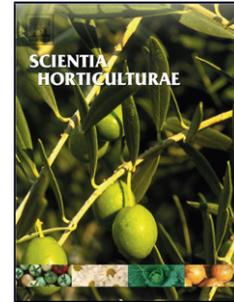


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Tomato seedling physiological responses under different percentages of blue and red photon flux ratios using LEDs and cool white fluorescent lamps

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Highlights

- Tomato seedling responses to blue and red photon flux (PF) are presented
- Tomato responses are comparable under treatments containing both blue and red photons
- LED light containing 30B:70R and 50B:50R photon flux have greater dry mass and growing efficacy than fluorescent lamps
- For the production of tomato seedlings in vertical farms 30B:70R and 50B:50R photon flux light qualities are recommended.

Abstract

Lamp spectral customization can be a strategy to achieve desirable plant characteristics when plants are grown under sole-source electric lighting. Vegetable transplants can be efficiently and economically grown under indoor-production systems with electrical lighting; however, species-specific light recipes have to be developed to improve plant growth, development and morphology, as well as to reduce electrical consumption. The objective of this study was to

evaluate the growth and morphology of tomato transplants to a broad range of blue to red (B:R) photon flux (PF) ratios under LEDs and cool white fluorescent lamps (CWF). Tomato ‘Komeett’ and ‘Beaufort’ seedlings were grown in a climate control growth chamber. Using LEDs, seven light treatments with different blue (B), green (G) and red (R) PF ratios were used: 100R, 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R, 75B:25R and 100B. In addition, a CWF treatment served as the control. Hypocotyl length of ‘Komeett’ decreased with the increase of percent B PF up to 75% B. Plant leaf area was 64-72% greater under treatments emitting both B and R PF than in the 100 B and 100 R treatments. Similarly, tomato ‘Komeett’ fresh mass, dry mass, leaf number and chlorophyll concentration was comparable among the treatments containing B and R PF and greater than in 100 B and 100 R treatments. However, plant compactness in the 30B:70R treatment was 42% greater than in the 10B:90R treatment. Anthocyanin concentration increased with the increase of percent B PF up to 75% B. Also, plants in 30B:70R and 50B:50R had 39% and 36% greater dry mass than in CWF, respectively. In addition, 30B:70R and 50B:50R LEDs had 172 % greater growing efficacy (g kWh^{-1}) than high output fluorescent lamps. The addition of G light did not have any effects on tomato physiological responses. ‘Beaufort’ plant morphology and growth were severely affected by intumescences development and intumescence severity decreased under higher percentages of B PF. In summary, 30B:70R, 50B:50R were the best spectrums to produce tomato seedlings under LEDs tested here; however, plant quality under CWF, 10B:90R, 20B:28G:52R, and 75B:25R was also acceptable.

Keywords: blue light; intumescences; *lycopersicum*; growing efficacy, light emitting diodes,

1. Introduction

With the continuing development of LEDs, the commercial horticulture sector has placed more emphasis on the production of plants under closed-type systems using sole-source electrical lighting commonly known as vertical farming (VF). One disadvantage of VF is the high electrical consumption. It is estimated that electrical lighting contributes with 25% of total production cost and 80% of total electricity consumption (Kozai, 2013). In addition, the high consumption of electricity also yields a high environmental impact in terms of carbon foot-print compared to greenhouse production (Harbick and Albright, 2016). For these reasons, it is imperative that lighting is used as efficiently as possible. With the rapid improvement of light emitting diodes, in terms of light efficiency, output, and fixture cost reduction (Haitz and Tsao, 2011), the application of the results of light quality research to the commercial sector of VF is more tangible than before. Currently, only high value, high density and compact crops are economically suitable for the production under VF conditions (Kozai, 2013). Among these crops is the production of horticultural transplants, which are grown under high density and the fine control of environmental conditions can increase transplant quality compared to traditional greenhouse production. However, plant light recipes have to be developed to improve plant growth, development, morphology and reduce electricity cost. Spectral recipes have to be independently developed for the different horticultural transplants since light quality requirements are known to be species specific.

Spectral customization can be used to increase desirable plant characteristics. For example, special light formulations can increase plant growth rate and production (Eguchi et al., 2016a; Hernández et al., 2016; Hernández and Kubota, 2016; Ouzounis et al., 2016; Runkle and Park,

2016), increase the concentration of secondary metabolites in plant tissue (Goto et al., 2016; Li and Kubota, 2009; Nicole et al., 2016; Noguchi and Amaki, 2016; Samuoliene et al., 2012), promote plant development (Gilberto et al., 2005), and generate desirable plant morphology (Chia and Kubota, 2010; Hernández and Kubota, 2015; Jeong et al., 2014; Yang et al., 2012).

In lettuce, Yorio et al. (1998) concluded that a minimum of $35 \mu\text{mol m}^{-2} \text{s}^{-1}$ of B light on a otherwise R spectrum was needed for normal plant development. Li and Kubota (2009) grew lettuce under fluorescent lamps and supplemented with UV-A, B, G, R, or Far-red LEDs and found an increase in phytochemical concentration with supplemental UV-A and B LED and decreased when supplemented with Far-red light; however, Far-red light increased lettuce fresh and dry mass. Son and Oh (2013) grew lettuce under increasing percent B PF from 0B to 59B and found that growth rate decreased with the increase of B PF. More recently, Jishi et al. (2016) grew lettuce under 50B:50R treatment and under a treatment with 100B for the first 4 to 7 hours followed by a 50B:50R spectrum and demonstrated that shifting the irradiation hours of B and R increase lettuce growth. Additional lettuce studies are needed specific for the production of lettuce transplants that will eventually be transferred to the greenhouse or field production.

For cucumber seedlings (*Cucumis sativus*), several studies have examined the physiological and morphological responses under different B and R PF ratios. Hogewoning et al. (2010) found greater leaf photosynthetic capacity (A_{max}), net photosynthetic rate (Pn), stomatal conductance (g_s), and chlorophyll concentration with the increase of percent B PF in cucumber seedlings (excluding 100% B PF). Savvides et al. (2012) showed higher hydraulic conductance, net photosynthetic rate (Pn), and stomata conductance (g_s) in cucumbers grown under a spectrum containing 30B:70R and 100B compared to those under 100R ($100 \mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod: 16 h). More recently, Hernández and Kubota (2016) showed that cucumber Pn increased as the

percent B PF increased in a study testing a broad range of percent B PF (0B, 10B, 30B, 50B, 75B, 100B) on an otherwise R light regime. They found that the plant dry mass decreased with the increase of B PF up to the 75% B. However, plant dry mass in the 100B treatment was not different from that in the 10B:90R treatment but both were greater than other treatments. All the aforementioned cucumber studies agreed that monochromatic blue (100B) or monochromatic red (100R) caused undesirable cucumber morphological and physiological responses. With the combined findings of these cucumber studies it is safe to conclude that the optimal growing spectrum for cucumber seedlings under sole-source lighting with blue and red LEDs is low B PF and high R PF (i.e.10B:90R).

Tomato (*Solanum lycopersicum*) is the most economically important plant species suitable for indoor transplant-production (Nanfelt, 2016). Several research groups reported tomato seedling growth and morphology under different ratios of B, green (G), and R PF, but inconsistent results are reported on growth rates. Liu et al. (2011) grew cherry tomato under B, yellow (Y), R, 1B:1R, and 3B:1G:3R (ratios calculated on energy basis) (PPF: $320 \mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod: 12 h) and found that tomato seedling dry mass was greater in the monochromatic B treatment than other treatments. Nanya et al. (2012) showed greater tomato shoot dry mass in seedlings grown by lowering percent B PF against R PF (in the range of 10-50%) (PPF: $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod: 16 h). Wollaeger and Runkle (2014) showed greater shoot dry mass in tomato seedlings grown under 100R than those grown under 50G:50R, 25B:25G:50R, 50B:50G, 50B:50R and 100B treatments (PPF: $160 \mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod: 18 h). In summary, Liu et al. (2011), Nanya et al. (2012), and Wollaeger and Runkle (2014) reported that 100B, 10B and 100R, respectively produced the greater dry mass in tomato seedlings. However, a limited range of B:R PF was used in the aforementioned studies.

The specific objective of this study is to evaluate plant responses of tomato transplants to the whole range of B:R PF ratios (from 0% to 100% B PF) under sole-source electrical LED lighting in order to optimize the spectrum of indoor tomato seedling production systems.

2 Materials and methods

2.1 Plant material and growing conditions

Tomato scion ‘Komeett’ (*Solanum lycopersicum*) and tomato rootstock ‘Beaufort’ (*Solanum lycopersicum* × *S. habrochaites* seeds) (DeRuiter, St. Louis, MO, USA) were sown in plastic trays (26.82 x 53.49 cm) with 98 cells (cell depth: 3.8 cm, cell top: 3.4 cm) (T.O. plastics, Clearwater, MN, USA) filled with peat moss plug substrate (sunshine mix #3) (Sun Gro Horticulture Agawam, MA, USA) and covered with vermiculite. Trays were kept at 28 °C in darkness for 48 hours for radicle emergence. Plants were manually irrigated using hydroponic solution with (mg L⁻¹) 90 N, 47 P, 144 K, 160 Ca, 60 Mg, 113 S, 105 Cl, as well as micro-nutrients. The canopy air temperature was measured in close proximity to the underside of the leaf (inside leaf boundary layer) with fine-wire thermocouples (type T, gauge 24, Omega Inc., Stamford, CT, USA). The room air temperature and relative humidity were measured in the chamber using a temperature/humidity probe (HMP110, Vaisala Inc., Helsinki, Finland) and CO₂ concentration was measured with a CO₂ analyzer (LI-800, LI-COR Biosciences, Lincoln, NE, USA). Environmental sensors were connected to a data-acquisition system (CR-23X, Campbell Scientific, Logan, UT, USA). Details of environmental conditions are described in Table 1.

2.2 Light treatments

The six fixtures used for the B:R LED treatments had 455 nm peak wavelength (full width at half maximum FWHM: 15 nm) for the B diodes and 661 nm peak wavelength (FWHM: 20 nm) for

the R diodes. The fixture used for the B:G:R treatment had 473 nm peak wavelength (FWHM: 25 nm) for the B diodes, 532 nm peak wavelength (FWHM: 37 nm) for the G diodes, and 660 nm peak wavelength (FWHM: 22 nm) for the R diodes (ISC-101-4, CCS Inc., Kyoto, Japan). Another treatment consisted of six cool-white-fluorescent (CWF) T12 tubes (F40T12 CW Supreme ALTO Plus, Philips Lighting, Somerset, NJ) (Fig. 1).

The eight light treatments were created inside a walk-in growth chamber using standard shelving units positioned and outfitted to prevent any light contamination. The LED fixtures (35 L x 34 W cm) were installed 19 cm from the top of the plant canopy and the distance was maintained by adjusting the height of the lamp throughout the experiment. Photon fluxes were measured in five locations of the growing area to achieve an average PF of $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (spectroradiometer, PAR-NIR, Apogee Instruments Inc., Logan, UT, USA) (Table 1). Plants were rotated daily in the growing area to ensure even light exposure to all plants. The measured percent photon flux and light spectrum of the six B:R LED treatments, one B:G:R LED treatment, and one CWF treatment are detailed in Table 1 and Fig 1. The Phytochrome photostationary state (P_{fr}/P_{total}) was calculated following the specifications described in (Sager et al., 1988).

2.3 Measurements and experimental design

The experiment was conducted for 21 days starting on 21 May 2014 and repeated on 11 September 2014 (two repetitions). Each repetition had a total of 144 plants with 18 tomato plants per cultivar per treatment as experimental units. Plant height, and hypocotyl length were measured using a rule. Stem diameter was measured below the cotyledons using a digital caliper. Shoot fresh mass was measured with an electronic balance and plant material was transferred to an oven (80 °C). After 48 hours shoot dry mass was quantified using an electronic balance. Chlorophyll concentration was quantified based on Moran and Porath (1980). Leaves greater

than one centimeter were recorded (number of leaves). Individual leaves were scanned and leaf area was estimated using LIA 32 software (Nagoya University, Japan). An index for plant compactness was calculated by dividing the total shoot dry mass by the total plant height. Anthocyanin concentration was quantified following the method described in Li and Kubota (2009). Leaf Pn, and g_s , were measured with a gas exchange system (CIRAS-2, PP System, MA, USA) at 25.0 ± 0.4 °C leaf temperature, ambient CO₂ concentration, and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PF provided by the treatment fixture. Due to equipment issues during repetition one, only Pn and g_s data for the second repetition is presented.

Analysis of variance ($P = 0.05$) and mean separations (Tukey-Kramer HSD $P = 0.05$) were implemented to identify any difference among treatments ($n=36$). No interactions between the treatments and the repetitions were detected. Regression was also applied to the quantitative response to increasing blue percent photon flux. Dunnett's test was used to compare LED treatments to the CWF control treatment ($P=0.05$). "How many percent the respective LED is statistically lower than the CWF treatment" was calculated by $(\text{CWF-LED})/\text{CWF}$ and "how many percent the respective LED is statistically greater than CWF" was calculated by $(\text{LED-CWF})/\text{LED}$ on Table 5. JMP software was used for all the statistical analysis (SAS Institute, Cary, NC, USA)

2.4 Intumescence injury assessment in 'Beaufort'

Some plants exhibited intumescence injury in leaves and/or stems under specific light qualities. Intumescence severity was assessed with three parameters. 1) *ratio of plants with intumescence* (number of plants with intumesce(s) over total number of plants). 2) *ratio of leaves with intumescences* (number of leaves with intumescences over total number of leaves). 3) *ratio of*

plants with intumescences in stem (number of plants with intumescences in stem over total number of plants).

2.5 Evaluation of electrical power consumption and growing efficacy

The electrical power consumption of the CWF and the LEDs were compared following the method and calculations described in detail by Hernández and Kubota (2015). Specifically, we computed areal electric power consumption (APC, kWh m⁻²) based on the fixture photon efficiency (μmol J⁻¹), and fixture-specific effective photon emission (EP, μmol s⁻¹). APC was then used to compute ‘fixture growing efficacy’ (FGE, g kWh⁻¹) to express the efficacy of the specific lamp fixture to convert electric energy to plant dry mass.

3 Results and discussion

3.1 Effects of B:R PF ratios on ‘Komeett’ tomato hypocotyl length.

In the present study, hypocotyl length of ‘Komeett’ decreased with the increase of percent B PF ($P < 0.0001$) up to 75% B (Fig. 2). Phytochrome photoreceptors are known to regulate hypocotyl extension. The phytochrome photostationary state (Pfr/Ptotal) is used to quantify the ratio of R and Far-Red light in the growing environment (R:FR ratio). Hypocotyl length linearly decreases with the increase of the Pfr/Ptotal (Runkle and Heins, 2001; Smith, 1982). In the present study, the reduction of hypocotyl length with increase in B PF cannot be directly attributed to the phytochrome response since the Pfr/Ptotal decreased with the increase of percent B PF (Table 1, Fig. 2). Therefore, the reduction of hypocotyl length by the increase of percent B PF can be attributed to cryptochrome photoreceptors. Cryptochrome photoreceptors have maximal absorption in the B range of 390-480 nm with the peak around 450 nm and are

known to decrease hypocotyl elongation when stimulated (Ahmad and Cashmore, 1996; Ahmad et al., 2002). The blue peak wavelength used in the present study (455 nm), falls in the range of maximal activity of the cryptochrome. Similar reduction of stem length caused by the increase of percent B PF has been reported for cucumber (Hernández and Kubota, 2016), pepper (Brown et al., 1995) and tomato (Liu et al., 2011; Nanya et al., 2012; Wollaeger and Runkle, 2014) seedlings.

In the present study, tomato seedling hypocotyl length of ‘Komeett’ grown under 100B treatment was 8.4 cm and it was comparable than hypocotyl length of seedlings grown under 10B:90R treatment (8.0 cm) while both being 34 %, 42 %, 45 %, and 56 % greater than the hypocotyl length of seedlings grown under 20B:28G:52R, 30B:70R, 50B:50R, and 75B:25R treatments, respectively ($P < 0.0001$) (Fig. 2). If cryptochrome stimulation was the main factor affecting hypocotyl length, then seedlings under the 100B treatment should have been the most compact of all treatments; however, in the present study this is not the case. The large hypocotyl length in the 100B treatment can be partially attributed to the phenomenon described as “coaction”. A combination of B light and high R:FR ratio suppress stem extension synergistically (Ahmad and Cashmore, 1997; Casal and Mazzella, 1999; Hernández and Kubota, 2016; Wollaeger and Runkle, 2013). Also, cryptochrome mediated responses do not occur in the absence of active phytochrome (Ahmad and Cashmore, 1997; Folta and Spalding, 2001; Neff and Chory, 1998; Whitelam et al., 1993). The lack of active phytochrome in the R absorbing form (Pr) caused by the lack of red light, could have contributed to the inhibition of stem reduction caused by cryptochrome stimulation. Another plausible explanation is the effect of B light on phytochrome far-red absorbing form (Pfr). When Pr is most abundant at the end of the day (EOD), it triggers hypocotyl elongation (Kendrick and Kronenberg, 1994). Sager et al.

(1988) used purified rye photochrome to demonstrate that Pfr has a maximal relative absorbance at 730-738 nm peak (far-red light) and that Pfr has an additional relative absorbance peak in the B region with the highest maximal relative absorbance at 400-420 nm. In the presence of EOD R light (all treatments except 100B), the Pfr absorbing form was the most abundant, which prevented stem elongation. However, when R light was removed (100B), the EOD light quality was B (peak: 455nm), which will make the Pr absorbing form more abundant and consequently lowering the suppression of hypocotyl elongation. Hypocotyl elongation by monochromatic B light has been documented in several studies. For example, when used as supplemental lighting, monochromatic B light caused cucumber plants a 46% greater hypocotyl length than did monochromatic R light (Hernández and Kubota, 2015). Under sole-source electrical lighting, cucumber seedlings under monochromatic B light had 69 % and 346 % greater hypocotyl than plants under monochromatic R and 75 % B light, respectively (Hernández and Kubota, 2016). Longer hypocotyl length was observed on dill (*Anethum graveolens*) under EOD B conditions when compared to EOD R (Fraszczak, 2013). Specifically for tomato seedlings, Liu et al. (2011) observed 31% greater plant height under 100B treatment than under 50B:50R treatment (energy basis). Similarly, Kim et al. (2014) showed greater stem length on cherry tomato seedlings grown under 100B than in 100R treatment. In contrast, Wollaeger and Runkle (2014) found no differences in plant height between plants grown under 100B and 50B:50R light treatments. The number of days the plants were under the treatments may have contributed to the differences in results between the Wollaeger and Runkle (2014) study (32 days) and the present study (21 days) since epicotyl extension can compensate for any initial hypocotyl elongation in older plants. In addition, tomato seedlings in the Wollaeger and Runkle (2014) study were kept in the greenhouse (broad-light spectrum) until cotyledon expansion and then moved to the light

treatments (*pers comm.* E. Runkle); in contrast to our study, our seedlings were always exposed to their respective light treatments from radicle emergence. The difference on the light quality before cotyledon expansion could have influenced the difference on final hypocotyl length between the present study and the Wollaeger and Runkle (2014) study.

3.2 Effects of percent B:R PF ratios on tomato 'Komeett' stem diameter and leaf area

Stem diameter is an important morphological characteristic for tomato seedlings, specifically if the seedlings are grown for grafting, producing a thicker stem in less time will allow the propagator to graft sooner. In addition, vegetable transplants with a thicker stem are often preferred in order to reduce stem breakage. In the present study, stem diameter under the 50B:50R treatment was 17%, 26%, 37%, and 46% greater than in 75B:25R, CWF, 100B and 100R, respectively (Table 2). Stem diameter was not different in the 10B:90R, 20B:28G:52R, 30B70R and 50B:50R treatments (Table 2).

Plants under treatments emitting both B and R PF showed no differences in leaf area and had 64-72 % greater leaf area than plants grown under monochromatic red and blue treatments (100R and 100B) (Table 2). Research in leaf expansion has shown that red and blue light stimulate leaf expansion by increasing the rate proton efflux on epidermal cells by separate mechanisms (Staal et al., 1994; Volkenburgh, 1999). Blue light directly stimulates the proton pump by direct interaction between the pump and a B-light photoreceptor (Elzenga, 1997), while, R-light influences the proton pump indirectly by modulating calcium and potassium channels (modulation of passive ion conductance) (Elzenga et al., 1997; Staal et al., 1994; Volkenburgh, 1999). Furthermore, research has shown that the effects of B and R light in leaf expansion are additive (Staal et al., 1994). In the present experiment, the plants grown under 100R or 100B may have lack the additive effect of leaf expansion present in plants under the treatments

containing both B and R PF, which caused the reduction in leaf area. Under supplemental LED lighting in a greenhouse, Gomez and Mitchell (2015) showed that ‘Kommeet’ tomato seedling’s leaf area under 5B:95R and 20B:80R was 41-54 % greater than tomatoes under the 100R treatment.

3.3 Effects of B:R PF ratios on tomato ‘Komeett’ chlorophyll and anthocyanin concentration.

Chlorophyll concentration per leaf area was not statistically different between plants in CWF, 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R, and 75B:25R (Table 3). In algae, research showed an increase of chlorophyll concentration with the increase of B PF (Jeffrey, 1980; Jeffrey and Vesk, 1981; Vesk and Jeffrey, 1977) and in other crops (Hernández and Kubota, 2014; Hernández and Kubota, 2016; Hogewoning et al., 2010; Matsuda et al., 2007). For example, under sole source lighting and supplemental lighting, cucumber seedlings showed increased chlorophyll concentration with the increase of B PF (Hernández et al., 2016; Hernández and Kubota, 2014; Hogewoning et al., 2010). However, similar to the present study, Wollaeger and Runkle (2014) showed no differences in relative chlorophyll concentration between 100R, 25B:25G:50R, 50B:50R in tomato seedlings,. Similarly, Liu et al. (2011) showed no differences in tomato chlorophyll content between 100R, 100B and 50B:50R.

Plants under the B:R treatments had an average of 31% and 57% greater chlorophyll content per leaf area than in the 100R and 100B treatments, respectively (Table 3). This response is similar to cucumber responses grown under similar experimental conditions (Hernández and Kubota, 2016; Hogewoning et al., 2010). The lack of a “coaction” effect of cryptochrome and phytochrome could have caused the reduction of chlorophyll biosynthesis under the 100B and

100R treatments (Neff and Chory, 1998). Another plausible possibility is the need for a qualitative response to B or R light for normal plant development by plants grown under monochromatic B or R light.

Anthocyanin increased with the increase of B PF from 0 % B (100R) up to 75 % B (Fig. 3) and anthocyanin concentration was mainly present in the abaxial part of the leaf. Previous research showed that anthocyanin concentration is greater when B light is present and that B light stimulates anthocyanin biosynthesis via the flavonoid biosynthetic pathway by promoting the gene expression of chalcone synthase (CHS) and dihydroflavonol-4-reductase (DFR) (Albert et al., 2009; Giliberto et al., 2005; Meng et al.; Ninu et al., 1999). Specifically for tomato, it was demonstrated that cryptochrome stimulated by B light regulates the biosynthesis of anthocyanin (Giliberto et al., 2005; Ninu et al., 1999). The role of anthocyanin in vegetative tissue is not fully understood. Vegetative tissues often biosynthesize anthocyanin under stress conditions such as low temperatures, nutrient deficiencies, high light, and pathogens (Chalker-Scott, 1999; Dixon and Paiva, 1995); however, in the present experiment, plants were not under stress conditions. Anthocyanin production of the vegetative tissue is attributed to high light conditions. For example, Albert et al. (2009) grew common petunia and a *Lc* petunia expressing *Leaf colour (LC)*, a bHLH anthocyanin regulator from maize responsible of anthocyanin production in vegetative tissue. Albert et al. (2009) found that plants under high solar light had greater anthocyanin concentration than when grown under low solar light. Further studies have shown that anthocyanin concentration serves as a light-attenuation mechanism to protect lower cells from photo-inhibition (Albert et al., 2009; Gould, 2004; Gould et al., 1995; Hughes et al., 2008).

We hypothesize that the accumulation of abaxial anthocyanin driven by the increase of B PF observed in the present study will help tomato seedlings adapt to higher light levels when

they are transplanted in the greenhouse or field conditions. Our current research is testing the performance of tomato seedlings with high anthocyanin concentration (grown under high B PF) and compared those to low anthocyanin concentration (grown under low B PF) after transplanted in greenhouses or field.

3.4 Effects of B:R PF ratios on net photosynthetic rate, stomata conductance, leaf number, shoot fresh mass, shoot dry mass and plant compactness of 'Komeett' tomato

No statistical differences were found between treatments in leaf Pn ($P=0.077$) and leaf g_s ($P=0.094$) (Table 3). McCree (1972) quantified the relative quantum yield efficiency (RQE) of growth-chamber grown tomatoes under different light quality (350-725 nm range, 25 nm increments). The tomato RQE curve shows that red light (600-700 nm) has 7 % and 27 % greater RQE than yellow and blue light, respectively. Based on McCree (1972), which reported that B light had lower RQE than red light, it is expected to observe a decrease on leaf Pn with the increase of percent B. However, in the present experiment no significant differences were found between the treatments. For tomato, Nanya et al. (2012) grew seedlings under 10B, 30B and 50B percent B PF (with remaining percent as red) (B: 450 nm peak, R: 660 nm peak, $150 \mu\text{mol m}^{-2} \text{s}^{-1}$) and found no differences in leaf Pn when plants were 11 days old; however, 17 day old plants had higher leaf Pn with the decrease of blue PF (10B>30B>50B). The Pn response can explain the growth rate response in Nanya et al. (2012). Similarly, in the present study, for the treatments containing both B and R PF the Pn and g_s responses match the growth rate responses such as fresh mass, dry mass, leaf number, and chlorophyll concentration. For 100B and 100R Pn and g_s responses do not match the growth rate responses since these two treatments had lower

growth rate than the treatments containing both B and R PF (see section 3.5 for further discussion).

For shoot fresh mass no differences were found between plants under the 10B:90R, 20B:28G:52R, 30B:70R and 50B:50R (Table 3). Plants under 10B:90R and 50B:50R had 33 % and 38 % greater fresh mass, respectively than plants under the 75B:25R treatment. Plants under the treatments 10B:90R, 20B:28G:52R, 30B:70R and 50B:50R had 62 %, 44 %, 50 %, and 67 % greater shoot fresh mass, respectively than plants under the CWF. Plants in 10B:90R, 20B:28G:52R, 30B:70R and 50B:50R had 91 %, 70 %, 76 %, 96 %, and 43% greater shoot fresh mass, respectively than plants in 100R. Plants in 10B:90R, 20B:28G:52R, 30B:70R and 50B:50R treatments had 59 %, 41 %, 47 %, 63 % and 19 % greater shoot fresh mass, respectively than plants in 100B.

For shoot dry mass, no differences were detected between plants under the 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R and 75B:25R treatments (Table 3). However, Plants under the treatments 30B:70R and 50B:50R had in average 61 %, 150 %, and 109 % greater dry mass than plants under CWF, 100R, and 100B, respectively.

For leaf number, no differences were found in plants under 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R, 75B:25R and CWF treatments (Table 2). Plants under 30B:70R, 20B:28G:52R and 50B:50R had 23 % greater leaf number than plants under 100R and 100B treatments. From the present study, tomato seedlings are able to have comparable growth rate (fresh mass, dry mass, leaf number) under the range of 10% to 50% B PF. Results on growth rate parameters of tomato seedlings under sole-source lighting vary in the literature. For example, Nanya et al. (2012) showed greater shoot dry mass under the 10B:90R treatment than under the 50B:50R treatment. Liu et al. (2011) showed no differences between plants in the 100R and in 50B:50R treatment.

Wollaeger and Runkle (2014) showed greater dry mass under the 100R treatment than 50B:50R and 100B treatments. None of the previous studies have tested a full range of B:R photon flux ratios; however, if growth rate is the main factor considered for seedling production under sole-source light conditions, based on previous studies and the present study, it is recommended a treatment containing low B and high R PF (i.e 10B:90R). However, other morphological (plant height), physiological (chlorophyll concentration) and potential plant disorders (intumescences) should be considered to find the most versatile spectrum.

No significant differences were found in plant compactness between plants in 20B:28G:52R, 30B:70R, 50B:50R, 75B:25R and CWF treatments (Table 2). Plants under 30B:70R had 42% greater plant compactness than in 10B:90R treatment (Table 2). Plant compactness, which is the relationship of dry mass and plant height, is another important parameter to determine seedling quality. A transplant with high dry mass and short height is considered as a high quality seedling (Currey et al., 2012; Vu et al., 2014). If plant compactness is used as the main parameter to select light quality for the production of tomato seedlings, we recommend to increase the B PF (decrease stem length) to no greater than 50%B to maintain high growth rate (fresh mass, dry mass, leaf number) and maintain a short plant (compactness).

3.5 Summary for 'Kommeet' physiological responses

In the present study, important parameters driving plant growth such as Pn, gs, leaf area (light intersection), and chlorophyll concentration were not statistically different between the treatments containing both B and R PF. This resulted in no-significant differences in plant growth in the LED treatments containing B, G and R PF (Table 2, 3). The main two factors that were affected quantitatively by the increase of B PF were hypocotyl length (plant height) and anthocyanin concentration in leaves. The decrease in plant height with the increase of B PF led

to the differences in plant compactness between plants in 10B:90R and 30B:70R. Plants in 100B and 100R had lower growth rate than plants under the treatments containing both B and R PF; however, plants in 100R, 100B and the other LED treatments (B:G:R) showed no significant differences in P_n , and g_s . In addition, after calculating the specific leaf area (SLA, leaf area per unit dry mass) no significant differences were detected between any of the treatments ($P=0.8685$). No significant differences between any of the treatments in P_n , g_s , and SLA, concludes that plants in all treatments have similar expected return on captured resources, in other words, similar capacity for growth rate (Westoby, 1998; Wilson et al., 1999). However, plants under the 100R and 100B had lower dry mass and fresh mass than other treatments. This can be explained by morphological traits since plants under 100R and 100B had lower leaf area and lower leaf number; which led to lower light intersection and consequently lower growth rate.

3.6 Effects of B:R PF ratios on intumescence for 'Beaufort' tomato

Severe intumescence symptoms led to leaf chlorosis and leaf abscission, which greatly affected 'Beaufort' growth rate. For example, plants under the CWF treatment (no intumescences) had 84% to 93% greater number of leaves, 116% to 237 % greater fresh mass, and 103% to 340% greater shoot dry mass than plants under the B:R treatments (data not shown). The 97% to 100% of plants in 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R and 75B:25R exhibited intumescences symptoms (Table 4). Plants under these treatments had 31-35% greater intumescence ratio than plants under 100R (Table 4). Plants grown under the combination of B and R PF had 51% to 66% leaves with intumescences (Fig. 4). Plants under 10B:90R, 20B:28G:52R, 30B:70R, and 50B:50R had 86% to 223% greater ratio of intumescences in stem (most severe symptom) than plants under 100R and 75B:25R treatments (Table 4). In the present study, the increase percent B PF in the growing spectrum had an inhibitory effect on the development of intumescences

(Fig. 4). The incidence of intumescences on leaves (*ratio of leaves with intumescences*) linearly decreased with the increase of percent B PF from the 10% B to 75% B ($P=0.0104$) (Fig. 4).

Also, the incidence of intumescence in the stem (*ratio of plants with intumescences in stem*) was significant lower in the 75B:25R treatment and in 100R treatment. Plants under CWF and 100B had no intumescences in leaves or stem (Fig. 4, Table 4).

Intumescences in tomatoes are described as a non-pathogenic disorder characterized by hypertrophy of spongy parenchyma, palisade, and epidermis cells (Lang and Esther Struckmeyer, 1983; Lang and Tibbitts, 1983; Morrow and Tibbitts, 1988). Intumescences in tomatoes are triggered by spectral quality, and high relative humidity can increase the severity of the symptoms (Lang and Tibbitts, 1983; Morrow and Tibbitts, 1988). Intumescence symptoms are known to be more common on wild type tomato (*S. habrochaites*). Tomato rootstock ‘Beaufort’ used in the present study is a cross between *Solanum lycopersicum* and *S. habrochaites*, which explains the higher incidence of intumescence symptoms compared to ‘Komeett’ (*Solanum lycopersicum*). Research showed that the absence of UV-B radiation is the main cause for intumescences development (Lang and Tibbitts, 1983). This is supported by the present study since the plants under the CWF treatment received a small amount of UV-B radiation coming from the fixture (aprox $0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$, 280-320 nm). Research also showed that far-red light could mitigate intumescence development (Eguchi et al., 2016a; Eguchi et al., 2016b; Morrow and Tibbitts, 1988). On a parallel study, we examined the effect of end-of-day far red (EOD-FR) on intumescence injury of ‘Beaufort’, and demonstrated that EOD-FR at a very low dosage ($1 \text{ mmol m}^{-2} \text{ d}^{-1}$) significantly decreases intumescence development compared to a 10B:90R treatment without EOD-FR treatment ((Eguchi et al., 2016a; Eguchi et al., 2016b).

In the present experiment, we found that severity of intumescences in leaves decreased as the percent B PF increased and intumescence symptoms were completely eliminated by 100B treatment. The decreased of intumescence development by the increase B PF has been reported before (Eguchi et al., 2016a; Eguchi et al., 2016b; Wollaeger and Runkle, 2014). For example, Wollaeger and Runkle (2014) showed that intumescence development in tomato ‘Early girl’ was lower under 50% B and 100% B than 0% B (100% R) treatment. In addition, Wollaeger and Runkle (2014) found that the addition of G light (50G:50R) reduced the incidence of intumescence while in the present study G light did not have an inhibitory effect on the incidence of intumescence in tomato ‘Beaufort’. Additional research is needed to understand the mechanism by which the increase of B PF decreases and eliminates (at 100% B) the incidence of intumescences on tomato seedlings grown under sole-source B and R light conditions.

In a parallel study, we presented spectra effectively suppressing intumescence development in tomato rootstocks ‘Beaufort’ and ‘Maxifort’ without compromising desirable seedling quality (Eguchi et al., 2016b). The spectrum consisted on the combination of low dosage EOD-FR ($1-4 \text{ mmol m}^{-2} \text{ d}^{-1}$) and high percent B PF (50B:50R or 75B:25R) during the growing spectrum, which can be used to grow tomato cultivars that are known to develop intumescence.

3.7 Tomato seedling response to the addition of green light

The 20B:28G:52R treatment had G light as a part of the spectrum. The total percent of G PF was 28%, and B and R consisted of 20% and 52% PF, respectively. In the present study, the physiological plant responses to the 20B:28G:52R treatment can be explained by the percent B PF, since the addition of G light did not have any effects on plant responses (shoot fresh mass,

shoot dry mass, leaf number, leaf area, hypocotyl length, stem diameter, chlorophyll concentration, anthocyanin, g_s , and leaf P_n)

Plant responses to G light are species specific. For example, Kim et al. (2006) concluded that 24% G increased lettuce (*Lactuca sativa* ‘Waldmann’s Green’) growth, and more than 50% G reduced lettuce growth. Johkan et al. (2012) grew lettuce under fluoresce light and under different G wavelengths (510, 520, 530 nm), under different light intensities (100, 200, 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and found that plants grown under lower (100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) light intensity had greater dry mass under fluorescence light; however when the intensity increased, plants under G light had comparable shoot dry mass (300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and higher root dry mass (200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) under the 510 nm G treatment. Ma et al. (2015) grew potato plantlets (*Solanum tuberosum*) in vitro under B:R and under B:G:R (300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and found that plants under B:G:R treatments had greater dry mass, stem diameter, and health index ([stem diameter/stem height]*dry mass) than plants under the B:R treatments. Future research should test the effect of G light on tomato seedlings at a higher PPF (300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) to identify any potential increased in growth rate or improved morphology.

More specifically for vegetable transplants, Hernández and Kubota (2016) found no effect of G light (20B:28G:52R) on cucumber seedling’s growth rate when compared to different ratios of B:R PF. Specifically for tomato, Wollaeger and Runkle (2013) found that tomato seedlings grown under G:R, B:G:R, and B:R had similar dry weight. Liu et al. (2011) found similar growth rate on cherry tomato when grown under B:R, B:G:R and G light.

Green light is also known to increase hypocotyl length in several plant species (Bouly et al., 2007; Wang and Folta, 2013; Wang et al., 2013). However, the hypocotyl response to G light is also species specific. For example, in cucumber seedlings, the addition of G light to a B:R

spectrum did not have an effect on hypocotyl length (Hernández and Kubota, 2016). In tomato, Wollaeger and Runkle (2013) found that plant height under a 50G:50R treatment was around 50% greater than plant height under 25B:25G:50R, 50B:50G and 50B:50R. This can be attributed to the absence of B light in the 50G:50R treatment since, from the present experiment, it is evident that the increase of B light decreases plant height (Fig. 2). Liu et al. (2011) found no differences between cherry tomato plants grown under B:R and B:G:R; however, plants grown under G light only had 64% and 89% greater plant height than plants in B:R and B:G:R, respectively.

3.8 Cool white fluorescent and LED comparison

Fluorescent lamps have been a widely used technology for the production of vegetable seedlings under indoor-production. For example, grafted plant propagators in Japan and US use fluorescent tubes for the production of tomato and cucurbit grafted seedlings (C. Kubota and J. Jackson *pers comm*). Cool white fluorescent fixtures have a broad spectrum (Fig. 1) with percent PF of 19B (400-500nm), 48G (500-600nm) and 32R (600-700 nm) (based on light measurements of the CWF used in the present study), which is suitable to grow plants. Fluorescent tubes are also easily available and inexpensive. Below we present a brief comparison of CWF and LEDs for the indoor production of tomato seedlings based on the results from this experiment.

Table 5 shows the pairing comparisons of tomato seedling's physiological responses when grown under CWF and different percentages of B:R PF using LEDs. The main differences between CWF and some of the LED treatments containing B:R were on plant hypocotyl length, stem diameter, fresh mass, and dry mass. Plants under the LED treatments had 16-53% longer hypocotyl length than plants under the CWF treatment (Table 5). However, plants under the 30B:70R and 50B:50R LED treatments had 39% and 36% greater dry mass, and 33% and 40 %

greater fresh mass than plants in CWF treatment, respectively. In summary, plants under the 30B:70R and 50B:50R LED treatments had greater growth rate, than plants under CWF. In order to further compare the two technologies, we estimated the electrical efficacies (g kWh^{-1}) between commercially available LEDs and High-Output fluorescent lamps (HO-FL), which have one of the highest advertised efficiencies (lumen per watt). Current LED indoor technology is advertised with efficiencies of up to $2.15 \mu\text{mol J}^{-1}$ (Emission rate: $62.5 \mu\text{mol s}^{-1}$, 29 W) (Philips, 2015) while HO-FL have an efficiency of $1.29 \mu\text{mol J}^{-1}$ (Emission rate: $70.2 \mu\text{mol s}^{-1}$, 54 W, T5-HO). Using these efficiencies, we calculated the areal-power-consumption (APC) and fixture-growing-efficacy (FGE). LEDs have 172% greater growing efficacy than HO-FL (Table 6).

Summarizing in terms of efficiencies and growing efficacy, current LEDs are the technology of choice for indoor-production. However, initial capital costs need to be considered before making the technology adoption since the LED fixtures used in this estimation are 3.2 times more expensive than the HO-FL.

4. Conclusion

Plants under higher percentages of B PF (up to 75% B PF) had desirable characteristics such as shorter stem length, greater plant compactness, and lower intumescence severity. However, growth rate parameters such as fresh mass, dry mass and number of leaves were comparable between the treatments containing both B:R PF (10B:90R, 20B:28G:52R, 30B:70R, 50B:50R, 75B:25R). Plants grown under monochromatic B and R light showed lower growth rate and undesirable plant height (100R,100B). Plants under CWF had comparable plant compactness to that of best LED treatments; however, also had lower dry mass than in 30B:70R, 50B:50R LED treatments and lower growing efficacy (g kWh^{-1}). In summary, 30B:70R, 50B:50R were the best

spectrums to produce tomato seedlings under VF conditions; however, plant quality under CWF, 10B:90R, 20B:28G:52R, 75B:25R is also acceptable.

Additional research is needed to determine the optimal growing spectrum in other specialty horticultural crops that are suitable for VF. In addition, further research is needed to understand the interaction of light quality and other environmental parameters to optimize production efficiency in which the total amount of energy consumed per unit mass of production is reduced.

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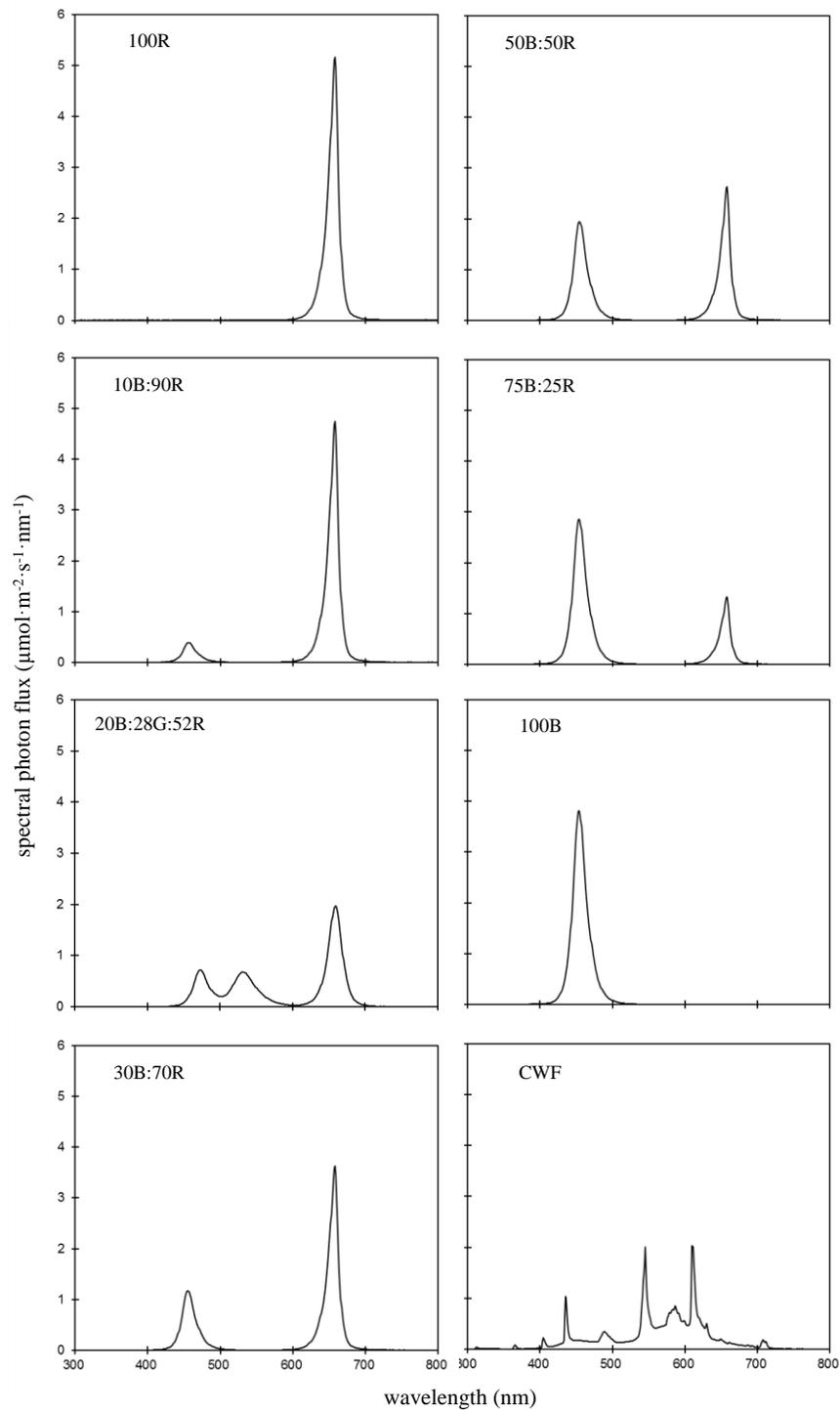


Fig 1. Spectral distribution of light treatments. B represents the blue PF ratio, G the green PF ratio and R the red PF ratio for each LED treatment. CWF represents the spectrum of the cool white fluorescent control. Spectra were measured using a spectroradiometer at the beginning and end of each repetition averaged at five locations at plant canopy height.

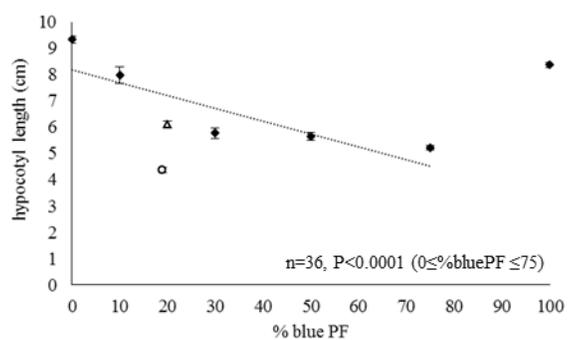


Fig 2. Effect of increase percent blue photon flux on hypocotyl length of tomato seedlings 'Komeett'. Diamonds represent the treatments containing B and R PF. Triangle represents the 20B:28G:52R treatment. Circle represents the CWF control treatment. CWF is not part of the regression analysis. Line represents statistically significant regression.

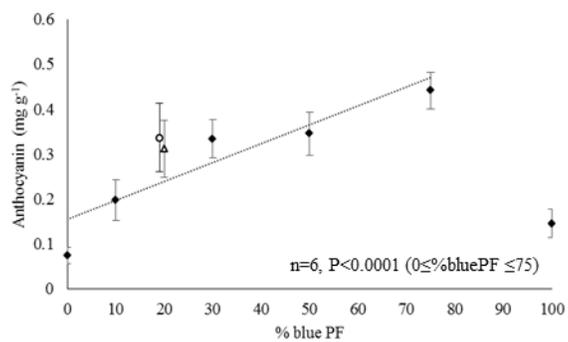


Fig 3. Effect of increase percent blue photon flux on the leaves anthocyanin concentration of tomato seedlings 'Komeett'. Diamonds represent the treatments containing B and R PF. Triangle represents the 20B:28G:52R treatment. Circle represents the CWF control treatment. 100B is not part of the regression analysis. Line represents statistically significant regression.

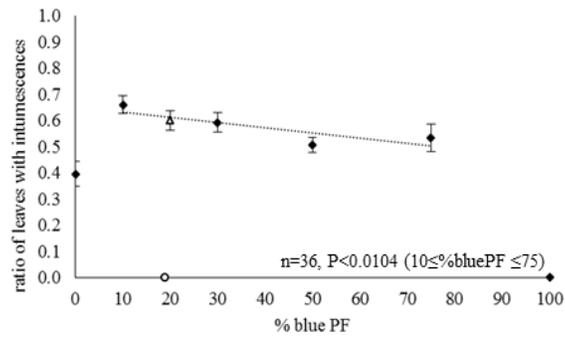


Fig 4. Effect of increase percent blue photon flux on the ratio of leaves with intumescences in tomato seedlings 'Beaufort'. Diamonds represent the treatments containing B and R PF. Triangle represents the 20B:28G:52R treatment. Circle represents the CWF control treatment. Line represents statistically significant linear regression.

Table 1. Light treatments with different blue (B), green (G) and red (R) percent PF and cool white fluorescent control (CWF), PPF per treatment, phytochrome photostationary state (P_{fr}/P_{total}), and growing environmental conditions

Parameter	Units	Treatments (photon flux ratio)							
		CWF	100R	10B:90R	20B:28G:52R	30B:70R	50B:50R	75B:25R	100B
PPF ^a (400-700 nm)	$\mu\text{mol m}^{-2} \text{s}^{-1}$	99.6 ± 3.1	99.8 ± 2.7	100.6 ± 1.6	100.4 ± 1.1	99.8 ± 1.0	101.8 ± 2.6	101.6 ± 3.3	98.7 ± 0.7
P_{fr}/P_{total} ^b		0.849	0.888	0.886	0.878	0.879	0.867	0.828	0.508
Canopy air T	°C	25.3 ± 0.5	25.2 ± 0.4	25.1 ± 0.4	25.2 ± 0.4	25.0 ± 0.4	25.0 ± 0.4	25.0 ± 0.5	25.2 ± 0.4
Photoperiod	hours	18							
Air T	°C	25.0 ± 0.4							
Relative Humidity	%	64.7 ± 10.2							
CO ₂ concentration	$\mu\text{mol mol}^{-1}$	509 ± 121							
Nutrient solution pH		6.0							
Nutrient solution EC	dS m ⁻¹	2.2							
Planting density	plants m ⁻²	700							

^a Average and standard deviation of sixteen measurements, four measurements at the beginning of the experiment and four measurements at the end of the experiment per treatment per repetition.

^b Phytochrome photostationary state (Sager et al., 1988)

Table 2. Effects of different light spectra on morphological responses of ‘Komeett’ (*Solanum lycopersicum*) greenhouse tomato. Means followed by different letters are significantly different at $P \leq 0.05$ (mean ± standard deviation).

Light treatment	Stem diameter	Leaf area per plant	Leaf number	Plant compactness
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	(mm)	(cm ²)	(> 1cm)	(g m ⁻¹)
CWF	2.9 ± 0.7 cd	46.3 ± 18.8 a	2.85 ± 0.66 abc	95.9 ± 43.1 ab
100R	2.5 ± 0.5 d	27.1 ± 11.4 b	2.72 ± 0.51 bc	41.6 ± 17.3 c
10B:90R	3.6 ± 0.6 ab	52.3 ± 16.0 a	3.11 ± 0.72 ab	83.8 ± 32.3 b
20B:28G:52R	3.4 ± 0.6 ab	48.8 ± 17.4 a	3.28 ± 0.70 a	87.2 ± 35.2 ab
30B:70R	3.4 ± 0.7 ab	52.0 ± 18.6 a	3.24 ± 0.65 a	119.2 ± 81.2 a
50B:50R	3.7 ± 0.6 a	53.8 ± 14.6 a	3.23 ± 0.65 a	102.2 ± 35.6 ab
75B:25R	3.2 ± 0.7 bc	46.5 ± 16.5 a	3.14 ± 0.60 ab	95.6 ± 56.6 ab
100B	2.7 ± 0.5 d	28.4 ± 13.0 b	2.57 ± 0.56 c	42.4 ± 18.0 c

Table 3 Effects of different light spectra on growth rate responses of ‘Komeett’ (*Solanum lycopersicum*) greenhouse tomato. Means followed by different letters are significantly different at $P \leq 0.05$ (mean ± standard deviation).

Light treatment	Shoot fresh mass (g)	Shoot dry mass (g)	Chlorophyll per leaf area (g m ⁻²)	Pn μmol CO ₂ m ⁻² s ⁻¹	gs mmol m ⁻² s ⁻¹
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CWF	1.55 ± 0.77 c	0.102 ± 0.057 bcd	0.265 ± 0.046 a	1.95 ± 0.69 a	47.0 ± 23.6 a
100R	1.32 ± 0.52 c	0.066 ± 0.032 d	0.218 ± 0.021 b	3.07 ± 0.38 a	94.2 ± 47.9 a
10B:90R	2.52 ± 0.86 a	0.147 ± 0.072 ab	0.264 ± 0.024 a	2.23 ± 1.11 a	82.5 ± 66.7 a
20B:28G:52R	2.25 ± 0.85 ab	0.134 ± 0.070 ab	0.294 ± 0.059 a	2.28 ± 0.79 a	94.5 ± 52.0 a
30B:70R	2.33 ± 1.05 ab	0.168 ± 0.091 a	0.284 ± 0.043 a	1.85 ± 0.87 a	51.8 ± 14.6 a
50B:50R	2.60 ± 0.83 a	0.161 ± 0.066 a	0.296 ± 0.058 a	2.1 ± 0.33 a	68.0 ± 41.8 a
75B:25R	1.89 ± 0.81 bc	0.120 ± 0.068 abc	0.298 ± 0.043 a	2.55 ± 0.49 a	133.7 ± 82.5 a
100B	1.59 ± 0.71 c	0.079 ± 0.048 cd	0.184 ± 0.081 b	1.75 ± 0.86 a	63.3 ± 36.8 a

Table 4. Effects of different light spectra on intumescence development of ‘Beaufort’ (*Solanum lycopersicum* x *S. habrochaites*) tomato rootstock. Means followed by different letters are significantly different at $P \leq 0.05$ (mean ± standard deviation).

Light treatment	ratio of plants with intumescences	ratio of plants with intumescences in stem
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CWF	0.00 ± 0.000 c	0.00 ± 0.000 c
100R	0.74 ± 0.443 b	0.49 ± 0.086 b
10B:90R	1.00 ± 0.000 a	0.91 ± 0.049 a
20B:28G:52R	0.97 ± 0.167 a	1.00 ± 0.000 a
30B:70R	0.97 ± 0.171 a	1.00 ± 0.000 a
50B:50R	0.97 ± 0.169 a	0.91 ± 0.048 a
75B:25R	0.97 ± 0.167 a	0.31 ± 0.078 b
100B	0.00 ± 0.000 c	0.00 ± 0.000 c

Table 5. Comparison of ‘Komeett’ physiological responses under cool white fluorescent (CWF) and LED light treatments. (-) Signifies how many percent the respective LED treatment is lower than the CWF treatment, (+) signifies how many percent the

respective LED is greater than the CWF treatment and (=) signifies no differences between CWF and the respective LED treatment. Statistical analysis based on comparisons with CWF (control) using Dunnett's method at $P \leq 0.05$.

Physiological parameter	Control	100R	10B:90R	20B:28G:52R	30B:70R	50B:50R	75B:25R	100B
Hypocotyl length (cm)	CWF	+ 53%	+ 45%	+ 28%	+ 24%	+ 22%	+ 16%	+ 48%
Stem diameter (mm)	CWF	- 14%	+19%	+ 15%	+ 15%	+ 21%	=	=
Leaf area (m ²)	CWF	- 41%	=	=	=	=	=	- 39%
Leaf number	CWF	=	=	+ 13%	=	=	=	=
Fresh mass	CWF	=	+ 38%	+ 31%	+ 33%	+ 40%	=	=
Dry mass	CWF	=	=	=	+ 39%	+ 36%	=	=
Chlorophyll per leaf area (g m ⁻²)	CWF	=	=	=	=	=	=	- 34%
Anthocyanin (mg g ⁻¹)	CWF	- 78%	=	=	=	=	=	- 57%
Leaf Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	CWF	=	=	=	=	=	=	=
g_s ($\text{mmol m}^{-2} \text{ s}^{-1}$)	CWF	=	=	=	=	=	=	=
Plant compactness (g cm ⁻¹)	CWF	- 57%	=	=	=	=	=	- 56%

Table 6. Estimation of 'areal power consumption' and 'fixture growing efficacy'. Tomato 'Komeett' seedlings were grown under 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photon flux, 0.0506 m² growing area, 18 h photoperiod, 21 growing days, and 700 plants m⁻² density. 'Fixture growing efficacy' was calculated using the growing area shoot-dry-mass means and the estimated total power consumption.

Lamp type and ballast	Input power (kW)	Fixture PPF efficiency ($\mu\text{mol J}^{-1}$)	Effective photons (EP, $\mu\text{mol s}^{-1}$) ^x	Areal power consumption (APC, kW m ⁻²)	Fixture growing efficacy (FGE, g kWh ⁻¹)
30B:70R and 50B:50R LEDs	0.029	2.15 ^z	62.5	0.0464	6.69
HO-T5 CWF	0.054	1.29 ^y	69.7	0.0775	2.46

^z Values obtained from spec-sheet of GP LED production DR/B 150 HB (Philips, 2015)

^y Values based on T5-HO, 5000 lumen, 54W, and a conversion factor derived from lux and quantum sensors empirical measurements

^x EP was considered as 100% of total photon emission of LEDs and CWF (assuming all photon were captured by plant canopy and similar fixture life)