying in intensity, R:FR (600–700 nm/700–780 nm), and duration on early leaf expansion and plug quality for petunia (*Petunia* × *hybrida*) ‘Wave Purple’ and ‘Dreams Midnight’. Seedlings were grown in 128-cell trays in a common greenhouse environment under a simulated winter DLI (~5.3 mol·m<sup>-2</sup>·s<sup>-1</sup>) and received one of four EOD-FR treatments, control conditions (no EOD-FR or supplemental lighting), or supplemental lighting (target photosynthetic photon flux density of 70 μmol·m<sup>-2</sup>·s<sup>-1</sup>). The EOD-FR treatments were provided for 3 weeks on cotyledon emergence and included the following: 10 μmol·m<sup>-2</sup>·s<sup>-1</sup> of far-red radiation for 30 minutes with a R:FR of ~0.8 (EOD<sub>FL</sub>), 10 or 20 μmol·m<sup>-2</sup>·s<sup>-1</sup> of far-red radiation for 30 minutes with a R:FR of ~0.15 (EOD<sub>10:30</sub> and EOD<sub>20:30</sub>, respectively), or 20 μmol·m<sup>-2</sup>·s<sup>-1</sup> of far-red radiation for 240 minutes with a R:FR of ~0.15 (EOD<sub>20:240</sub>). Destructive data were collected 14 and 21 days after cotyledon emergence. Seedlings that received EOD-FR treatments did not show any increase in leaf area compared with control or supplemental lighting treatments. Stem length generally increased under EOD-FR treatments compared with supplemental lighting and control treatments; greater elongation was observed when the R:FR decreased from 0.8 to 0.15, and when treatment duration increased from 30 minutes to 240 minutes. However, at a R:FR of 0.15 and a treatment duration of 30 minutes, an increase in far-red radiation intensity from 10 to 20 μmol·m<sup>-2</sup>·s<sup>-1</sup> did not promote further stem elongation resulting in similar stem lengths for both cultivars under EOD<sub>10:30</sub> and EOD<sub>20:30</sub>. Results of this study indicate that under low DLIs, EOD-FR radiation applied in the first 3 weeks of seedling production does not promote early leaf area expansion, and generally decreases seedling quality for petunia. As responses to far-red radiation may vary based on study taxa, incident radiation, and DLI, future research examining EOD-FR-induced morphological changes is warranted.

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Poel and Runkle 2017a) also decrease. Increasing the DLI when natural light is low requires the use of supplemental lighting, but the costs of supplemental lighting can be extensive (van Iersel and Gianino 2017). Oh et al. (2010) showed that supplemental lighting does not provide equal benefit at all stages of seedling development; in this study, supplemental lighting provided to seedlings of petunia (*Petunia* × *hybrida*) ‘Madness Red’ and pansy (*Viola* × *wittrockiana*) ‘Delta Premium Yellow’ during the four to six and three to four leaf stage, respectively, led to greater or similar dry mass at transplant compared with when supplemental lighting was applied while cotyledons were developing and during the one to three or one to two leaf stage. Thus, it may be advantageous to promote early leaf expansion in young plants to facilitate increased radiation capture when DLI is low or lighting costs are limiting to growers, and to increase the efficacy of supplemental lighting by reducing wasted radiation that may strike substrate, plug trays, or bench space.

A decreased ratio of red relative to far-red radiation (R:FR) perceived by the photoreceptor family phytochrome is one important signal for plants of current or future vegetational shade; this decrease under forest canopies or in dense plantings is due to the relatively lower transmission of red radiation and higher transmission and reflectance of far-red radiation, and shade-avoiding plants exposed to decreased R:FR undergo a variety of shade avoidance responses such as hypocotyl, internode, and petiole elongation to improve radiation capture (Ballaré and Pierik 2017; Casal 2013; Franklin 2008; Smith and Whitelam 1997). Increases, decreases, and minimal effects of shade light quality or supplemental far-red radiation on leaf area expansion have also been reported and vary interspecifically and with leaf age or photosynthate availability (Casal and Smith 1989; Casal et al. 1987; Demotes-Mainard et al. 2016; Park and Runkle 2017).

The addition of far-red radiation in sole source lighting (SSL) environments has been shown to increase leaf area in *Arabidopsis* (*Arabidopsis thaliana*) (Franklin et al. 2003; Patel et al. 2013), snapdragon (*Antirrhinum majus*), geranium (*Pelargonium* × *hortorum*), petunia (Park and Runkle 2016, 2017, 2018), and tomato (*Solanum lycopersicum*) (Kalaitzoglou et al. 2019). For example, Kalaitzoglou et al. (2019) found that an addition of 54 μmol·m<sup>-2</sup>·s<sup>-1</sup> of far-red to a background photosynthetic photon flux density (PPFD; 400–700 nm) of 149 μmol·m<sup>-2</sup>·s<sup>-1</sup> increased leaf area of tomato ‘Komeett’ by 3%, resulting in an increase in whole plant radiation absorption by 10% compared with plants with no added far-red radiation. Similarly, Park and Runkle (2018) found that leaf area of petunia ‘Wave Blue’ seedlings increased as the R:FR decreased. In the previously mentioned experiments, significant increases in plant height often accompanied any leaf area expansion and is an undesirable response for annual bedding plant seedlings.

The recommended daily light integral (DLI) to produce high-quality young annual bedding plants (plugs) is 10 to 12 mol·m<sup>-2</sup>·d<sup>-1</sup> (Lopez and Runkle 2008; Pramuk and Runkle 2005). However, plug production often begins in midwinter to early spring when the ambient DLI in northern latitude greenhouses may be limited due to naturally short photoperiods and a low angle of incidence; further decreases occur due to greenhouse infrastructure, increasing latitude, and the presence of cloud cover (Both and Faust 2017; Faust and Logan 2018; Lopez and Runkle 2008; Pramuk and Runkle 2005; Styer 2003).

As DLI decreases, many metrics of plug quality, such as average shoot dry mass per internode (Pramuk and Runkle 2005), stem diameter (Craver et al. 2019), root dry mass (RDM), and shoot dry mass (Oh et al. 2010;

An SSL research environment allows for the relative customization of radiation quality to promote plant morphological change, but using supplemental lighting to achieve the same within greenhouses is more difficult, especially when the relative contribution of the supplemental radiation to total radiation is low (Craver et al. 2019; Hernández and Kubota 2014; Poel and Runkle 2017a, 2017b). Thus, the use of end-of-day (EOD) treatments with a low R:FR may be more effective in eliciting desirable responses in a greenhouse environment. End-of-day far-red (EOD-FR) treatments have been found to promote shade avoidance responses such as hypocotyl elongation (Chia and Kubota 2010; Mizuno et al. 2015; Yang et al. 2012), leaf expansion (Casal and Sadras 1987; Casal et al. 1987), and internode elongation (Kalaitzoglou et al. 2019). In addition, lower R:FR applied as EOD-FR or as simulated shade during the day often increases the intensity of elongation responses (Chia and Kubota 2010; Kalitzoglou et al. 2019; Lund et al. 2007), whereas other responses such as leaf area expansion may in part depend on resource availability or age of the leaves (Casal and Sadras 1987; Casal et al. 1987; Park and Runkle 2018). Responses to far-red radiation such as hypocotyl elongation also show a far-red dose (far-red photon flux density × duration of treatment) response in some species (Chia and Kubota 2010; Yang et al. 2012).

Because of the costs of lighting and the importance of timing supplemental radiation application, it is worth examining whether EOD-FR can elicit increases in the leaf area index (LAI) of annual bedding plant plugs to improve radiation capture and more efficiently use supplemental lighting. In addition, as prolonged EOD-FR treatments may lead to intense elongation responses, it is necessary to examine leaf area expansion at multiple time points. Thus, the objectives of this study were to 1) investigate the effects of EOD-FR radiation (R:FR, far-red intensity, and duration) on early leaf expansion under a low DLI; 2) investigate if increasing DLI through supplemental lighting increases plug quality post cessation of EOD-FR treatments if early leaf expansion occurs; and 3) quantify detrimental shade avoidance responses such as excessive elongation, attributable to EOD-FR treatments. To improve the applicability of this study to greenhouse production, commercially available flowering lamps in addition to tunable light-emitting diode (LED) fixtures were used to examine the effects of

differing R:FR (600–700 nm/700–780 nm). As past research has shown that leaf expansion and stem elongation in *Petunia* spp. have occurred in response to supplemental far-red radiation and EOD-FR, we selected two petunia cultivars, Wave Purple (WP) and Dreams Midnight (DM), to examine treatment responses.

## Materials and Methods

**Plant material and greenhouse environment.** Seeds of petunia ‘WP’ and ‘DM’ were sown between 12 Sep and 7 Oct 2020, in 128-cell trays (15-mL individual cell volume) using a commercial soilless germination medium (BM2 Germinating Mix; Berger Horticultural Products Ltd., Saint-Modeste, QC, Canada). Trays were germinated under a translucent plastic tarp in a common greenhouse environment at the Colorado State University Horticulture Center (Fort Collins, CO, USA). On cotyledon emergence, trays were transferred underneath shadecloth-covered polyvinyl chloride (PVC) structures to simulate a winter DLI.

Greenhouse air temperature was controlled using a Veristep integrated environmental control system (Wadsworth Control Systems, Arvada, CO, USA) with a target air temperature of 21/19 °C (D/N). Seedlings were irrigated as needed using tap water with added water-soluble fertilizer (Jack’s 13N–0.9P–10.8K Plug LX; J.R. Peters, Inc., Allentown, PA, USA) providing (in mg·L<sup>-1</sup>) 150 nitrogen (N), 23 phosphorus (P), 150 potassium (K), 69 calcium (Ca), 34 magnesium (Mg), 0.15 boron (B), 0.07 copper (Cu), 0.75 iron (Fe), 0.37 manganese (Mn), 0.07 molybdenum (Mo), and 0.37 zinc (Zn). The appropriate pH and electrical conductivity (EC) of the water-soluble fertilizer was confirmed using a handheld meter (GroLine H19814; Hanna Instruments, Woonsocket, RI, USA). The average ± SD pH and EC were 1.34 ± 0.06 and 6.56 ± 0.11, respectively.

**Greenhouse supplemental radiation and EOD-FR treatments.** Shade structures described previously were used to simulate the light environment commonly reported in northern hemisphere greenhouse production facilities during the winter season. Two shade structures were deployed per experimental replication with one serving as a wintertime control (WTC) and the other serving as wintertime control with supplemental lighting (WSL). The WSL environment was created by hanging a supplemental lighting fixture

(Phillips GreenPower LED Toplighting Linear 2.1; Signify, Eindhoven, The Netherlands) 1.15 m above the greenhouse bench (6 cm above shade structures) for the duration of the study. The fixture provided a target total photon flux density (TPFD; 400–780 nm) of 70 μmol·m<sup>-2</sup>·s<sup>-1</sup> with a 14-h photoperiod (0600–2000 HR). Radiation intensity and spectrum were measured using a spectrometer (LI-180; LI-COR Biosciences, Lincoln, NE, USA), and mean TPFD, photon flux density (PFD; blue, 400–500 nm; green, 500–600 nm; red, 600–700 nm; far-red, 700–780 nm), and R:FR (600–700 nm/700–780 nm) for the WSL environment are reported in Table 1. For the duration of the study, one plug tray per replication per cultivar was placed underneath the WTC to serve as a low DLI control (CN) from 0800 to 1830 HR (moved under blackout at 1830 for a 10.5-h photoperiod), and one plug tray per replication per cultivar was placed underneath the WSL to serve as a supplemental lighting control (SR). All trays receiving EOD-FR were placed under the WTC shade structure during the day. Tray position was randomized every day to minimize any effects of uneven radiation distribution.

Two PVC structures covered with blackout cloth to prevent outside radiation interference were used to apply EOD-FR treatments. Under the first blackout structure, three flowering lamps (FL; Philips GreenPower LED DR/W/FR; Signify) were mounted 0.68 m above the greenhouse bench to provide a target far-red PFD of 10 μmol·m<sup>-2</sup>·s<sup>-1</sup> at canopy height. Under the second blackout structure, a tunable LED fixture (tunable fixtures; Elixia; Heliospectra, Gothenburg, Sweden) was mounted 0.7 m above the greenhouse bench to provide two EOD-FR radiation environments based on proximity to the fixture with a target far-red PFD of 10 and 20 μmol·m<sup>-2</sup>·s<sup>-1</sup> at canopy height. A summary of mean TPFD, PFD, and R:FR for each EOD-FR environment is reported in Table 1, and spectral quality of WSL and EOD-FR environments are reported in Fig. 1.

Using the EOD-FR environments described previously, four treatments were established varying in far-red PFD (10 or 20 μmol·m<sup>-2</sup>·s<sup>-1</sup>), R:FR (0.15 or 0.80), and duration of EOD-FR treatment (30 or 240 min). EOD-FR treatments are designated as “EOD” with subscripts describing the radiation source as with FL (EOD<sub>FL</sub>), or in the case of tunable fixtures, describing the intensity of far-red radiation and the

Table 1. Total (TPFD; 400–780 nm), blue (BPDF; 400–500 nm), green (GPFD; 500–600 nm), red (RPFD; 600–700 nm), and far-red photon flux densities (FRPFD; 700–780 nm) (μmol·m<sup>-2</sup>·s<sup>-1</sup>), and the ratio of red relative to far-red radiation (R:FR) provided by supplemental lighting fixtures (supplemental fixtures; Philips GreenPower LED Toplighting Linear 2.1; Signify, Eindhoven, The Netherlands), photoperiodic flowering lamps (flowering lamps; Philips GreenPower LED DR/W/FR; Signify), and tunable LED fixtures (tunable fixtures; Elixia; Heliospectra, Gothenburg, Sweden). Subscripts “a” and “b” represent spectral scans taken 1 m away from and directly under the tunable fixtures, respectively. Values are an average of at least nine spectral scans per replication.

Light source	TPFD	BPDF	GPFD	RPFD	FRPFD	R:FR
Supplemental fixtures	73.5 ± 3.1	7.2 ± 0.6	3.9 ± 0.3	61.5 ± 2.6	–	69 ± 4.6
Flowering lamps	21.6 ± 2.1	1.3 ± 0.1	2.8 ± 0.3	7.7 ± 0.8	9.7 ± 0.9	0.79 ± 0.03
Tunable fixtures <sub>a</sub>	11.3 ± 0.2	–	–	1.6 ± 0.2	9.7 ± 1.2	0.16 ± 0.02
Tunable fixtures <sub>b</sub>	23.5 ± 0.6	–	–	3.1 ± 0.1	20.4 ± 0.5	0.15 ± 0.00

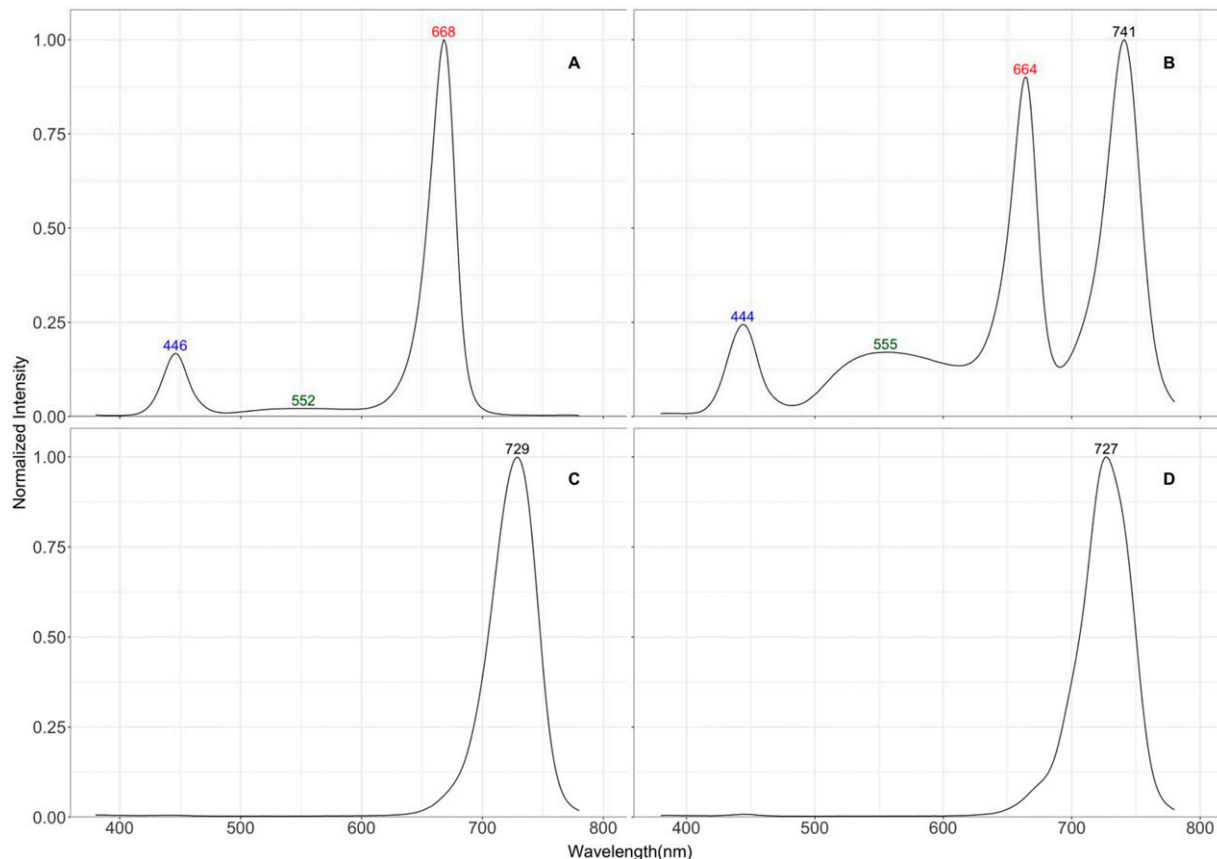


Fig. 1. Normalized spectral distribution from 400 to 800 nm measured at canopy height for supplemental lighting fixtures (Philips GreenPower LED Top-lighting Linear 2.1; Signify, Eindhoven, The Netherlands) (A), photoperiodic flowering lamps (Philips GreenPower LED DR/W/FR; Signify) (B), and programmable LED fixtures (Elixia; Heliospectra, Gothenburg, Sweden) providing a far-red (700–780 nm) photon flux density of 10 (C) or 20  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (D). Data were averaged across four experimental replications with peak wavelengths in the blue (400–500 nm), green (500–600 nm), red (600–700 nm), and far-red regions shown above their respective peaks.

duration of the EOD radiation treatment. Thus, EOD treatments included EOD<sub>FL</sub> (30 min of EOD-FR under FL), EOD<sub>10:30</sub> (30 min of EOD-FR with far-red PFD 10  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), EOD<sub>20:30</sub> (30 min of EOD-FR with far-red PFD of 20  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), and EOD<sub>20:240</sub> (240 min of EOD-FR with far-red PFD of 20  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). All EOD treatments began on cotyledon emergence.

At 1800 HR every evening, all EOD-FR treatments were removed from the WTC and placed under their respective radiation sources. Trays were positioned randomly every evening to minimize any effect of uneven radiation distribution. At the end of the EOD period, treatments were placed under blackout cloth until 0800 HR the following day at which time they were returned to the WTC. EOD-FR treatments ceased after 21 d due to no observable effect on leaf area compared with CN seedlings.

A dynamic lighting treatment was also initiated to examine if early leaf expansion promoted by EOD-FR treatments during the first 14 d could benefit from supplemental lighting due to a potential increased radiation capture capacity. Specifically, after 14 d, one tray from EOD<sub>20:240</sub> was moved to the WSL structure and received no further EOD-FR for the duration of the experiment (EOD<sub>2</sub>SR<sub>1</sub>;

subscripts describe the number of weeks under EOD-FR and supplemental lighting conditions).

Air temperature and PPFD were measured every 15 s using precision thermistors [fan-aspirated solar radiation shields (ST-110; Apogee Instruments, Inc., Logan, UT, USA)] and quantum sensors (LI-190R; LI-COR Biosciences), respectively, and the average was logged every 15 min by a data logger (CR1000X; Campbell Scientific, Inc., Logan, UT, USA). The mean  $\pm$  SD canopy air temperature (D/N), WTC DLI, and WSL DLI averaged across four replications was  $21.2 \pm 0.9^\circ\text{C}$ / $18.9 \pm 0.4^\circ\text{C}$ ,  $5.3 \pm 2.3 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , and  $9.0 \pm 1.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , respectively.

**Seedling data collection.** Seedling data were collected 14 and 21 d after cotyledon emergence, and five seedlings from each treatment per cultivar were randomly selected for measurement and analysis. Roots of selected seedlings were thoroughly washed and measurements were taken including stem length (centimeters; measured from the base of the hypocotyl to the shoot apical meristem), stem diameter [millimeters; measured directly under and perpendicular to cotyledons using a digital caliper (Fisherbrand™ Traceable™; Thermo Fisher Scientific, Waltham, WA, USA)], and relative chlorophyll

content [RCC; measured on the youngest fully expanded leaf using a SPAD chlorophyll meter (Chlorophyll Meter SPAD-502Plus; Konica Minolta, Inc., Chiyoda City, Tokyo, Japan)]. Leaves were removed from seedlings at the node to be counted, and leaf area (square centimeters) was determined using a leaf area meter (LI-3100; LI-COR Biosciences). Leaves and roots of each measured seedling were separated and dried at  $70^\circ\text{C}$  to determine the dry mass of each using an analytical microbalance (Analytical Balance ME54E; Mettler-Toledo, LLC, Columbus, OH, USA). Leaf area index was calculated by dividing individual seedling leaf area by the area of a tray cell (9 cm<sup>2</sup>), and leaf mass per unit area (LMA; grams per square meter) was calculated by dividing individual seedling leaf area by leaf dry mass (LDM).

**Statistical analysis.** This experiment was a randomized complete block design with EOD-FR, CN, and SR (seven levels) as treatment factors and replication (four levels) as a blocking variable; the blocking variable was included in the analysis and cultivars were evaluated separately. Four experimental replications were conducted from early Sep to late Nov 2020 with replications one/two and three/four occurring over the same period in separate locations in the greenhouse bay with

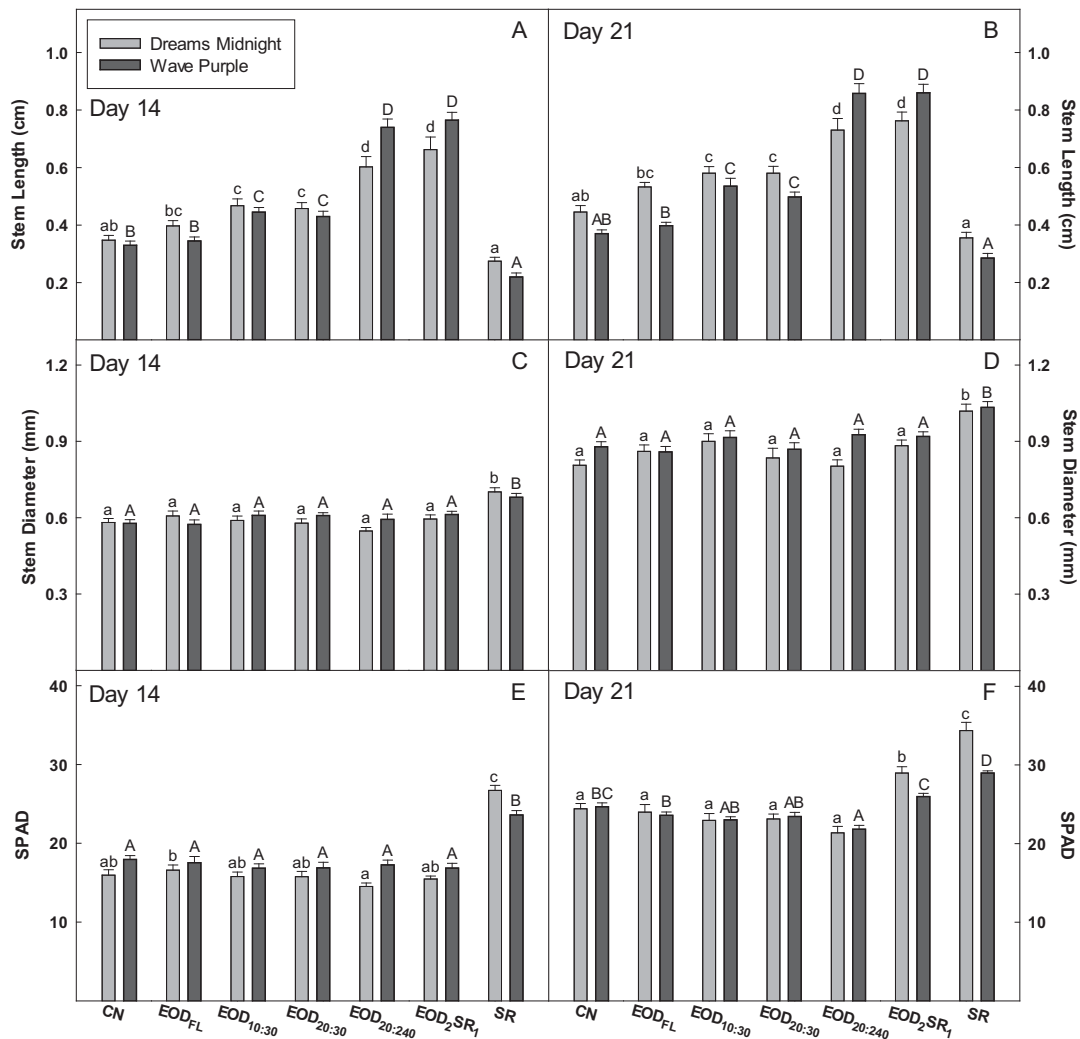


Fig. 2. Stem length, stem diameter, and relative chlorophyll content (SPAD) of *Petunia ×hybrida* ‘Wave Purple’ and ‘Dreams Midnight’ seedlings 14 (A, C, and E) and 21 d (B, D, and F) after cotyledon emergence under end-of-day far-red (EOD-FR) treatments including control (CN; no EOD-FR), EOD<sub>FL</sub> [30 min of EOD-FR under flowering lamps (FL) with a far-red PFD of 10  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.8$ ], EOD<sub>10:30</sub> (30 min of EOD-FR under a far-red PFD of 10  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.15$ ), EOD<sub>20:30</sub> (30 min of EOD-FR under a far-red PFD of 20  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.15$ ), and EOD<sub>20:240</sub> (240 min of EOD-FR under a far-red PFD of 20  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.15$ ). Lighting treatments also included seedlings under supplemental lighting with no EOD-FR (SR) and seedlings subjected to 2 weeks of EOD<sub>20:240</sub> and 1 week of supplemental lighting (EOD<sub>2</sub>SR<sub>1</sub>). Means within a cultivar sharing a letter are not statistically different by Tukey’s honestly significant difference test at  $P \leq 0.05$ . Error bars represent one standard error of the mean.

similar radiation and temperature conditions. For replication three at day 21, treatments EOD<sub>20:30</sub> and EOD<sub>20:240</sub> for ‘DM’ were found to have pest presence and were excluded from analysis. The effects of EOD-FR and dynamic lighting treatments on the parameters described previously were compared by two-way analysis of variance using R statistical software and pairwise comparison of estimated marginal means averaged over replication using Tukey’s honestly significant difference at  $P < 0.05$  (R Core Team 2022).

## Results

**Stem length and diameter.** Generally, EOD-FR radiation treatments promoted stem elongation in both cultivars (Fig. 2A and B). Specifically, at day 14 and 21, seedlings under EOD<sub>20:240</sub>, EOD<sub>20:30</sub>, and EOD<sub>10:30</sub> had longer stems compared with CN seedlings. In

addition, stem length in EOD<sub>20:240</sub> was longer than all other treatments sans EOD<sub>2</sub>SR<sub>1</sub>. For example, stem length of petunia ‘DM’ was 25%, 26%, 37%, 64%, and 105% longer under EOD<sub>20:240</sub> compared with EOD<sub>10:30</sub>, EOD<sub>20:30</sub>, EOD<sub>FL</sub>, CN, and SR, respectively, at day 21. Similarly, petunia ‘WP’ under EOD<sub>2</sub>SR<sub>1</sub> had stems that were 60%, 72%, 115%, 132%, and 201% longer than EOD<sub>10:30</sub>, EOD<sub>20:30</sub>, EOD<sub>FL</sub>, CN, and SR, respectively, at day 21. In contrast to the other EOD-FR treatments, seedlings of both cultivars grown under EOD<sub>FL</sub> did not display longer stems compared with CN for any harvest week. Stem diameter for both cultivars was not significantly impacted by the duration, far-red PFD, or R:FR of EOD-FR treatments compared with CN (Fig. 2C and D).

Supplemental lighting generally promoted increased stem diameter in both cultivars compared with all other treatments, with

larger values observed under SR at days 14 and 21 (Fig. 2C and D). For example, stem diameter for petunia ‘WP’ under SR at day 21 was 20%, 19%, 18%, 13%, 12%, and 12% greater compared with EOD<sub>FL</sub>, EOD<sub>20:30</sub>, CN, EOD<sub>10:30</sub>, EOD<sub>2</sub>SR<sub>1</sub>, and EOD<sub>10:30</sub>, respectively. Similarly, stem diameter for petunia ‘DM’ at day 21 was 27%, 26%, 22%, 18%, 15%, and 13% greater under SR than EOD<sub>20:240</sub>, CN, EOD<sub>20:30</sub>, EOD<sub>FL</sub>, EOD<sub>2</sub>SR<sub>1</sub>, and EOD<sub>10:30</sub>, respectively.

**Leaf area, leaf number, and RCC.** End-of-day far-red radiation did not significantly promote leaf area expansion for any treatment compared with CN in either cultivar (data not shown, see Fig. 3C and D for LAI). Seedlings that received supplemental lighting for the duration of the study had greater leaf area than all other treatments at each measurement day. Similarly, leaf number was generally not impacted by EOD-FR radiation compared

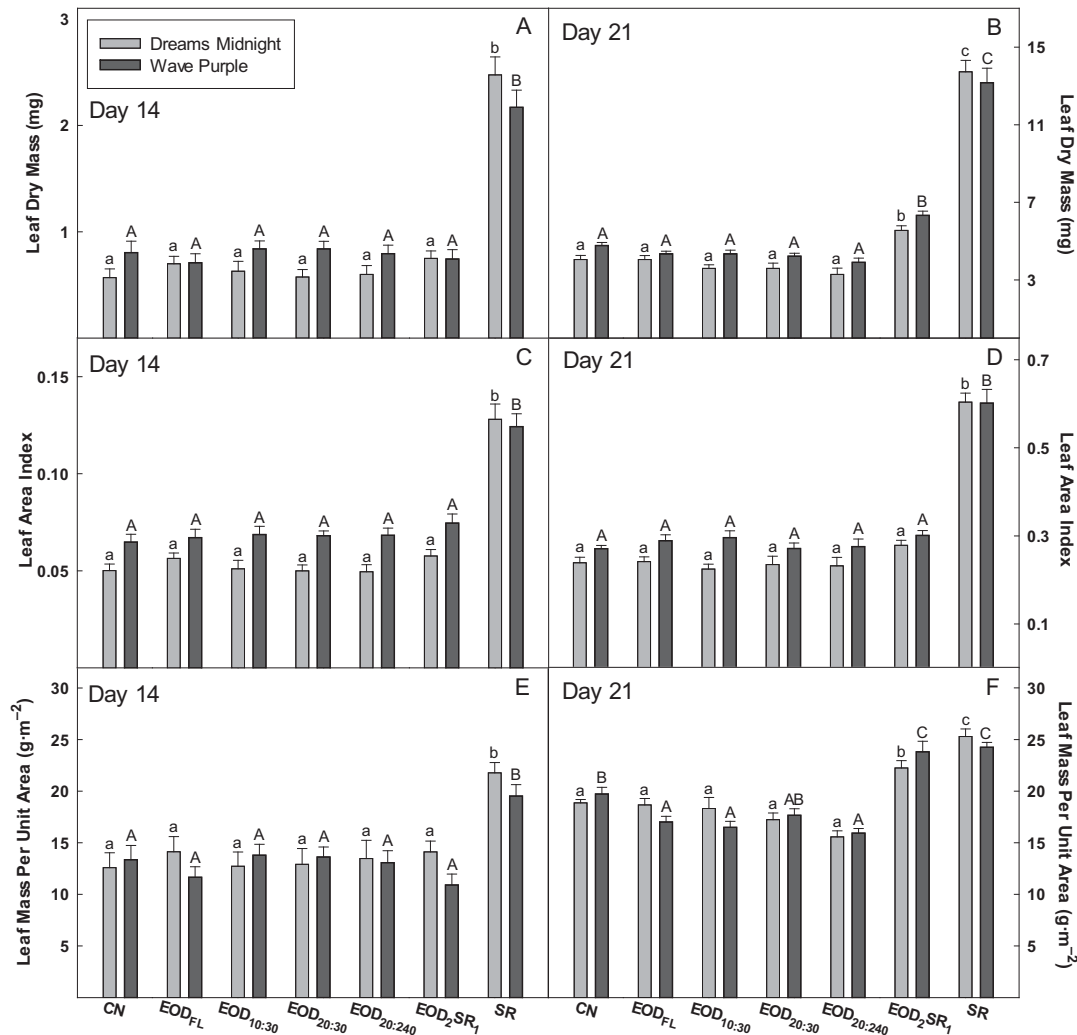


Fig. 3. Leaf dry mass, leaf mass per unit area, and leaf area index of *Petunia ×hybrida* ‘Wave Purple’ and ‘Dreams Midnight’ seedlings 14 (A, C, and E) and 21 d (B, D, and F) after cotyledon emergence under end-of-day far-red (EOD-FR) treatments including control (CN); no EOD-FR or supplemental lighting), EOD<sub>FL</sub> [30 min of EOD-FR under flowering lamps (FL) with a far-red PFD of 10  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.8$ ], EOD<sub>10:30</sub> (30 min of EOD-FR under a far-red PFD of 10  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.15$ ), EOD<sub>20:30</sub> (30 min of EOD-FR under a far-red PFD of 20  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.15$ ), and EOD<sub>20:240</sub> (240 min of EOD-FR under a far-red PFD of 20  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and R:FR of  $\sim 0.15$ ). Lighting treatments also included seedlings under supplemental lighting with no EOD-FR (SR) and seedlings subjected to 2 weeks of EOD<sub>20:240</sub> and 1 week of supplemental lighting (EOD<sub>2SR<sub>1</sub></sub>). Means within a cultivar sharing a letter are not statistically different by Tukey’s honestly significant difference test at  $P \leq 0.05$ . Error bars represent one standard error of the mean.

with CN, but supplemental lighting resulted in seedlings under SR having significantly more leaves than all other treatments at day 21 for both cultivars (data not shown).

No difference in RCC was observed between any EOD-FR treatment and CN at day 14 and 21 for petunia ‘DM’ (Fig. 2E and F). However, petunia ‘WP’ grown under CN was found to have 13% greater RCC than EOD<sub>20:240</sub> at day 21. In addition, RCC was greater under EOD<sub>FL</sub> compared with EOD<sub>20:240</sub> at day 14 for petunia ‘DM’ and at day 21 for petunia ‘WP’. RCC was promoted in seedlings that received supplemental lighting in both cultivars for all weeks, with the highest values observed under SR (Fig. 2E and F). At day 21, petunia ‘DM’ under EOD<sub>2SR<sub>1</sub></sub> had significantly greater RCC than all other treatments sans SR. Specifically, petunia ‘DM’ under EOD<sub>2SR<sub>1</sub></sub> had 19%, 20%, 21%, 26%, and 30% greater RCC than CN, EOD<sub>20:30</sub>, EOD<sub>FL</sub>, EOD<sub>10:30</sub>,

and EOD<sub>20:240</sub>, respectively. For petunia ‘WP’, no difference was observed for RCC between CN and EOD<sub>2SR<sub>1</sub></sub>, but seedlings under EOD<sub>2SR<sub>1</sub></sub> had greater RCC than all other EOD-FR treatments.

**Dry mass.** EOD-FR did not significantly impact RDM for either cultivar compared with CN (data not shown). However, supplemental lighting applied for the duration of the study promoted a significantly greater dry mass in seedlings compared with all other treatments at day 21 for both cultivars. EOD-FR treatments did not significantly affect LDM compared with CN for either cultivar, whereas supplemental lighting increased LDM for both cultivars (Fig. 3A and B). In both cultivars, seedlings under SR had significantly greater LDM compared with all other treatments at day 14 and 21, and EOD<sub>2SR<sub>1</sub></sub> had greater LDM compared with CN at day 21 (Fig. 3A and B).

**LAI and LMA.** No significant difference in LAI was found between any EOD-FR treatment and CN at day 14 and 21 in either cultivar. In contrast, SR seedlings of both cultivars had significantly greater LAI compared with all other treatments at day 14 and 21 (Fig. 3C and D). Specifically, LAI for petunia ‘DM’ under SR was 168%, 167%, 164%, 153%, and 150% greater than EOD<sub>10:30</sub>, EOD<sub>20:240</sub>, EOD<sub>20:30</sub>, CN, and EOD<sub>2SR<sub>1</sub></sub>, respectively, on day 21. Similarly, LAI for petunia ‘WP’ under SR on day 21 was 122%, 122%, 118%, 108%, 103%, and 100% greater than CN, EOD<sub>20:30</sub>, EOD<sub>20:240</sub>, EOD<sub>FL</sub>, EOD<sub>10:30</sub>, and EOD<sub>2SR<sub>1</sub></sub>, respectively. LMA was only reduced under EOD-FR compared with CN at day 21 for petunia ‘WP’ (Fig. 3E and F). Specifically, petunia ‘WP’ under CN had 16%, 19%, and 24% greater LMA than EOD<sub>20:240</sub>, EOD<sub>10:30</sub>, and EOD<sub>FL</sub>, respectively, at

day 21. Supplemental lighting generally promoted an increase in LMA.

## Discussion

For annual bedding plants, low ambient DLI at northern latitudes necessitates supplemental lighting use in the production of high-quality compact plugs for transplant and shipping, but the low LAI early in production reduces radiation interception and thus the efficacy of supplemental radiation. In this study, no EOD-FR treatment resulted in an increase in LAI for petunia 'WP' and 'DM' (Fig. 3C and D). Leaf dry mass of seedlings of both cultivars was similar under EOD-FR compared with CN plants, and stem elongation was generally promoted by EOD-FR resulting in stretched and fragile seedlings (Fig. 2A and B). Shade avoidance responses to a low R:FR are primarily regulated by the phytochrome family of photoreceptors with phytochrome B (phyB) shown to generally be the most important (Casal 2013; Franklin 2008). When phyB is inactivated by low R:FR due to direct shading or by an increased reflectance of far-red radiation by nearby neighbors, increased auxin synthesis and subsequently enhanced elongation responses occur (Casal 2013; Fernández-Milmanda and Ballaré 2021; Küpers et al. 2020).

Previous studies indicate that petunia has elongation responses to far-red radiation (Illias and Rajapakse 2005; Park and Runkle 2017). All EOD-FR treatments showed increased stem length compared with SR seedlings for both cultivars, but cultivar-specific responses were apparent between EOD-FR treatments (Fig. 2A and B). For example, seedlings of both cultivars under EOD<sub>10:30</sub> were found to have greater stem length than CN; but compared with EOD<sub>FL</sub> (R:FR of ~0.8), only 'WP' EOD<sub>10:30</sub> resulted in seedlings with longer stems.

Neither petunia cultivar showed differential stem elongation responses to increased intensity of far-red radiation when the R:FR and duration of treatment were ~0.15 and 30 min, respectively; this lack of further elongation under higher intensities may have been the result of a saturated EOD-FR dose response that has been examined in species such as tomato and the squash hybrid, *Cucurbita maxima* × *Cucurbita moschata* 'Tetsukabuto' (Chia and Kubota 2010; Yang et al. 2012). Chia and Kubota (2010) used a Michaelis-Menten-type model to estimate the far-red radiation dose required to achieve 90% maximum hypocotyl elongation for tomato rootstock cultivars 'Aloha' and 'Maxifort' to be 5 to 14 mmol·m<sup>-2</sup>·d<sup>-1</sup> and 8 to 15 mmol·m<sup>-2</sup>·d<sup>-1</sup>, respectively, and the "practical near saturation dose" resulting in similar hypocotyl elongation for both cultivars was only 2 to 4 mmol·m<sup>-2</sup>·d<sup>-1</sup>; the near saturating dose of squash 'Tetsukabuto' was found to be 4 mmol·m<sup>-2</sup>·d<sup>-1</sup> (Chia and Kubota 2010; Yang et al. 2012).

The approximate far-red dose received by 'DM' and 'WP' under EOD<sub>10:30</sub> and EOD<sub>20:30</sub> was 20 and 40 mmol·m<sup>-2</sup>·d<sup>-1</sup>,

respectively. Based on these results from EOD treatments lasting 30 min before the dark period, the saturating far-red dose for petunia stem elongation was likely achieved at or below 20 mmol·m<sup>-2</sup>·d<sup>-1</sup>, resulting in no further significant increase at 40 mmol·m<sup>-2</sup>·d<sup>-1</sup>. The further increase in stem elongation under EOD<sub>20:240</sub> compared with EOD<sub>10:30</sub> and EOD<sub>20:30</sub> may indicate that there is an overall higher far-red dose ceiling for petunia stem elongation at or below the 290 mmol·m<sup>-2</sup>·d<sup>-1</sup> of far-red radiation received by EOD<sub>20:240</sub>, but the timing and the duration of the EOD treatment may also be important to explain this finding. An EOD-FR pulse can promote shade avoidance responses because the pulse reduces the proportion of active phyB before night (Franklin 2008), but there is also known to be a reduced sensitivity to far-red radiation at the beginning of the night caused by the evening complex that reduces the expression of PIF4 and PIF5; this is thought to prevent confusion between shade and night (Casal 2013). This aligns with findings by Sellaro et al. (2012) who showed that for wild-type *Arabidopsis* seedlings grown under sunlight for an 8-h photoperiod, a 2-h "afternoon shade event" at the end of the photoperiod at a R:FR of 0.1 more effectively promoted hypocotyl elongation compared with a 10-min pulse of red and far-red radiation with the same R:FR. The 4-h duration of EOD<sub>20:240</sub> makes this treatment more akin to an "afternoon shade event" than a far-red pulse at EOD while also increasing the far-red dose. Thus, both the higher far-red dose as well as the increased duration of EOD<sub>20:240</sub> may have played a role in the increased stem elongation under EOD<sub>20:240</sub> compared with EOD<sub>10:30</sub> and EOD<sub>20:30</sub>. However, because we did not design treatments with additional far-red doses at this longer treatment duration, this hypothesis was not explicitly tested.

Last, similarity in stem length between EOD<sub>FL</sub> and CN seedlings for both cultivars after 2 and 3 weeks of EOD-FR treatments may be due to the lower R:FR that naturally occurs at dusk (Franklin 2008). Although dusk radiation quality for CN seedlings was not measured in this study, Lund et al. (2007) showed that chrysanthemum (*Chrysanthemum morifolium*) internode length under a simulated twilight (R:FR of ~0.7, 30-min duration) was increased compared with a treatment with an R:FR of ~2.4. In our study, the EOD<sub>FL</sub> treatment had an R:FR of ~0.8, perhaps explaining the similar stem length between the two treatments.

In this study, leaf number between EOD-FR and CN seedlings did not significantly differ after 2 and 3 weeks (data not shown), thus individual leaf expansion determined total leaf area. The LAI did not differ between CN and any EOD-FR treatment at day 14 and 21 (Fig. 3C and D), and this may have been due to multiple factors. In shade-avoiding plants, leaf area responses to lower R:FR vary by species, but in many cases a reduction in leaf development occurs in tandem with elongation growth (Franklin

2008; Smith and Whitelam 1997). Two cellular processes that control leaf size are cell division and cell expansion that primarily occur earlier and later in development, respectively, and both processes have extensive regulatory mechanisms (Gonzales et al. 2012). Carabelli et al. (2007) found that under a low R:FR, new leaf primordia in young *Arabidopsis* plants showed inhibited cell proliferation and that the resulting smaller leaves were due to decreased cell number rather than smaller cells. Similarly, for *Petunia axillaris* EOD-FR had a promotive effect on leaf area of individual leaves at the late development stage, whereas younger leaves were less affected by treatments (Casal et al. 1987).

It has also been suggested that expansion of leaves under lower R:FR may be related to radiation availability or competition with the plant stem; leaf development may be inhibited in tandem with promoted stem elongation when PPFD is low, and added far-red radiation under a sufficient PPFD for normal growth may promote leaf expansion (Casal et al. 1987; Demotes-Mainard et al. 2016; Park and Runkle 2017). The low DLI experienced by CN and EOD-FR seedlings in our study may have influenced resource investment in the elongation of stems, further limiting leaf area expansion. However, the lack of an increase in leaf area for tomato (Kalaitzoglou et al. 2019) in EOD-FR-treated plants compared with plants with far-red included in the normal spectrum may indicate a lack of a leaf area expansion response under EOD-FR even when PPFD or DLI is not limiting for some species. The promotion of leaf area expansion under both EOD-FR and far-red included in the spectrum in lettuce (Zou et al. 2019) supports interspecific responses to low R:FR radiation quality applied differentially during production.

Compared with CN seedlings, EOD-FR treatments did not significantly increase or decrease stem diameter (Fig. 2C and D), LDM (Fig. 3A and B), or RDM (data not shown); all three parameters increased under higher relative to lower DLI. The lack of a differential stem diameter response in either cultivar to EOD-FR treatments compared with CN is similar to the aforementioned far-red dose response experiments for tomato and squash as well as the EOD-FR response of chrysanthemum (Chia and Kubota 2010; Lund et al. 2007; Yang et al. 2012). For example, no significant difference in stem diameter was reported in tomato 'Aloha' seedlings under EOD-FR treatments with an R:FR of 0.47 compared with 0.05 (Chia and Kubota 2010). The lower DLI experienced by CN and EOD-FR seedlings is the likely cause for the reduced stem diameter in all treatments compared with SR, as studies have demonstrated that stem diameter and average stem dry weight per internode of annual bedding seedlings increases under higher DLIs, contributing to higher seedling quality (Craver et al. 2018, 2019; Pramuk and Runkle 2005).

A decrease in leaf chlorophyll content is a common response in shade-avoiding species



grown under a low R:FR (Franklin 2008; Smith and Whitelam 1997); this decrease in chlorophyll content is very apparent in SSL environments, especially when compared with plants receiving no far-red radiation (Kalaitzoglou et al. 2019; Park and Runkle 2017, 2018; Patel et al. 2013). EOD-FR has also notably been found to reduce leaf chlorophyll content in plants such as *Petunia axillaris* and tomato (Casal et al. 1987; Kalaitzoglou et al. 2019). However, Kalaitzoglou et al. (2019) observed a clear reduction in chlorophyll content from EOD-FR treatment (15 min) compared with a control (90:10 red:blue LEDs) in an SSL experiment that was not apparent in a second experiment where ~25% of total radiation received by plants was solar in origin (including  $\sim 11 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  of far-red); this may indicate that short EOD-FR periods may not severely reduce total leaf chlorophyll content in some shade-avoiding plants when grown with small amounts of far-red radiation. Alternatively, a high R:FR applied at EOD may reduce chlorophyll biosynthesis inhibition by increasing active phyB levels before night; this may partly explain the consistent high RCC seen in SR plants, as SR used in this study extended the natural photoperiod and created a light environment with a R:FR of ~69 (Table 1). The blue radiation included in the SR spectrum (~10% of total PPFD) may also have led to increased leaf chlorophyll content (Bantis et al. 2018).

Both shade-avoiding and shade-tolerant species have been found to exhibit an increase in specific leaf area (SLA; the inverse of LMA) in response to shade as a strategy of maximizing radiation interception; in nature this response may be advantageous in regard to radiation capture in shaded environments but decreased biomass per unit leaf area can also make leaves more vulnerable to mechanical stressors (Gommers et al. 2013). In a horticultural context, a reduced LMA is a negative attribute for young plants, as they may be more easily damaged during shipping and transplant. Regarding radiation, LMA seems to be positively related to the daily photon irradiance (DPI; analogous to DLI) (Poorter et al. 2009), and a decrease in LMA due to decreased PPFD has been shown in petunia (Park and Runkle 2018). In SSL experiments, a reduction in LMA is also observed when far-red radiation is added to the spectrum without a reduction in PPFD (Kalaitzoglou et al. 2019; Zou et al. 2019); Kalaitzoglou et al. (2019) showed that although total leaf dry weight was generally similar in tomato leaves between SSL treatments with and without included far-red, LMA was reduced under treatments including far-red. In our study, the lower DLI in CN and EOD-FR-treated seedlings compared with SR plants was likely the cause of the reduced LMA.

Dynamic lighting strategies for plant production include those in which radiation intensity, quality, and the timing of both may be altered throughout the production process; some examples include Oh et al. (2010) restricting supplemental lighting use to different

periods during seedling development, Hurt et al. (2019) using instantaneous threshold lighting to only use supplemental lighting when natural light drops below a certain level, or the use of EOD-FR or night interruption lighting with a low R:FR to promote flowering in long-day plants (Craig and Runkle 2012; Demotes-Mainard et al. 2016). The dynamic lighting treatment in this study was designed to test if or when in young petunia seedling development EOD-FR might promote early leaf expansion under a low DLI, and whether supplemental lighting provided post cessation of EOD-FR treatments would enhance plug quality if EOD-FR treatments increased LAI. However, no EOD-FR treatment promoted leaf area expansion and thus the effects on measured parameters post cessation of EOD-FR treatments are likely the result of a shift from lower to higher DLI after 2 weeks (EOD<sub>2</sub>SR<sub>1</sub>) in tandem with any residual effects on seedlings from EOD-FR treatments. Similar to the findings of Oh et al. (2010), seedlings that received 1 week of supplemental lighting after periods of overall low DLI showed a significant increase in overall quality, such as increased dry mass and stem diameter, compared with CN plants. However, detrimental aspects of shade avoidance, such as elongated stems, still reduced overall seedling quality, which was evident under EOD<sub>2</sub>SR<sub>1</sub> (Fig. 2A and B)

## Conclusion

Under greenhouse conditions, lighting at the end of the natural photoperiod is one way that radiation quality can be manipulated to elicit desired plant responses. Although the addition of far-red radiation in SSL environments and the use of EOD-FR has been shown to induce leaf expansion in some species, including *Petunia* spp., the EOD-FR treatments in the present study were ineffective in promoting early leaf area expansion under a low DLI. In addition, characteristics deemed negative with regard to seedling quality were common across EOD-FR treatments compared with plants receiving supplemental lighting. However, the effect of the “afternoon shade event” seen here on stem elongation compared with shorter EOD-FR periods may be of use in rootstock production for crops such as tomato and squash (Chia and Kubota 2010; Yang et al. 2012); if this response can be promoted with commercially available lamps with relatively low R:FR output, then this strategy may be more easily implemented. Further research into responses of seedlings to different EOD radiation quality treatments at different seedling development stages may yet yield beneficial applications in the production of annual bedding plants under greenhouse conditions. In addition, examination of the effects of EOD lighting applications under varying DLI may further elucidate how resource availability interacts with photomorphological responses for seedling production.

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