

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

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10 Abstract

11 Lamp spectral customization can be a strategy to achieve desirable plant characteristics when
12 plants are grown under sole-source electric lighting. Vegetable transplants can be efficiently and
13 economically grown under indoor-production systems with electrical lighting; however, species-
14 specific light recipes have to be developed to improve plant growth, development and
15 morphology, as well as to reduce electrical consumption. The objective of this study was to
16 evaluate the growth and morphology of tomato transplants to a broad range of blue to red (B:R)
17 photon flux (PF) ratios under LEDs and cool white fluorescent lamps (CWF). Tomato ‘Komeett’
18 and ‘Beaufort’ seedlings were grown in a climate control growth chamber. Using LEDs, seven
19 light treatments with different blue (B), green (G) and red (R) PF ratios were used: 100R,
20 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R, 75B:25R and 100B. In addition, a CWF treatment
21 served as the control. Hypocotyl length of ‘Komeett’ decreased with the increase of percent B PF
22 up to 75% B. Plant leaf area was 64-72% greater under treatments emitting both B and R PF than
23 in the 100 B and 100 R treatments. Similarly, tomato ‘Komeett’ fresh mass, dry mass, leaf

24 number and chlorophyll concentration was comparable among the treatments containing B and R
25 PF and greater than in 100 B and 100 R treatments. However, plant compactness in the 30B:70R
26 treatment was 42% greater than in the 10B:90R treatment. Anthocyanin concentration increased
27 with the increase of percent B PF up to 75% B. Also, plants in 30B:70R and 50B:50R had 39%
28 and 36% greater dry mass than in CWF, respectively. In addition, 30B:70R and 50B:50R LEDs
29 had 172 % greater growing efficacy (g kWh^{-1}) than high output fluorescent lamps. The addition
30 of G light did not have any effects on tomato physiological responses. ‘Beaufort’ plant
31 morphology and growth were severely affected by intumescences development and
32 intumescence severity decreased under higher percentages of B PF. In summary, 30B:70R,
33 50B:50R were the best spectrums to produce tomato seedlings under LEDs tested here; however,
34 plant quality under CWF, 10B:90R, 20B:28G:52R, and 75B:25R was also acceptable.

35

36 1. Introduction

37 With the continuing development of LEDs, the commercial horticulture sector has placed more
38 emphasis on the production of plants under closed-type systems using sole-source electrical
39 lighting commonly known as vertical farming (VF). One disadvantage of VF is the high
40 electrical consumption. It is estimated that electrical lighting contributes with 25% of total
41 production cost and 80% of total electricity consumption (Kozai, 2013). In addition, the high
42 consumption of electricity also yields a high environmental impact in terms of carbon foot-print
43 compared to greenhouse production (Harbick and Albright, 2016). For these reasons, it is
44 imperative that lighting is used as efficiently as possible. With the rapid improvement of light
45 emitting diodes, in terms of light efficiency, output, and fixture cost reduction (Haitz and Tsao,
46 2011), the application of the results of light quality research to the commercial sector of VF is

47 more tangible than before. Currently, only high value, high density and compact crops are
48 economically suitable for the production under VF conditions (Kozai, 2013). Among these crops
49 is the production of horticultural transplants, which are grown under high density and the fine
50 control of environmental conditions can increase transplant quality compared to traditional
51 greenhouse production. However, plant light recipes have to be developed to improve plant
52 growth, development, morphology and reduce electricity cost. Spectral recipes have to be
53 independently developed for the different horticultural transplants since light quality
54 requirements are known to be species specific.

55 Spectral customization can be used to increase desirable plant characteristics. For example,
56 special light formulations can increase plant growth rate and production (Eguchi et al., 2016a;
57 Hernández et al., 2016; Hernández and Kubota, 2016; Ouzounis et al., 2016; Runkle and Park,
58 2016), increase the concentration of secondary metabolites in plant tissue (Goto et al., 2016; Li
59 and Kubota, 2009; Nicole et al., 2016; Noguchi and Amaki, 2016; Samuoliene et al., 2012),
60 promote plant development (Gilberto et al., 2005), and generate desirable plant morphology
61 (Chia and Kubota, 2010; Hernández and Kubota, 2015; Jeong et al., 2014; Yang et al., 2012).

62 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
63 otherwise R spectrum was needed for normal plant development. Li and Kubota (2009) grew
64 lettuce under fluorescent lamps and supplemented with UV-A, B, G, R, or Far-red LEDs and
65 found an increase in phytochemical concentration with supplemental UV-A and B LED and
66 decreased when supplemented with Far-red light; however, Far-red light increased lettuce fresh
67 and dry mass. Son and Oh (2013) grew lettuce under increasing percent B PF from 0B to 59B
68 and found that growth rate decreased with the increase of B PF. More recently, Jishi et al. (2016)
69 grew lettuce under 50B:50R treatment and under a treatment with 100B for the first 4 to 7 hours

70 followed by a 50B:50R spectrum and demonstrated that shifting the irradiation hours of B and R
71 increase lettuce growth. Additional lettuce studies are needed specific for the production of
72 lettuce transplants that will eventually be transferred to the greenhouse or field production.

73 For cucumber seedlings (*Cucumis sativus*), several studies have examined the physiological
74 and morphological responses under different B and R PF ratios. Hogewoning et al. (2010) found
75 greater leaf photosynthetic capacity (A_{\max}), net photosynthetic rate (Pn), stomatal conductance
76 (g_s), and chlorophyll concentration with the increase of percent B PF in cucumber seedlings
77 (excluding 100% B PF). Savvides et al. (2012) showed higher hydraulic conductance, net
78 photosynthetic rate (Pn), and stomata conductance (g_s) in cucumbers grown under a spectrum
79 containing 30B:70R and 100B compared to those under 100R ($100 \mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod: 16
80 h). More recently, Hernández and Kubota (2016) showed that cucumber Pn increased as the
81 percent B PF increased in a study testing a broad range of percent B PF (0B, 10B, 30B, 50B,
82 75B, 100B) on an otherwise R light regime. They found that the plant dry mass decreased with
83 the increase of B PF up to the 75% B. However, plant dry mass in the 100B treatment was not
84 different from that in the 10B:90R treatment but both were greater than other treatments. All the
85 aforementioned cucumber studies agreed that monochromatic blue (100B) or monochromatic red
86 (100R) caused undesirable cucumber morphological and physiological responses. With the
87 combined findings of these cucumber studies it is safe to conclude that the optimal growing
88 spectrum for cucumber seedlings under sole-source lighting with blue and red LEDs is low B PF
89 and high R PF (i.e.10B:90R).

90 Tomato (*Solaneum lycopersicum*) is the most economically important plant species suitable
91 for indoor transplant-production (Nanfelt, 2016). Several research groups reported tomato
92 seedling growth and morphology under different ratios of B, green (G), and R PF, but

93 inconsistent results are reported on growth rates. Liu et al. (2011) grew cherry tomato under B,
94 yellow (Y), R, 1B:1R, and 3B:1G:3R (ratios calculated on energy basis) (PPF: 320 $\mu\text{mol m}^{-2} \text{s}^{-1}$,
95 photoperiod: 12 h) and found that tomato seedling dry mass was greater in the monochromatic B
96 treatment than other treatments. Nanya et al. (2012) showed greater tomato shoot dry mass in
97 seedlings grown by lowering percent B PF against R PF (in the range of 10-50%) (PPF: 150
98 $\mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod: 16 h). Wollaeger and Runkle (2014) showed greater shoot dry mass in
99 tomato seedlings grown under 100R than those grown under 50G:50R, 25B:25G:50R, 50B:50G,
100 50B:50R and 100B treatments (PPF: 160 $\mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod: 18 h). In summary, Liu et
101 al. (2011), Nanya et al. (2012), and Wollaeger and Runkle (2014) reported that 100B, 10B and
102 100R, respectively produced the greater dry mass in tomato seedlings. However, a limited range
103 of B:R PF was used in the aforementioned studies.

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

107

108 2 Materials and methods

109 2.1 Plant material and growing conditions

110 Tomato scion 'Komeett' (*Solanum lycopersicum*) and tomato rootstock 'Beaufort' (*Solanum*
111 *lycopersicum* \times *S. habrochaites* seeds) (DeRuiter, St. Louis, MO, USA) were sown in plastic trays
112 (26.82 x 53.49 cm) with 98 cells (cell depth: 3.8 cm, cell top: 3.4 cm) (T.O. plastics, Clearwater,
113 MN, USA) filled with peat moss plug substrate (sunshine mix #3) (Sun Gro Horticulture
114 Agawam, MA, USA) and covered with vermiculite. Trays were kept at 28 °C in darkness for 48
115 hours for radicle emergence. Plants were manually irrigated using hydroponic solution with (mg

116 L⁻¹) 90 N, 47 P, 144 K, 160 Ca, 60 Mg, 113 S, 105 Cl, as well as micro-nutrients. The canopy air
117 temperature was measured in close proximity to the underside of the leaf (inside leaf boundary
118 layer) with fine-wire thermocouples (type T, gauge 24, Omega Inc., Stamford, CT, USA). The
119 room air temperature and relative humidity were measured in the chamber using a
120 temperature/humidity probe (HMP110, Vaisala Inc., Helsinki, Finland) and CO₂ concentration
121 was measured with a CO₂ analyzer (LI-800, LI-COR Biosciences, Lincoln, NE, USA).
122 Environmental sensors were connected to a data-acquisition system (CR-23X, Campbell
123 Scientific, Logan, UT, USA). Details of environmental conditions are described in Table 1.

124 *2.2 Light treatments*

125 The six fixtures used for the B:R LED treatments had 455 nm peak wavelength (full width at half
126 maximum FWHM:15 nm) for the B diodes and 661 nm peak wavelength (FWHM: 20 nm) for
127 the R diodes. The fixture used for the B:G:R treatment had 473 nm peak wavelength (FWHM:
128 25 nm) for the B diodes, 532 nm peak wavelength (FWHM: 37 nm) for the G diodes, and 660
129 nm peak wavelength (FWHM: 22 nm) for the R diodes (ISC-101-4, CCS Inc., Kyoto, Japan).
130 Another treatment consisted of six cool-white-fluorescent (CWF) T12 tubes (F40T12 CW
131 Supreme ALTO Plus, Philips Lighting, Somerset, NJ) (Fig. 1).

132 The eight light treatments were created inside a walk-in growth chamber using standard shelving
133 units positioned and outfitted to prevent any light contamination. The LED fixtures (35 L x 34 W
134 cm) were installed 19 cm from the top of the plant canopy and the distance was maintained by
135 adjusting the height of the lamp throughout the experiment. Photon fluxes were measured in five
136 locations of the growing area to achieve an average PF of 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (spectroradiometer,
137 PAR-NIR, Apogee Instruments Inc., Logan, UT, USA) (Table 1). Plants were rotated daily in the
138 growing area to ensure even light exposure to all plants. The measured percent photon flux and

139 light spectrum of the six B:R LED treatments, one B:G:R LED treatment, and one CWF
140 treatment are detailed in Table 1 and Fig 1. The Phytochrome photostationary state (Pfr/Ptotal)
141 was calculated following the specifications described in (Sager et al., 1988).

142 *2.3 Measurements and experimental design*

143 The experiment was conducted for 21 days starting on 21 May 2014 and repeated on 11
144 September 2014 (two repetitions). Each repetition had a total of 144 plants with 18 tomato plants
145 per cultivar per treatment as experimental units. Plant height, and hypocotyl length were
146 measured using a rule. Stem diameter was measured below the cotyledons using a digital caliper.
147 Shoot fresh mass was measured with an electronic balance and plant material was transferred to
148 an oven (80 °C). After 48 hours shoot dry mass was quantified using an electronic balance.
149 Chlorophyll concentration was quantified based on Moran and Porath (1980). Leaves greater
150 than one centimeter were recorded (number of leaves). Individual leaves were scanned and leaf
151 area was estimated using LIA 32 software (Nagoya University, Japan). An index for plant
152 compactness was calculated by dividing the total shoot dry mass by the total plant height.
153 Anthocyanin concentration was quantified following the method described in Li and Kubota
154 (2009). Leaf Pn, and g_s , were measured with a gas exchange system (CIRAS-2, PP System, MA,
155 USA) at 25.0 ± 0.4 °C leaf temperature, ambient CO₂ concentration, and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PF
156 provided by the treatment fixture. Due to equipment issues during repetition one, only Pn and g_s
157 data for the second repetition is presented.

158 Analysis of variance ($P = 0.05$) and mean separations (Tukey-Kramer HSD $P = 0.05$)
159 were implemented to identify any difference among treatments (n=36). No interactions between
160 the treatments and the repetitions were detected. Regression was also applied to the quantitative
161 response to increasing blue percent photon flux. Dunnett's test was used to compare LED

162 treatments to the CWF control treatment (P=0.05). “How many percent the respective LED is
163 statistically lower than the CWF treatment” was calculated by (CWF-LED)/CWF and “how
164 many percent the respective LED is statistically greater than CWF” was calculated by (LED-
165 CWF)/LED on Table 5. JMP software was used for all the statistical analysis (SAS Institute,
166 Cary, NC, USA)

167 *2.4 Intumescence injury assessment in ‘Beaufort’*

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

174 *2.5 Evaluation of electrical power consumption and growing efficacy*

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

181

182 3 Results and discussion

183 *3.1 Effects of B:R PF ratios on 'Komeett' tomato hypocotyl length.*

184 In the present study, hypocotyl length of 'Komeett' decreased with the increase of
185 percent B PF ($P < 0.0001$) up to 75% B (Fig. 2). Phytochrome photoreceptors are known to
186 regulate hypocotyl extension. The phytochrome photostationary state (Pfr/Ptotal) is used to
187 quantify the ratio of R and Far-Red light in the growing environment (R:FR ratio). Hypocotyl
188 length linearly decreases with the increase of the Pfr/Ptotal (Runkle and Heins, 2001; Smith,
189 1982). In the present study, the reduction of hypocotyl length with increase in B PF cannot be
190 directly attributed to the phytochrome response since the Pfr/Ptotal decreased with the increase
191 of percent B PF (Table 1, Fig. 2). Therefore, the reduction of hypocotyl length by the increase of
192 percent B PF can be attributed to cryptochrome photoreceptors. Cryptochrome photoreceptors
193 have maximal absorption in the B range of 390-480 nm with the peak around 450 nm and are
194 known to decrease hypocotyl elongation when stimulated (Ahmad and Cashmore, 1996; Ahmad
195 et al., 2002). The blue peak wavelength used in the present study (455 nm), falls in the range of
196 maximal activity of the cryptochrome. Similar reduction of stem length caused by the increase of
197 percent B PF has been reported for cucumber (Hernández and Kubota, 2016), pepper (Brown et
198 al., 1995) and tomato (Liu et al., 2011; Nanya et al., 2012; Wollaeger and Runkle, 2014)
199 seedlings.

200 In the present study, tomato seedling hypocotyl length of 'Komeett' grown under 100B
201 treatment was 8.4 cm and it was comparable than hypocotyl length of seedlings grown under
202 10B:90R treatment (8.0 cm) while both being 34 %, 42 %, 45 %, and 56 % greater than the
203 hypocotyl length of seedlings grown under 20B:28G:52R, 30B:70R, 50B:50R, and 75B:25R
204 treatments, respectively ($P < 0.0001$) (Fig. 2). If cryptochrome stimulation was the main factor
205 affecting hypocotyl length, then seedlings under the 100B treatment should have been the most

206 compact of all treatments; however, in the present study this is not the case. The large hypocotyl
207 length in the 100B treatment can be partially attributed to the phenomenon described as
208 “coaction”. A combination of B light and high R:FR ratio suppress stem extension
209 synergistically (Ahmad and Cashmore, 1997; Casal and Mazzella, 1999; Hernández and Kubota,
210 2016; Wollaeger and Runkle, 2013). Also, cryptochrome mediated responses do not occur in the
211 absence of active phytochrome (Ahmad and Cashmore, 1997; Folta and Spalding, 2001; Neff
212 and Chory, 1998; Whitelam et al., 1993). The lack of active phytochrome in the R absorbing
213 form (Pr) caused by the lack of red light, could have contributed to the inhibition of stem
214 reduction caused by cryptochrome stimulation. Another plausible explanation is the effect of B
215 light on phytochrome far-red absorbing form (Pfr). When Pr is most abundant at the end of the
216 day (EOD), it triggers hypocotyl elongation (Kendrick and Kronenberg, 1994). Sager et al.
217 (1988) used purified rye photochrome to demonstrate that Pfr has a maximal relative absorbance
218 at 730-738 nm peak (far-red light) and that Pfr has an additional relative absorbance peak in the
219 B region with the highest maximal relative absorbance at 400-420 nm. In the presence of EOD
220 R light (all treatments except 100B), the Pfr absorbing form was the most abundant, which
221 prevented stem elongation. However, when R light was removed (100B), the EOD light quality
222 was B (peak: 455nm), which will make the Pr absorbing form more abundant and consequently
223 lowering the suppression of hypocotyl elongation. Hypocotyl elongation by monochromatic B
224 light has been documented in several studies. For example, when used as supplemental lighting,
225 monochromatic B light caused cucumber plants a 46% greater hypocotyl length than did
226 monochromatic R light (Hernández and Kubota, 2015). Under sole-source electrical lighting,
227 cucumber seedlings under monochromatic B light had 69 % and 346 % greater hypocotyl than
228 plants under monochromatic R and 75 % B light, respectively (Hernández and Kubota, 2016).

229 Longer hypocotyl length was observed on dill (*Anethum graveolens*) under EOD B conditions
230 when compared to EOD R (Fraszczak, 2013). Specifically for tomato seedlings, Liu et al. (2011)
231 observed 31% greater plant height under 100B treatment than under 50B:50R treatment (energy
232 basis). Similarly, Kim et al. (2014) showed greater stem length on cherry tomato seedlings
233 grown under 100B than in 100R treatment. In contrast, Wollaeger and Runkle (2014) found no
234 differences in plant height between plants grown under 100B and 50B:50R light treatments. The
235 number of days the plants were under the treatments may have contributed to the differences in
236 results between the Wollaeger and Runkle (2014) study (32 days) and the present study (21 days)
237 since epicotyl extension can compensate for any initial hypocotyl elongation in older plants. In
238 addition, tomato seedlings in the Wollaeger and Runkle (2014) study were kept in the
239 greenhouse (broad-light spectrum) until cotyledon expansion and then moved to the light
240 treatments (*pers comm.* E. Runkle); in contrast to our study, our seedlings were always exposed
241 to their respective light treatments from radicle emergence. The difference on the light quality
242 before cotyledon expansion could have influenced the difference on final hypocotyl length
243 between the present study and the Wollaeger and Runkle (2014) study.

244 *3.2 Effects of percent B:R PF ratios on tomato 'Komeett' stem diameter and leaf area*

245 Stem diameter is in an important morphological characteristic for tomato seedlings, specifically
246 if the seedlings are grown for grafting, producing a thicker stem in less time will allow the
247 propagator to graft sooner. In addition, vegetable transplants with a thicker stem are often
248 preferred in order to reduce stem breakage. In the present study, stem diameter under the
249 50B:50R treatment was 17%, 26%, 37%, and 46% greater than in 75B:25R, CWF, 100B and
250 100R, respectively (Table 2). Stem diameter was not different in the 10B:90R, 20B:28G:52R,
251 30B70R and 50B:50R treatments (Table 2).

252 Plants under treatments emitting both B and R PF showed no differences in leaf area and had 64-
253 72 % greater leaf area than plants grown under monochromatic red and blue treatments (100R
254 and 100B) (Table 2). Research in leaf expansion has shown that red and blue light stimulate leaf
255 expansion by increasing the rate proton efflux on epidermal cells by separate mechanisms (Staal
256 et al., 1994; Volkenburgh, 1999). Blue light directly stimulates the proton pump by direct
257 interaction between the pump and a B-light photoreceptor (Elzenga, 1997), while, R-light
258 influences the proton pump indirectly by modulating calcium and potassium channels
259 (modulation of passive ion conductance) (Elzenga et al., 1997; Staal et al., 1994; Volkenburgh,
260 1999). Furthermore, research has shown that the effects of B and R light in leaf expansion are
261 additive (Staal et al., 1994). In the present experiment, the plants grown under 100R or 100B
262 may have lack the additive effect of leaf expansion present in plants under the treatments
263 containing both B and R PF, which caused the reduction in leaf area. Under supplemental LED
264 lighting in a greenhouse, Gomez and Mitchell (2015) showed that ‘Kommeet’ tomato seedling’s
265 leaf area under 5B:95R and 20B:80R was 41-54 % greater than tomatoes under the 100R
266 treatment.

267

268 *3.3 Effects of B:R PF ratios on tomato ‘Komeett’ chlorophyll and anthocyanin concentration.*

269 Chlorophyll concentration per leaf area was not statistically different between plants in CWF,
270 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R, and 75B:25R (Table 3). In algae, research showed
271 an increase of chlorophyll concentration with the increase of B PF (Jeffrey, 1980; Jeffrey and
272 Vesk, 1981; Vesk and Jeffrey, 1977) and in other crops (Hernández and Kubota, 2014;
273 Hernández and Kubota, 2016; Hogewoning et al., 2010; Matsuda et al., 2007). For example,
274 under sole source lighting and supplemental lighting, cucumber seedlings showed increased

275 chlorophyll concentration with the increase of B PF (Hernández et al., 2016; Hernández and
276 Kubota, 2014; Hogewoning et al., 2010). However, similar to the present study, Wollaeger and
277 Runkle (2014) showed no differences in relative chlorophyll concentration between 100R,
278 25B:25G:50R, 50B:50R in tomato seedlings,. Similarly, Liu et al. (2011) showed no differences
279 in tomato chlorophyll content between 100R, 100B and 50B:50R.

280 Plants under the B:R treatments had an average of 31% and 57% greater chlorophyll
281 content per leaf area than in the 100R and 100B treatments, respectively (Table 3). This response
282 is similar to cucumber responses grown under similar experimental conditions (Hernández and
283 Kubota, 2016; Hogewoning et al., 2010). The lack of a “coaction” effect of cryptochrome and
284 phytochrome could have caused the reduction of chlorophyll biosynthesis under the 100B and
285 100R treatments (Neff and Chory, 1998). Another plausible possibility is the need for a
286 qualitative response to B or R light for normal plant development by plants grown under
287 monochromatic B or R light.

288 Anthocyanin increased with the increase of B PF from 0 % B (100R) up to 75 % B (Fig.
289 3) and anthocyanin concentration was mainly present in the abaxial part of the leaf. Previous
290 research showed that anthocyanin concentration is greater when B light is present and that B
291 light stimulates anthocyanin biosynthesis via the flavonoid biosynthetic pathway by promoting
292 the gene expression of chalcone synthase (CHS) and dihydroflavonol-4-reductase (DFR) (Albert
293 et al., 2009; Giliberto et al., 2005; Meng et al.; Ninu et al., 1999). Specifically for tomato, it was
294 demonstrated that cryptochrome stimulated by B light regulates the biosynthesis of anthocyanin
295 (Giliberto et al., 2005; Ninu et al., 1999). The role of anthocyanin in vegetative tissue is not fully
296 understood. Vegetative tissues often biosynthesize anthocyanin under stress conditions such as
297 low temperatures, nutrient deficiencies, high light, and pathogens (Chalker-Scott, 1999; Dixon

298 and Paiva, 1995); however, in the present experiment, plants were not under stress conditions.
299 Anthocyanin production of the vegetative tissue is attributed to high light conditions. For
300 example, Albert et al. (2009) grew common petunia and a *Lc* petunia expressing *Leaf colour*
301 (*LC*), a bHLH anthocyanin regulator from maize responsible of anthocyanin production in
302 vegetative tissue. Albert et al. (2009) found that plants under high solar light had greater
303 anthocyanin concentration than when grown under low solar light. Further studies have shown
304 that anthocyanin concentration serves as a light-attenuation mechanism to protect lower cells
305 from photo-inhibition (Albert et al., 2009; Gould, 2004; Gould et al., 1995; Hughes et al., 2008).

306 We hypothesize that the accumulation of abaxial anthocyanin driven by the increase of B
307 PF observed in the present study will help tomato seedlings adapt to higher light levels when
308 they are transplanted in the greenhouse or field conditions. Our current research is testing the
309 performance of tomato seedlings with high anthocyanin concentration (grown under high B PF)
310 and compared those to low anthocyanin concentration (grown under low B PF) after transplanted
311 in greenhouses or field.

312

313 *3.4 Effects of B:R PF ratios on net photosynthetic rate, stomata conductance, leaf number, shoot*
314 *fresh mass, shoot dry mass and plant compactness of 'Komeett' tomato*

315 No statistical differences were found between treatments in leaf Pn (P=0.077) and leaf g_s
316 (P=0.094) (Table 3). McCree (1972) quantified the relative quantum yield efficiency (RQE) of
317 growth-chamber grown tomatoes under different light quality (350-725 nm range, 25 nm
318 increments). The tomato RQE curve shows that red light (600-700 nm) has 7 % and 27 % greater
319 RQE than yellow and blue light, respectively. Based on McCree (1972), which reported that B

320 light had lower RQE than red light, it is expected to observe a decrease on leaf Pn with the
321 increase of percent B. However, in the present experiment no significant differences were found
322 between the treatments. For tomato, Nanya et al. (2012) grew seedlings under 10B, 30B and 50B
323 percent B PF (with remaining percent as red) (B: 450 nm peak, R: 660 nm peak, $150 \mu\text{mol m}^{-2}$
324 s^{-1}) and found no differences in leaf Pn when plants were 11 days old; however, 17 day old
325 plants had higher leaf Pn with the decrease of blue PF (10B>30B>50B). The Pn response can
326 explain the growth rate response in Nanya et al. (2012). Similarly, in the present study, for the
327 treatments containing both B and R PF the Pn and *gs* responses match the growth rate responses
328 such as fresh mass, dry mass, leaf number, and chlorophyll concentration. For 100B and 100R
329 Pn and *gs* responses do not match the growth rate responses since these two treatments had lower
330 growth rate than the treatments containing both B and R PF (see section 3.5 for further
331 discussion).

332 For shoot fresh mass no differences were found between plants under the 10B:90R,
333 20B:28G:52R, 30B:70R and 50B:50R (Table 3). Plants under 10B:90R and 50B:50R had 33 %
334 and 38 % greater fresh mass, respectively than plants under the 75B:25R treatment. Plants under
335 the treatments 10B:90R, 20B:28G:52R, 30B:70R and 50B:50R had 62 %, 44 %, 50 %, and 67 %
336 greater shoot fresh mass, respectively than plants under the CWF. Plants in 10B:90R,
337 20B:28G:52R, 30B:70R and 50B:50R had 91 %, 70 %, 76 %, 96 %, and 43% greater shoot fresh
338 mass, respectively than plants in 100R. Plants in 10B:90R, 20B:28G:52R, 30B:70R and 50B:50R
339 treatments had 59 %, 41 %, 47 %, 63 % and 19 % greater shoot fresh mass, respectively than
340 plants in 100B.

341 For shoot dry mass, no differences were detected between plants under the 10B:90R,
342 20B:28G:52R, 30B:70R, 50B:50R and 75B:25R treatments (Table 3). However, Plants under the

343 treatments 30B:70R and 50B:50R had in average 61 %, 150 %, and 109 % greater dry mass than
344 plants under CWF, 100R, and 100B, respectively.

345 For leaf number, no differences were found in plants under 10B:90R, 20B:28G:52R, 30B:70R,
346 50B:50R, 75B:25R and CWF treatments (Table 2). Plants under 30B:70R, 20B:28G:52R and
347 50B:50R had 23 % greater leaf number than plants under 100R and 100B treatments. From the
348 present study, tomato seedlings are able to have comparable growth rate (fresh mass, dry mass,
349 leaf number) under the range of 10% to 50% B PF. Results on growth rate parameters of tomato
350 seedlings under sole-source lighting vary in the literature. For example, Nanya et al. (2012)
351 showed greater shoot dry mass under the 10B:90R treatment than under the 50B:50R treatment.
352 Liu et al. (2011) showed no differences between plants in the 100R and in 50B:50R treatment.
353 Wollaeger and Runkle (2014) showed greater dry mass under the 100R treatment than 50B:50R
354 and 100B treatments. None of the previous studies have tested a full range of B:R photon flux
355 ratios; however, if growth rate is the main factor considered for seedling production under sole-
356 source light conditions, based on previous studies and the present study, it is recommended a
357 treatment containing low B and high R PF (i.e 10B:90R). However, other morphological (plant
358 height), physiological (chlorophyll concentration) and potential plant disorders (intumescences)
359 should be considered to find the most versatile spectrum.

360 No significant differences were found in plant compactness between plants in 20B:28G:52R,
361 30B:70R, 50B:50R, 75B25R and CWF treatments (Table 2). Plants under 30B:70R had 42%
362 greater plant compactness than in 10B:90R treatment (Table 2). Plant compactness, which is the
363 relationship of dry mass and plant height, is another important parameter to determined seedling
364 quality. A transplant with high dry mass and short height is considered as a high quality seedling
365 (Currey et al., 2012; Vu et al., 2014). If plant compactness is used as the main parameter to select

366 light quality for the production of tomato seedlings, we recommend to increase the B PF
367 (decrease stem length) to no greater than 50%B to maintain high growth rate (fresh mass, dry
368 mass, leaf number) and maintain a short plant (compactness).

369 *3.5 Summary for 'Kommeet' physiological responses*

370 In the present study, important parameters driving plant growth such as Pn, *gs*, leaf area
371 (light intersection), and chlorophyll concentration were not statistically different between the
372 treatments containing both B and R PF. This resulted in no-significant differences in plant
373 growth in the LED treatments containing B, G and R PF (Table 2, 3). The main two factors that
374 were affected quantitatively by the increase of B PF were hypocotyl length (plant height) and
375 anthocyanin concentration in leaves. The decrease in plant height with the increase of B PF led
376 to the differences in plant compactness between plants in 10B:90R and 30B:70R. Plants in 100B
377 and 100R had lower growth rate than plants under the treatments containing both B and R PF;
378 however, plants in 100R, 100B and the other LED treatments (B:G:R) showed no significant
379 differences in Pn, and *gs*. In addition, after calculating the specific leaf area (SLA, leaf area per
380 unit dry mass) no significant differences were detected between any of the treatments
381 ($P=0.8685$). No significant differences between any of the treatments in Pn, *gs*, and SLA,
382 concludes that plants in all treatments have similar expected return on captured resources, in
383 other words, similar capacity for growth rate (Westoby, 1998; Wilson et al., 1999). However,
384 plants under the 100R and 100B had lower dry mass and fresh mass than other treatments. This
385 can be explained by morphological traits since plants under 100R and 100B had lower leaf area
386 and lower leaf number; which led to lower light intersection and consequently lower growth rate.

387 *3.6 Effects of B:R PF ratios on intumescence for 'Beaufort' tomato*

388 Severe intumescence symptoms led to leaf chlorosis and leaf abscission, which greatly affected
389 ‘Beaufort’ growth rate. For example, plants under the CWF treatment (no intumescences) had
390 84% to 93% greater number of leaves, 116% to 237 % greater fresh mass, and 103% to 340%
391 greater shoot dry mass than plants under the B:R treatments (data not shown). The 97% to 100%
392 of plants in 10B:90R, 20B:28G:52R, 30B:70R, 50B:50R and 75B:25R exhibited intumescences
393 symptoms (Table 4). Plants under these treatments had 31-35% greater intumescence ratio than
394 plants under 100R (Table 4). Plants grown under the combination of B and R PF had 51% to
395 66% leaves with intumescences (Fig. 4). Plants under 10B:90R, 20B:28G:52R, 30B:70R, and
396 50B:50R had 86% to 223% greater ratio of intumescences in stem (most severe symptom) than
397 plants under 100R and 75B:25R treatments (Table 4). In the present study, the increase percent
398 B PF in the growing spectrum had an inhibitory effect on the development of intumescences
399 (Fig. 4). The incidence of intumescences on leaves (*ratio of leaves with intumescences*) linearly
400 decreased with the increase of percent B PF from the 10% B to 75% B ($P=0.0104$) (Fig. 4).
401 Also, the incidence of intumescence in the stem (*ratio of plants with intumescences in stem*) was
402 significant lower in the 75B:25R treatment and in 100R treatment. Plants under CWF and 100B
403 had no intumescences in leaves or stem (Fig. 4, Table 4).

404 Intumescences in tomatoes are described as a non-pathogenic disorder characterized by
405 hypertrophy of spongy parenchyma, palisade, and epidermis cells (Lang and Esther Struckmeyer,
406 1983; Lang and Tibbitts, 1983; Morrow and Tibbitts, 1988). Intumescences in tomatoes are
407 triggered by spectral quality, and high relative humidity can increase the severity of the
408 symptoms (Lang and Tibbitts, 1983; Morrow and Tibbitts, 1988). Intumescence symptoms are
409 known to be more common on wild type tomato (*S. habrochaites*). Tomato rootstock ‘Beaufort’
410 used in the present study is a cross between *Solanum lycopersicum* and *S. habrochaites*, which

411 explains the higher incidence of intumescence symptoms compared to ‘Komeett’ (*Solanum*
412 *lycopersicum*). Research showed that the absence of UV-B radiation is the main cause for
413 intumescences development (Lang and Tibbitts, 1983). This is supported by the present study
414 since the plants under the CWF treatment received a small amount of UV-B radiation coming
415 from the fixture (aprox $0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$, 280-320 nm). Research also showed that far-red light
416 could mitigate intumescence development (Eguchi et al., 2016a; Eguchi et al., 2016b; Morrow
417 and Tibbitts, 1988). On a parallel study, we examined the effect of end-of-day far red (EOD-
418 FR) on intumescence injury of ‘Beaufort’, and demonstrated that EOD-FR at a very low dosage
419 ($1 \text{ mmol m}^{-2} \text{d}^{-1}$) significantly decreases intumescence development compared to a 10B:90R
420 treatment without EOD-FR treatment ((Eguchi et al., 2016a; Eguchi et al., 2016b).

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

432 In a parallel study, we presented spectra effectively suppressing intumescence
433 development in tomato rootstocks ‘Beaufort’ and ‘Maxifort’ without compromising desirable

434 seedling quality (Eguchi et al., 2016b). The spectrum consisted on the combination of low
435 dosage EOD-FR ($1-4 \text{ mmol m}^{-2} \text{ d}^{-1}$) and high percent B PF (50B:50R or 75B:25R) during the
436 growing spectrum, which can be used to grow tomato cultivars that are known to develop
437 intumescence.

438 *3.7 Tomato seedling response to the addition of green light*

439 The 20B:28G:52R treatment had G light as a part of the spectrum. The total percent of G PF was
440 28%, and B and R consisted of 20% and 52% PF, respectively. In the present study, the
441 physiological plant responses to the 20B:28G:52R treatment can be explained by the percent B
442 PF, since the addition of G light did not have any effects on plant responses (shoot fresh mass,
443 shoot dry mass, leaf number, leaf area, hypocotyl length, stem diameter, chlorophyll
444 concentration, anthocyanin, g_s , and leaf Pn)

445 Plant responses to G light are species specific. For example, Kim et al. (2006) concluded
446 that 24% G increased lettuce (*Lactuca sativa* 'Waldmann's Green') growth, and more than 50%
447 G reduced lettuce growth. Johkan et al. (2012) grew lettuce under fluoresce light and under
448 different G wavelengths (510, 520, 530 nm), under different light intensities ($100, 200, 300 \mu\text{mol}$
449 $\text{m}^{-2} \text{ s}^{-1}$) and found that plants grown under lower ($100 \mu\text{mol m}^{-2} \text{ s}^{-1}$) light intensity had greater
450 dry mass under fluorescence light; however when the intensity increased, plants under G light
451 had comparable shoot dry mass ($300 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and higher root dry mass ($200 \mu\text{mol m}^{-2} \text{ s}^{-1}$)
452 under the 510 nm G treatment. Ma et al. (2015) grew potato plantlets (*Solanum tuberosum*) in
453 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
454 treatments had greater dry mass, stem diameter, and health index ([stem diameter/stem
455 height]*dry mass) than plants under the B:R treatments. Future research should test the effect of

456 G light on tomato seedlings at a higher PPF ($300 \mu\text{mol m}^{-2} \text{s}^{-1}$) to identify any potential increased
457 in growth rate or improved morphology.

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

463 Green light is also known to increase hypocotyl length in several plant species (Bouly et
464 al., 2007; Wang and Folta, 2013; Wang et al., 2013). However, the hypocotyl response to G light
465 is also species specific. For example, in cucumber seedlings, the addition of G light to a B:R
466 spectrum did not have an effect on hypocotyl length (Hernández and Kubota, 2016). In tomato,
467 Wollaeger and Runkle (2013) found that plant height under a 50G:50R treatment was around
468 50% greater than plant height under 25B:25G:50R, 50B:50G and 50B:50R. This can be
469 attributed to the absence of B light in the 50G:50R treatment since, from the present experiment,
470 it is evident that the increase of B light decreases plant height (Fig. 2). Liu et al. (2011) found no
471 differences between cherry tomato plants grown under B:R and B:G:R; however, plants grown
472 under G light only had 64% and 89% greater plant height than plants in B:R and B:G:R,
473 respectively.

474 *3.8 Cool white fluorescent and LED comparison*

475 Fluorescent lamps have been a widely used technology for the production of vegetable seedlings
476 under indoor-production. For example, grafted plant propagators in Japan and US use fluorescent
477 tubes for the production of tomato and cucurbit grafted seedlings (C. Kubota and J. Jackson *pers*

478 *comm*). Cool white fluorescent fixtures have a broad spectrum (Fig. 1) with percent PF of 19B
479 (400-500nm), 48G (500-600nm) and 32R (600-700 nm) (based on light measurements of the
480 CWF used in the present study), which is suitable to grow plants. Fluorescent tubes are also
481 easily available and inexpensive. Below we present a brief comparison of CWF and LEDs for the
482 indoor production of tomato seedlings based on the results from this experiment.

483 Table 5 shows the pairing comparisons of tomato seedling's physiological responses
484 when grown under CWF and different percentages of B:R PF using LEDs. The main differences
485 between CWF and some of the LED treatments containing B:R were on plant hypocotyl length,
486 stem diameter, fresh mass, and dry mass. Plants under the LED treatments had 16-53% longer
487 hypocotyl length than plants under the CWF treatment (Table 5). However, plants under the
488 30B:70R and 50B:50R LED treatments had 39% and 36% greater dry mass, and 33% and 40 %
489 greater fresh mass than plants in CWF treatment, respectively. In summary, plants under the
490 30B:70R and 50B:50R LED treatments had greater growth rate, than plants under CWF. In order
491 to further compare the two technologies, we estimated the electrical efficacies (g kWh^{-1}) between
492 commercially available LEDs and High-Output fluorescent lamps (HO-FL), which have one of
493 the highest advertised efficiencies (lumen per watt). Current LED indoor technology is
494 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,
495 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-
496 HO). Using these efficiencies, we calculated the areal-power-consumption (APC) and fixture-
497 growing-efficacy (FGE). LEDs have 172% greater growing efficacy than HO-FL (Table 6).

498 Summarizing in terms of efficiencies and growing efficacy, current LEDs are the technology
499 of choice for indoor-production. However, initial capital costs need to be considered before

500 making the technology adoption since the LED fixtures used in this estimation are 3.2 times
501 more expensive than the HO-FL.

502 4.Conclusion

503 Plants under higher percentages of B PF (up to 75% B PF) had desirable characteristics such as
504 shorter stem length, greater plant compactness, and lower intumescence severity. However,
505 growth rate parameters such as fresh mass, dry mass and number of leaves were comparable
506 between the treatments containing both B:R PF (10B:90R, 20B:28G:52R, 30B:70R, 50B:50R,
507 75B:25R). Plants grown under monochromatic B and R light showed lower growth rate and
508 undesirable plant height (100R,100B). Plants under CWF had comparable plant compactness to
509 that of best LED treatments; however, also had lower dry mass than in 30B:70R, 50B:50R LED
510 treatments and lower growing efficacy (g kWh^{-1}). In summary, 30B:70R, 50B:50R were the best
511 spectrums to produce tomato seedlings under VF conditions; however, plant quality under CWF,
512 10B:90R, 20B:28G:52R, 75B:25R is also acceptable.

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

517

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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)

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

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

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

Light treatment	Shoot fresh mass (g)	Shoot dry mass (g)	Chlorophyll per leaf area (g m ⁻²)	Pn $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	<i>gs</i> $\text{mmol m}^{-2} \text{ s}^{-1}$
CWF	1.55 \pm 0.77 c	0.102 \pm 0.057 bcd	0.265 \pm 0.046 a	1.95 \pm 0.69 a	47.0 \pm 23.6 a
100R	1.32 \pm 0.52 c	0.066 \pm 0.032 d	0.218 \pm 0.021 b	3.07 \pm 0.38 a	94.2 \pm 47.9 a
10B:90R	2.52 \pm 0.86 a	0.147 \pm 0.072 ab	0.264 \pm 0.024 a	2.23 \pm 1.11 a	82.5 \pm 66.7 a
20B:28G:52R	2.25 \pm 0.85 ab	0.134 \pm 0.070 ab	0.294 \pm 0.059 a	2.28 \pm 0.79 a	94.5 \pm 52.0 a
30B:70R	2.33 \pm 1.05 ab	0.168 \pm 0.091 a	0.284 \pm 0.043 a	1.85 \pm 0.87 a	51.8 \pm 14.6 a
50B:50R	2.60 \pm 0.83 a	0.161 \pm 0.066 a	0.296 \pm 0.058 a	2.1 \pm 0.33 a	68.0 \pm 41.8 a
75B:25R	1.89 \pm 0.81 bc	0.120 \pm 0.068 abc	0.298 \pm 0.043 a	2.55 \pm 0.49 a	133.7 \pm 82.5 a
100B	1.59 \pm 0.71 c	0.079 \pm 0.048 cd	0.184 \pm 0.081 b	1.75 \pm 0.86 a	63.3 \pm 36.8 a

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

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

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50 **Table 5.** Comparison of ‘Komeett’ physiological responses under cool white fluorescent (CWF) and LED light treatments. (-)
 51 Signifies how many percent the respective LED treatment is lower than the CWF treatment, (+) signifies how many percent the
 52 respective LED is greater than the CWF treatment and (=) signifies no differences between CWF and the respective LED treatment.
 53 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 (μmol CO ₂ m ⁻² s ⁻¹)	CWF	=	=	=	=	=	=	=
g _s (mmol m ⁻² s ⁻¹)	CWF	=	=	=	=	=	=	=
Plant compactness (g cm ⁻¹)	CWF	- 57%	=	=	=	=	=	- 56%

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66 **Table 6.** Estimation of ‘areal power consumption’ and ‘fixture growing efficacy’. Tomato ‘Komeett’ seedlings were grown under 100
 67 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photon flux, 0.0506 m^2 growing area, 18 h photoperiod, 21 growing days, and 700 plants m^{-2} density. ‘Fixture growing
 68 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

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

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

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

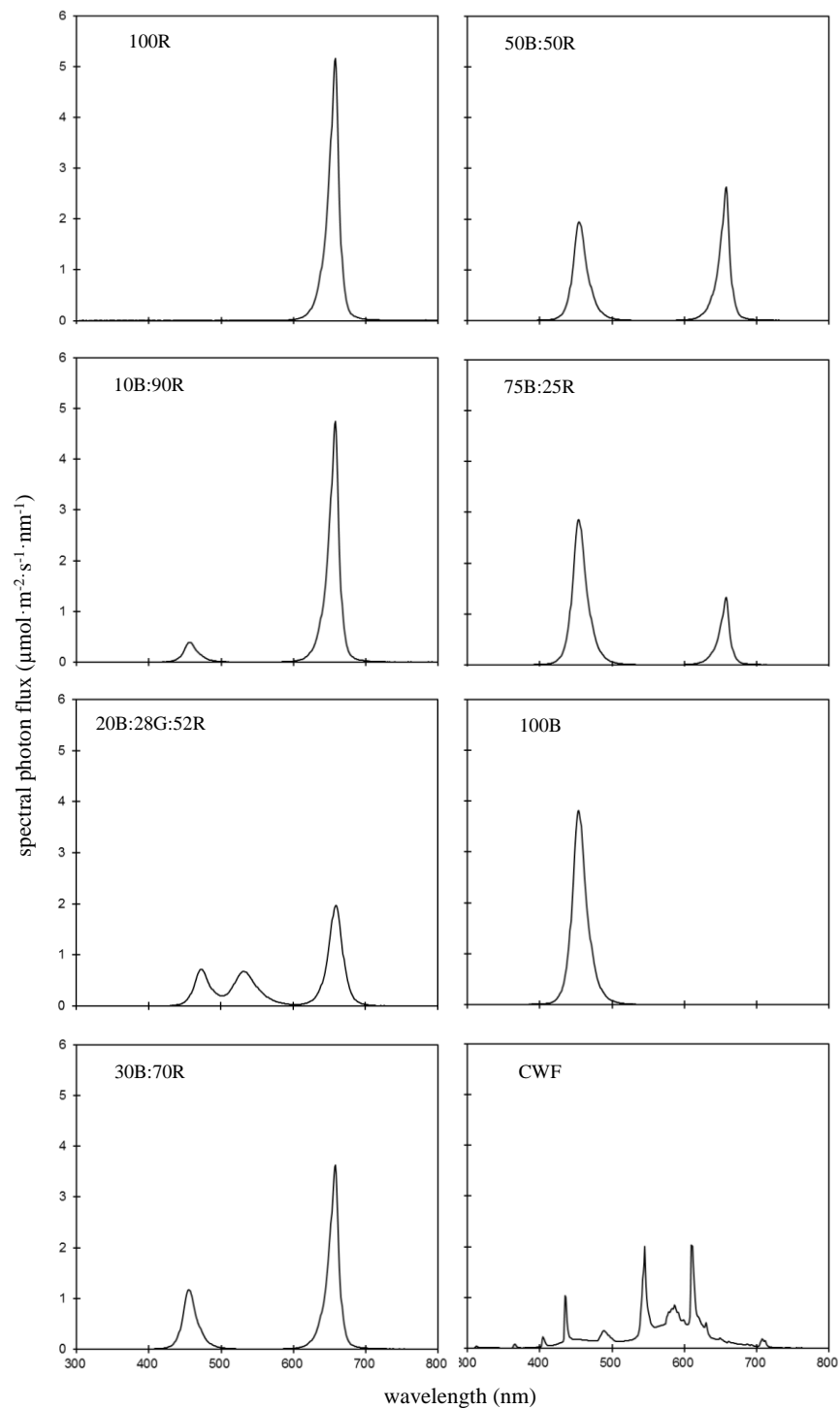


Fig 1. Spectral distribution of light treatments. B represents the blue PF ratio, G the green PF ratio and R the red PF ratio for each LED treatment. CWF represents the spectrum of the cool white fluorescent control. Spectra were measured using a spectroradiometer at the beginning and end of each repetition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

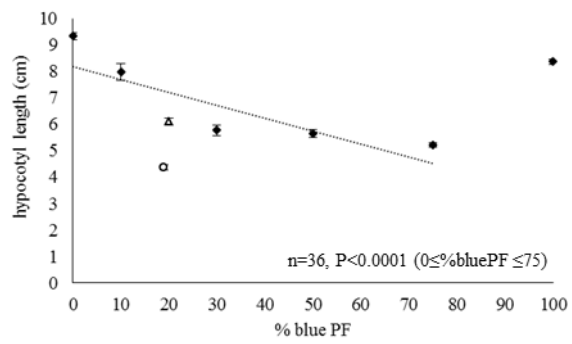


Fig 2. Effect of increase percent blue photon flux on hypocotyl length of tomato seedlings 'Komeett'. Diamonds represent the treatments containing B and R PF. Triangle represents the 20B:28G:52R treatment. Circle represents the CWF control treatment. CWF is not part of the regression analysis. Line represents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

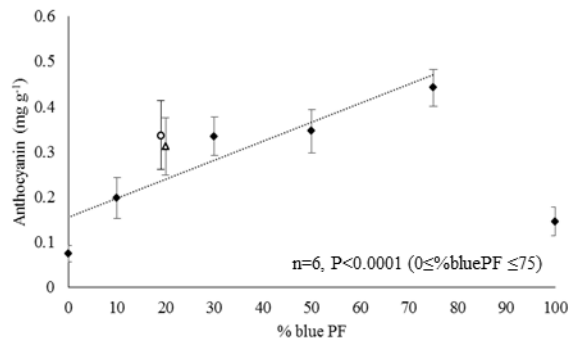


Fig 3. Effect of increase percent blue photon flux on the leaves anthocyanin concentration of tomato seedlings 'Komeett'. Diamonds represent the treatments containing B and R PF. Triangle represents the 20B:28G:52R treatment. Circle represents the CWF control treatment. 100B is not part of the regression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

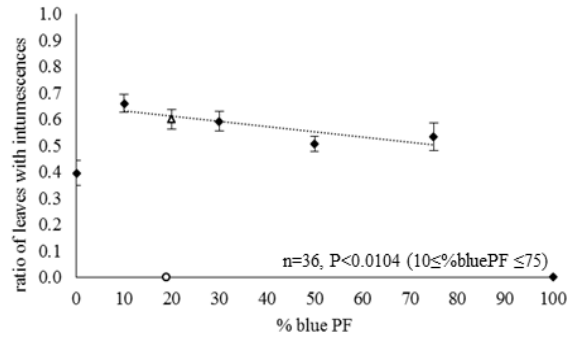


Fig 4. Effect of increase percent blue photon flux on the ratio of leaves with intumescences in tomato seedlings 'Beaufort'. Diamonds represent the treatments containing B and R PF. Triangle represents the 20B:28G:52R treatment. Circle represents the CWF control treatment. Line represents statistically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