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Yield, resource use efficiency or flavour: trade-offs of varying blue-to-red lighting ratio in urban plant factories --Manuscript Draft--

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Abstract:	<p>With increasing urbanisation and consumer concerns over food miles, indoor urban plant factories are gaining popularity. These offer precise regulation of the crop environment, but optimal light requirements vary between species and according to grower specifications. Here we introduce a novel assessment framework to optimise light quality in urban plant factories accounting for yield, resource use efficiency and flavour, factors that have only been studied separately in previous research. Yield, water and energy use efficiency and flavour of sweet basil (<i>Ocimum basilicum</i> cv. Genovese) and tomato (<i>Solanum lycopersicum</i> cv. Micro-Tom) were determined for plants grown supplied with 100% blue, 66% blue + 33% red, 33% blue + 66% red, or 100% red lighting. In both species, 66% red and 100% red optimised water use efficiency and energy use respectively. For basil, 100% blue light maximised leaf biomass, while 66% red enhanced leaf flavouring volatiles. In Micro-Tom, all treatments produced similar fruit biomass, but 100% red light enhanced flavour-related volatiles in foliage. By considering trade-offs between yield, efficiency and flavour, growers can select bespoke lighting treatments to optimise their product according to specific market demands and minimise environmental impacts.</p>

1 Yield, resource use efficiency or flavour: trade-offs of varying blue- 2 to-red lighting ratio in urban plant factories

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10 Abstract

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12 factories are gaining popularity. These offer precise regulation of the crop environment, but
13 optimal light requirements vary between species and according to grower specifications. Here
14 we introduce a novel assessment framework to optimise light quality in urban plant factories
15 accounting for yield, resource use efficiency and flavour, factors that have only been studied
16 separately in previous research. Yield, water and energy use efficiency and flavour of sweet
17 basil (*Ocimum basilicum* cv. Genovese) and tomato (*Solanum lycopersicum* cv. Micro-Tom)
18 were determined for plants grown supplied with 100% blue, 66% blue + 33% red, 33% blue +
19 66% red, or 100% red lighting. In both species, 66% red and 100% red optimised water use
20 efficiency and energy use respectively. For basil, 100% blue light maximised leaf biomass,
21 while 66% red enhanced leaf flavouring volatiles. In Micro-Tom, all treatments produced
22 similar fruit biomass, but 100% red light enhanced flavour-related volatiles in foliage. By
23 considering trade-offs between yield, efficiency and flavour, growers can select bespoke
24 lighting treatments to optimise their product according to specific market demands and
25 minimise environmental impacts.

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27 **Keywords:** Crop improvement, Light emitting diodes (LEDs), *Ocimum basilicum*, Plant
28 factories, *Solanum lycopersicum*.

29 **Introduction**

30 Increasing urbanisation has prompted interest in urban agriculture to reduce the length of food
31 supply chains (Satterthwaite et al., 2010) and promote urban ecology and sustainable
32 development (Nogueira-McRae et al., 2018). Urban greenhouses and plant factories with
33 artificial lighting (PFALs) create controlled environments, increasing crop production, and
34 improving land, water, energy and nutrient use efficiency compared with outdoor production
35 (Ting et al., 2016; Touliatos et al., 2016). From the grower's perspective, controlled-
36 environment urban agriculture involves more than simply generating biomass; resource
37 management and efficiency, target market, final desired product and post-harvest processing
38 are also critical to the economics of the business (Ting et al., 2016). Modern urban agriculture
39 increasingly uses artificial light from light emitting diodes (LEDs) as they have more efficient
40 energy to photon conversion, customisable spectra, long service life, and low maintenance costs,
41 improving crop productivity and profitability (Bardsley et al., 2014; Hayashi, 2016; Kozai,
42 2016).

43 The light environment affects plant morphology, canopy structure, biomass, reproduction and
44 metabolite production (hence nutrient and flavour quality) differently for different species and
45 genotypes (Fankhauser and Chory, 1997; Ouzounis et al., 2016). Thus, an individual PFAL can
46 be customised for specific crops and specific business models, e.g., to improve profitability, to
47 meet specific market sector preferences or to enhance the nature of industrial products (Elevitch
48 and Love, 2013; Fisher and Runkle, 2004). Urban PFALs can produce whole plants or raw
49 products (e.g., lettuce leaves), but also specific components associated with further financial
50 returns such as essential oils, herbal supplements, soft fruits, and nutritional or pharmaceutical
51 products (Fang, 2016; Hayashi, 2016).

52 Indoor cultivation of green leafy vegetables and fruiting crops enables control of lighting to
53 optimise yield, resource use efficiency and flavour according to the target market. Both light

1 54 intensity (the photosynthetic photon flux density, PPF), and the spectral distribution of UV-
2 55 B (280-315nm), UV-A (315-400 nm), blue (400-500 nm), red (620-700 nm) and far-red (700-
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4 56 850 nm) light affect plant growth and development (Higuchi and Hisamatsu, 2016). LEDs of
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6 57 differing wavelengths can be used to control plant morphogenesis and enhance the production
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8 58 of secondary metabolites, increasing efficiency and adding value to crops by enhancing nutrient
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10 59 content and/or taste (Kozai and Zhang, 2016; Lu and Mitchell, 2016). Monochromatic blue and
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12 60 red light induce specific light signalling responses in plants, significantly affecting
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14 61 morphological, physiological and biochemical processes through alterations in photosynthetic
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16 62 activities and/or photoreceptors (Higuchi and Hisamatsu, 2016). Blue light is mainly absorbed
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18 63 by phototropins, chloroplasts and cryptochromes causing responses including phototropism,
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20 64 enhanced efficiency of chlorophylls and carotenes (Liu et al., 2012), and stomatal opening
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22 65 (Shimazaki et al., 2007). Red light is absorbed by phytochromes, regulating major
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24 66 developmental transitions (e.g. germination and flowering) (Smith, 1995), and plant vegetative
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26 67 and reproductive growth . Blue and red lights can act synergistically to amplify their individual
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28 68 signalling effects (Fankhauser and Chory, 1997).

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32 69 Changing the ratio of blue-to-red light has differing effects on plant growth and development
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34 70 both within and between species (Lu and Mitchell, 2016; Olle and Viršile, 2013). Maximal
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36 71 stomatal conductance of sweet basil (*Ocimum basilicum*) occurs under mixed ~33% red and
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38 72 66% blue lighting (Pennisi et al., 2019), while increasing the proportion of blue light enhances
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40 73 biomass production, stomatal conductance and net photosynthesis rate of other species
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42 74 (Hogewoning et al., 2010; Matsuda et al., 2004). However, the response to red light appears
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44 75 less uniform across species. Compared to monochromatic or high percentage blue light, high
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46 76 proportions ($\geq 50\%$) of red light reduced basil yield by restricting leaf area and biomass
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48 77 (Carvalho et al., 2016; Piovene et al., 2015), while decreases in blue proportions restricted
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50 78 tomato stomatal conductance (Lanoue et al., 2017), but had no effect on shoot biomass of either
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52 79 basil (Pennisi et al., 2019) or tomato (*Solanum lycopersicum*) (Hernández et al., 2016). Thus,
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54 80 the ratio of blue to red light affects leaf physiology and overall growth in complex ways.

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57 81 Different wavelengths of light also appear to alter secondary metabolism, associated with crop
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1 82 nutrient and volatile composition, but reports are inconsistent (Olle and Viršile, 2013; Shimizu,
2 83 2016) and it should be noted that the volatiles associated with olfactory quality (“nose”) of
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4 84 vegetables or fruits often differ from gustatory quality (“flavour”) (Klee, 2010; Tieman et al.,
5
6 85 2017). Foliar volatile emissions, a major product of secondary metabolism, are associated with
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8 86 aroma and flavour (Bertoli et al., 2013; Kim et al., 2014) while the aromatic composition of
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10 87 ripening fruits or volatile content of tissue reflects flavour or quality (Selli et al., 2014). The
11
12 88 main aromatic compounds are terpenoids (e.g. monoterpenes: linalool, sesquiterpenes: α -
13
14 89 bergamotene) and oxygenated terpenoids (e.g. eugenol) (Carvalho et al., 2016; Selli et al.,
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16 90 2014), and flavour is also dependent on the concentration, emission rate, and composition of
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18 91 aromatic compounds (Mulder-Krieger et al., 1988). Combinations of blue and red light
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20 92 enhanced aromatic volatile emissions from sweet basil compared to monochromatic light
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22 93 (Carvalho et al., 2016), but the reverse was found in tea (*Camellia sinensis*) (Fu et al., 2015).
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24 94 Basil leaves grown under combined red and blue light had a higher essential oil content than
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26 95 those grown under white LEDs (Aldarkazali et al., 2019), but long-term treatment (70 days)
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28 96 with monochromatic LEDs (blue or red) is also reported to promote essential oil production
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30 97 (Amaki et al., 2011). Short-term exposure to red light during the fruiting stage altered fruit
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32 98 volatile profile in tomato (Colquhoun et al., 2013), enhancing the flavour (Tieman et al., 2012).
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34 99 Thus there is scope to select specific lighting treatments to enhance product “quality”.

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38 100 Red-rich LEDs are currently used in most facilities as they have low initial and operating
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40 101 (energy) costs (Kozai and Zhang, 2016) e.g. high photosynthetic photon efficiency (Ibaraki,
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42 102 2016). Water and nutrient use efficiency (WUE, NUE) depend on physiological (e.g. stomatal
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44 103 and metabolic) characteristics , and although relatively high (and constant) across PFALs, can
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46 104 still be improved through lighting choice (Brandon et al., 2016). Increasing energy costs, the
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48 105 location of PFALs in the urban environment with high water costs and consumer demand for
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50 106 low environmental footprint may prompt growers to prioritise the efficiency of their operation.
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53 107 Previous studies of crop responses to different LED lights in indoor controlled environments
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55 108 have generally focused on a single factor (crop productivity, resource use efficiency, and/or
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57 109 quality). Relatively few have simultaneously investigated these factors, and differences in
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1 110 experimental conditions, research facilities and interests have resulted in inconsistent
2 111 conclusions and recommendations (Carvalho et al., 2016; Lanoue et al., 2017; Pennisi et al.,
3 112 2019) with most of the data from plant factories and companies not publicly accessible. There
4 113 is a clear need, therefore, for a flexible evaluation framework to assist the grower in optimising
5 114 light conditions for indoor crop cultivation.

6 115 Here we introduce such a framework that aim to determine the optimum ratio of blue-to-red
7 116 LED light for tomato (*Solanum lycopersicum* cv. Micro-Tom) and sweet basil (*Ocimum*
8 117 *basilicum* cv. Genovese) for: 1) **yield** through morphological changes; 2) **resource use**
9 118 **efficiency** taking energy and water use efficiencies as examples; and 3) **flavour**, here using
10 119 leaf-level volatile emissions as a proxy. This framework allows growers to identify the LED
11 120 combination(s) most suited to their specific product requirements.

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13 122 **2. Methods**

14 123 **2.1. Plant materials and growth conditions**

15 124 Fifty seeds per treatment of sweet basil (*Ocimum basilicum* cv. Genovese) and tomato (*Solanum*
16 125 *lycopersicum* cv. Micro-Tom) were sown one seed to a pot (11 cm top, 9 cm base, 8.4 cm height)
17 126 with 0.5 L Levington® Advance M3 compost (ICL Everris Ltd, UK). They were germinated
18 127 and grown in a controlled environment growth facility at Stockbridge Technology Centre
19 128 (Cawood, Selby, UK). After three weeks, outliers were removed leaving a minimum of 40
20 129 morphologically uniform seedlings, and were randomised into one rack for each treatment. Two
21 130 batches of basil plants were sown for each treatment and treated as independent experiments
22 131 for (a) morphological assessment; and (b) gas exchange and volatile sampling, considering the
23 132 short growth cycle of basil.

24 133 The hydroponic growth racks were lit with mixed LED lighting and maintained at constant
25 134 temperature (20±2 °C) and relative humidity (60±10%). Hydroponic irrigation was initially
26 135 supplied using an ebb and flow system with tap water every four days, gradually increasing to

1 136 daily. Plants were rotated every two weeks in racks. Philips GreenPower® LED research
2 137 module strips (Philips Ltd, UK) were installed on the top of each rack, 40 cm above the bench.
3
4 138 Racks were irradiated for 14h from 6:00 a.m. to 8:00 p.m. using combinations of blue (400-500
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6 139 nm) and red (600-700 nm) LEDs. The four treatments were 100% blue (B), 66% blue + 33%
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8 140 red (BR), 33 % blue + 66% red (RB) and 100% red (R). The total photon flux density at leaf
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10 141 level height ranged from 115 to 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$ according to leaf distance to the lighting
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12 142 module, and was constant across treatments. The distribution of quantum energy (Figure S1)
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14 143 was measured using a Jaz spectrometer (Ocean Optics Inc, UK), the spectral distributions are
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16 144 consistent in racks and shown in Table S1 together with the average vertical profile.

20 145 **2.2. Morphological measurements**

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23 146 Morphological measurements of plant height (H), total leaf area (LA) and fresh/dry weight
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25 147 (FW/DW) of leaf and stem (basil, tomato), and fruit (tomato), were recorded following
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27 148 destructive harvesting of 9-10 replicates weekly from Week 3 for basil and fortnightly from
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29 149 Week 5 for Micro-Tom (reflecting the different growth rates of the two species). Plant height
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31 150 was measured from soil surface to shoot apex using a tape measure. Leaf area was determined
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33 151 using a LI-3100C Leaf Area Meter (LI-COR, UK). Sampling continued for 6 weeks for basil
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35 152 and 13 for tomato. Harvest index (HI) was calculated as leaf to shoot (including leaf and stem)
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37 153 dry mass for basil, and fruit to shoot (including leaf, fruit, and stem) dry mass for Micro-Tom.

41 154 **2.3. Leaf-level gas exchange and resource use efficiency**

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44 155 Physiological responses and volatile emissions were sampled in-situ for two consecutive weeks
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46 156 in both species (Weeks 4 and 5 for basil, and 6 and 7 for Micro-Tom). The newest fully
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48 157 developed leaf from each of 3 randomly selected replicates per treatment was sampled using a
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50 158 Li-6400XT (Li-COR Inc., USA), three hours after the lights were switched on. The leaf was
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52 159 placed in a 2 x 3 cm clear-top chamber under conditions that closely replicated the growing
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54 160 environment (leaf temperature 22°C, relative humidity 50-60%, and CO₂ concentration 400 μL
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56 161 L⁻¹). Following a 5-minute period of stabilisation, net photosynthesis (*P_n*), stomatal
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58 162 conductance (*G_s*) and transpiration rates (*T_r*) were logged. The Li-6400XT cuvette remained

1 163 on the leaf for a further 15 minutes to finish volatile sample collection. Any tomato leaves
2 164 insufficiently large to fill the chamber were photographed in-situ and the sampled leaf area
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4 165 subsequently calculated using Image J software (Schneider et al., 2012). Water use efficiency
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6 166 was estimated as instantaneous water-use-efficiency (iWUE) defined as the ratio of
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8 167 photosynthesis to transpiration. Energy efficiency was estimated as the relative energy usage
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10 168 based on the power consumption of LED modules from manufacture's product manual (Royal
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12 169 Philips N.V.; 2015).

16 170 **2.4. Volatile sampling and analysis**

18 171 Simultaneously with the gas exchange measurements, samples of the chamber headspace gas
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20 172 were drawn from the Li-6400XT outlet and collected in stainless steel thermal desorption
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22 173 sorbent tubes (Markes International Ltd, Llantrisant, UK) packed with 0.2 g Tenax® Porous
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24 174 Polymer and 0.1 g Carbopack™ Adsorbent matrix (Sigma Aldrich Ltd, UK). Two litres of air
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26 175 were drawn through at a flow rate of 100 ml min⁻¹. The volatile samples were subsequently
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28 176 thermally desorbed from the tubes using an Auto Thermal Desorber (TurboMatrix150,
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30 177 PerkinElmer, Beaconsfield, UK) and concentrated in a cryo-trap prior to injection into a Gas
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32 178 Chromatograph-Mass Spectrometer (Autosystem XL-TurboMass Gold; PerkinElmer,
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34 179 Beaconsfield, UK) following the protocol established by Harley et al. (2003) and Hellén et al.
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36 180 (2012). Calibration standards containing a mixture of 14 common terpenoids were included
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38 181 with each batch of samples analysed to allow positive identification and quantification of
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40 182 chromatograph peaks. Full details of the system settings and uncertainties of the method are
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42 183 given in the Supplementary Material. Compounds were identified against the standards and by
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44 184 comparison with known spectra available in the NIST 2008 Library. The mass of each
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46 185 compound was determined by comparing the chromatograph peak area against those of the
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48 186 calibration standards following the methodology developed for biogenic volatiles by Ruiz-
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50 187 Hernández et al. (2018) (Method 2).

55 188 **2.5. Assessment framework**

58 189 A framework was developed, using the measured data, to enable growers to evaluate the

1 190 performance of the different treatments against three key factors: (1) yield; (2) efficiency; (3)
2 191 flavour. The framework uses total leaf area and leaf biomass (basil), fruit biomass (tomato), as
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4 192 measures of **yield**; iWUE and relative energy usage as proxies for production **efficiency** and
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6 193 potential cost; headspace concentration of total volatile and aroma compounds as an indicator
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8 194 of crop **flavour**. Fig. 1 describes each factor of the assessment framework and the commercial
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10 195 implications. Individual growers can then weight each indicator in the framework according to
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12 196 the market requirements for their products, and hence select the optimum LED lighting
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14 197 conditions to best meet these requirements.
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18 198 **2.6. Data analysis**

19 199 All statistical analyses were performed in SPSS® 25. A General Linear Model with one-way
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21 200 ANOVA with Bonferroni correction and Tukey adjustment was applied to the variances from
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23 201 the morphological, gas exchange and volatile concentrations in each single rack between
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25 202 treatments, and two-way ANOVA for treatments x sampling weeks interactions. Error bars
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27 203 indicate the standard error of mean. Significant differences were taken to be $p < 0.05$.
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32 204 33 34 35 205 **3. Results**

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38 206 There were no significant physiological light response differences between two sampling weeks
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40 207 for both species, as well as no morphological differences in Week 5 and 6 for basil, and Weeks
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42 208 7-13 for Micro-Tom (data not shown). Morphological data from the final harvest (Week 6 and
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44 209 13), and physiological and volatile data close to the final harvest for the last gas exchange
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46 210 sampling (Week 5 and 7) for sweet basil and Micro-Tom, respectively, were used to analyse
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48 211 'Yield', 'Efficiency' (iWUE) and 'Flavour' within the assessment framework.
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52 212 **3.1. Yield**

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55 213 Yields strongly depended on the light treatment (e.g. proportion of blue-to-red light) in both
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57 214 crops, but there were species differences. In sweet basil, blue light significantly ($p < 0.05$)
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215 enhanced height, leaf area and total biomass, with plants grown under B were more than double
216 the height of those grown under R(Fig. 2a). Total leaf area (Fig. 2b) and leaf and stem dry
217 weight (Fig. 2c) showed similar trends, with leaf area and biomass of plants grown under R
218 only one-third of those grown under B.

219 Micro-Tom grown under R were twice the height of those grown with other treatments (Fig.
220 2d) but had significantly lower (~20-38%) total leaf area (Fig. 2e) and dry weight (Fig. 2f).
221 Blue light enhanced both leaf area and dry weight with plants in treatment RB having the
222 greatest values, although not statistically different from those grown under BR and B conditions
223 (Fig. 2e, f). Light treatment did not affect fruit dry weight (Fig. 2f), which was not correlated
224 with height or dry weight.

225 **3.2. Efficiency**

226 Basil grown under BR had 7-18% higher net photosynthesis (P_n) than the other three treatments,
227 which had similar values (Fig. 3a). Stomatal conductance (G_s) varied more between treatments,
228 with G_s under B almost double that of RB (Fig 3b). Consequently, plant instantaneous water
229 use efficiency ($iWUE = P_n / Tr$) was greatest under the RB treatment, and lowest under B,
230 which was only half of those plants under BR and RB treatments (Fig. 3c).

231 Micro-Tom grown under RB had the highest P_n , more than double that of R (Fig 3d). G_s was
232 approximately one-third that observed for basil and was greatest under BR (Fig. 3e). Plants
233 grown under RB light had significantly higher $iWUE$ than BR and R treatments, which were
234 similar (Fig. 3f).

235 Energy usage was dependent on the power consumption of the LED modules. The individual
236 blue and red LED light modules used here provided almost identical light intensity (photon
237 flux). However, the blue LED module consumed nearly 50% more power than the red module
238 (Table. 1), resulting in relatively higher running costs. Hence, increasing the ratio of red light
239 improves energy use regardless of species, minimising running costs.

240 In summary, light treatment RB increased $iWUE$ and R increased relative energy use for both
241 species.

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242 **3.3. Flavour**

243 More than 40 different compounds were identified in sweet basil, and 25 in Micro-Tom. For
244 both species, emissions were dominated by benzenoids, fatty aldehydes, fatty alcohols,
245 monoterpenoids, sesquiterpenoids, and oxygenated terpenoids. Mono-, sesqui-, oxygenated
246 terpenoids and fatty aldehydes are generally considered the most aromatic plant volatiles and
247 are here to determine 'Flavour'. Full lists of volatile identification and quantification are
248 reported in Table S2.

249 In sweet basil, mono- and oxygenated terpenoids were the most abundant (>80% of the total
250 emissions), followed by sesquiterpenoids (~9%) and benzenoids (~3%, Fig. 4a). The greatest
251 proportion and quantity of flavour volatiles were produced under RB treatments. Although
252 plants grown under BR generated a similar volatile profile (94.8% aroma compounds), the
253 emission rate ($1740 \text{ ng m}^{-2} \text{ leaf s}^{-1}$) was the lowest.

254 Total leaf-level emission rates were substantially lower from Micro-Tom than sweet basil.
255 Mono- and sesquiterpenoids accounted for >55% of major volatile emissions (Fig. 4b), with
256 fatty aldehydes (~5%) and oxygenated terpenoids (~3%) contributing for flavour profile. By
257 contrast to sweet basil, the highest proportion of benzenoids (26.2%) emitted by Micro-Tom
258 leaf volatile emission rate increased as rate of red light increases, with treatment R generating
259 the greatest proportion and emission rate of flavour volatiles.

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262 **4. Discussion**

263 **4.1. Yield**

264 For sweet basil, all yield-related parameters (height, leaf area, leaf and stem dry weight)
265 increased as the ratio of blue light increased. Under B light, basil plants were tall (~35cm) with
266 large, well expanded leaves, compared with only ~16cm under R light, which also showed the

1 267 lowest fresh weight per unit height (“compactness”; see Fig. S2a). This “red light syndrome”
2 268 of stunted height and small crumpled leaves has been reported previously in basil and other
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4 269 species (Brown et al., 1995; Naznin et al., 2019), and limits production with leaf biomass of
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6 270 basil grown under R attaining only 28% of that of B light (Fig. 2c). The causes of this plant
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8 271 physiological disorder are still under investigation (Hogewoning et al., 2010; Shengxin et al.,
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10 272 2016). Blue light generated the greatest yield (Fig. 5a), and therefore direct market value of
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12 273 sweet basil, and would be recommended for growers seeking to maximise harvest.

14
15 274 In Micro-Tom, individual yield parameters responded differently to different light treatments.
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17 275 Red light increased plant height (Fig. 2d) but resulted in a very loose structure (Fig. S2b), as in
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19 276 other tomato cultivars and genotypes (Hernández et al., 2016; X. Y. Liu et al., 2011; Ouzounis
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21 277 et al., 2016), with curling leaves and less total leaf area. All light treatments produced similar
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23 278 fresh and dry fruit (unripe) biomass, indicating similar fruit production efficiency between
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25 279 different light treatments. However, RB light produced the greatest leaf area (Fig. 2e) and shoot
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27 280 biomass (Fig. 2f), and we therefore tentatively recommend it (Fig. 5b). While monochromatic
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29 281 red light has been shown to enhance shoot dry biomass and leaf area of tomato (Wollaeger and
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31 282 Runkle, 2014), our results suggest greater leaf biomass production under polychromatic (BR
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33 283 and RB) light treatments, increasing with increasing proportion of red light. This reflects the
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35 284 agronomic reality of commercial crop production in indoor growth facilities. In practice, other
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37 285 parameters associated with yield should also be considered. Previous research indicated that
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39 286 plant growth and differences in biomass accumulation may differentially change the light
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41 287 interception and intensity from top to base, thus accelerating differences in total carbon
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43 288 assimilation and distribution across the treatments, and further affecting crop production per
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45 289 unit area in the facility (Papadopoulos and Pararajasingham, 1997; Toulaitos et al., 2016). This
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47 290 reflects the agronomic reality of commercial crop production in indoor growth facilities.

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51 291 Light-mediated differences in yield-related variables allow growers to select the light treatment
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53 292 that best suits their market interests and requirements. For example, factories targeting food
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55 293 producers who use dried basil leaves, and markets selling packed fresh leaves, might select
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57 294 monochromatic blue light as it enhanced both total leaf area and biomass. However, growers
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1 295 who market fresh potted plants for ornamental or indoor fragrance might prefer compact plants
2 296 with an attractive structure, as produced under BR light. For potted ornamental dwarf tomato
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4 297 (cv. Micro-Tom), the RB treatment produced the most attractive compact and leafy tomatoes.
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6 298 Unmatured fruit yields did not differ between treatments, however, trade-offs between
7
8 299 horizontal and vertical growing space should also be considered. Although the taller Micro-
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10 300 Tom grown under R light required >50% more vertical space than the other treatments, their
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12 301 low total leaf area (Fig. 2e) and expansion (see Fig. S4) required less horizontal space per plant.
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14 302 Space limitations in either direction would require further trials to determine the lighting
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16 303 combination that maximises yield density (Papadopoulos and Pararajasingham, 1997).
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18 304 Experiments are needed with other tomato genotypes used in PFALs (Ouzounis et al., 2016) to
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20 305 test consistency of results.
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24 306 **4.2. Efficiency**

27 307 Instantaneous (photosynthetic) water use efficiency (iWUE), calculated as the leaf-level carbon
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29 308 assimilation rate (CO₂) divided by the water transpiration (H₂O) rate, was used as an efficiency
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31 309 indicator. RB produced the highest iWUE in both species and is recommended for indoor
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33 310 cultivation (Fig. 5). The least efficient treatments were B in sweet basil (Fig. 3c), R and BR for
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35 311 Micro-Tom (Fig. 3f), consistent with previous studies of both species (Pennisi et al., 2019)
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37 312 (Lanoue et al., 2017). In both species, a combination of blue and red LED light promoted
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39 313 photosynthesis. Although blue light increased stomatal conductance of sweet basil, net
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41 314 photosynthesis rate was greatest under BR lights (Fig. 3b, a). Micro-Tom also showed varied
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43 315 photosynthetic and stomatal responses, with maxima occurring under RB and BR light
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45 316 respectively (Fig. 3d, e). Therefore commercial growers need to consider the trade-off between
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47 317 total carbon assimilation (yield) and total resource usage. The iWUE is a physiological
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49 318 parameter that we applied in this framework to estimate leaf-level water usage. However, the
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51 319 efficiency of water use in productivity (ratio of biomass to total water use) is frequently used
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53 320 in real growth facilities to calculate overall WUE throughout the growth cycle or season of
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55 321 specific species, and therefore could be more realistic for indoor crop production and specific
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57 322 facilities. Light treatment can (marginally) improve whole plant water usage, but optimising
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1 323 energy efficiency per unit area is much more dependent on the choice of lighting system and
2 324 likely of more interest to growers since the main costs for PFALs are associated with electricity
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4 325 for lighting, as well as environmental control systems. RB light optimised iWUE of both species,
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6 326 but R treatment delivers the best energy use (Table. 1). Hence R light is recommended for
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8 327 saving costs (Fig. 5). Unit mass WUE and energy use efficiency (EUE) are already generally
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10 328 high in plant factories or vertical farms (Pennisi et al., 2019; Ting et al., 2016). If commercial
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12 329 growers are trying to improve the overall resource use efficiency of PFALs, the trade-off
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14 330 between WUE and EUE would need to be carefully considered, as well as additional indicators
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16 331 such as nutrient use and the costs of environmental regulation such as cooling and
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18 332 dehumidification.
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22 333 **4.3. Flavour**

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25 334 The dominant compounds in plant aroma profiles are mono-, sesqui- and oxygenated terpenoids
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27 335 and fatty aldehydes. Foliar emissions of these were used to assess flavour (Fig. 4) although
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29 336 post-harvest volatile emissions are arguably more relevant than those during cultivation. The
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31 337 constitution of aroma compounds from sweet basil was little affected by light treatment,
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33 338 although RB treatment would be recommended for maximising total emission rates of aromatic
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35 339 volatiles (Fig. 4a, 5). Similarly, low intensity red or high intensity blue light enhanced the
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37 340 concentration of volatiles in basil essential oils and leaf extracts (Amaki et al., 2011; Pennisi et
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39 341 al., 2019). Although total emission rates were lower, red light enhanced production of eugenol,
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41 342 an oxygenated terpenoid and powerful antioxidant, which is an important component of
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43 343 essential oil and therefore flavour (Gülçin et al., 2012). Both emission rate and proportion of
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45 344 leaf aromatic volatiles were stimulated by R light in Micro-Tom (Fig. 4b), which is therefore
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47 345 our recommendation (Fig. 5b).
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51 346 Of considerably more importance to the grower, however, is the flavour of the final product
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53 347 (tomato fruits and basil leaves post-harvest), which is highly consumer taste oriented. Long-
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55 348 term post-harvest dynamics related to these treatments are currently unknown, and it is not clear
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57 349 how good a proxy foliar emission during cultivation is. In addition to volatiles, mineral, sugar
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1 350 and acid content (e.g. glutamate, malate) also determine the flavour of fruits or leaves (Petro-
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3 351 Turza, 1986) and these were not measured here. Future trials should therefore adopt fruit or leaf
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5 352 tissue extractions to determine more realistic flavour profiles, and growers seeking to optimise
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7 353 flavour should undertake taste-testing of the final marketable product accounting for its
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9 354 intended use (e.g. whether used raw or cooked, fresh or dried) (Klee and Tieman, 2018).
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11 355 Moreover, the emission rate and composition of volatile contents can be expected to change
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13 356 before and after harvest, and during storage (Spadafora et al., 2019). Greater emissions do not
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15 357 necessarily equate to a better flavour (Mulder-Krieger et al., 1988), rather the relative
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17 358 proportions and concentrations of particular compounds determine the aromatic and flavour
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19 359 characteristics. Hence, flavour changes during production, storage, and distribution, as well as
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21 360 the most appropriate volatile composition profile should also be assessed.

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24 361 This study identified an optimum combination of blue-to-red LED light based on maximising
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26 362 each of **yield**, **efficiency** and **flavour** for an herb (sweet basil) and a model crop (Micro-Tom)
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28 363 grown in indoor plant factory. In so doing, we demonstrated for the first time how each can be
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30 364 selectively enhanced through different wavelengths of light. No light treatment simultaneously
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32 365 optimised all assessment criteria for either species, implying that growers can design bespoke
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34 366 light treatments to optimise the specific attribute that best meets their market requirement.
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36 367 Although a few previous studies (Aldarkazali et al., 2019; Pennisi et al., 2019) have
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38 368 demonstrated the possibility of optimising light quality for multiple assessment factors in
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40 369 environment-controlled growth facilities, none have demonstrated how this knowledge should
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42 370 be applied by the growers. Hence, we emphasise the practical acquisition of observations
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44 371 required to quantify each factor, and established a systematic, highly flexible framework for all
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46 372 indoor growers and plant factories.

51 373 **5. Conclusion**

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54 374 We developed an innovative highly flexible framework that includes all three key factors (yield,
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56 375 efficiency and flavour) of indoor crop production to assess optimum lighting regimes. The
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58 376 framework is a user-friendly tool that can be universally applied across the indoor agriculture

1 377 sector. The parameters used to assess each factor can be modified to target the specific demands
2 378 of the intended market. Individual growers can then identify the optimum trade-off between
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4 379 those three factors based on their final markets and consumers acceptance. Our
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6 380 recommendations are summarised in Fig. 5. Basil “yield” was maximised under 100% blue,
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8 381 while “flavour” was enhanced under 33% blue + 66% red. In Micro-Tom, “yield” was
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10 382 maximised under 33% blue + 66 % red, whereas “flavour” was enhanced under 100% red.
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12 383 Efficiency in both species was optimised under 33% blue + 66% red (water-use-efficiency) and
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14 384 100% red (energy-use-efficiency) lights. Depending on the market requirements, trials with
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16 385 specific cultivars and final consumer taste or acceptability tests may be needed to determine the
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18 386 ideal lighting regime for different indoor growing facilities.
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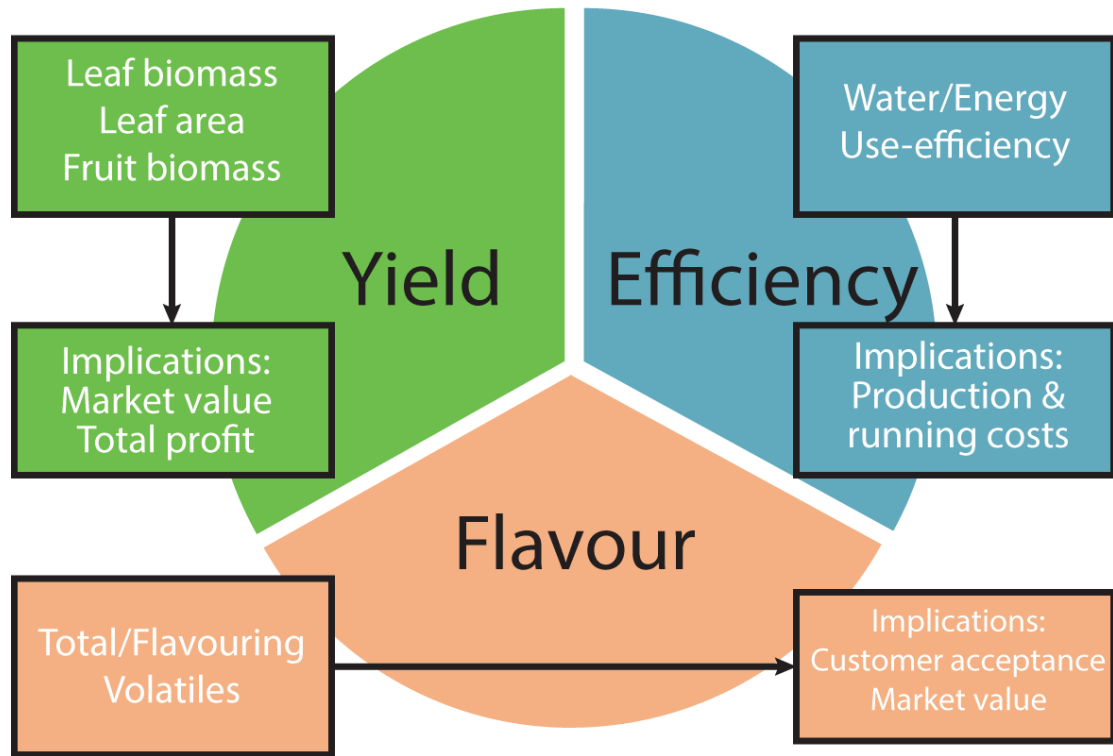
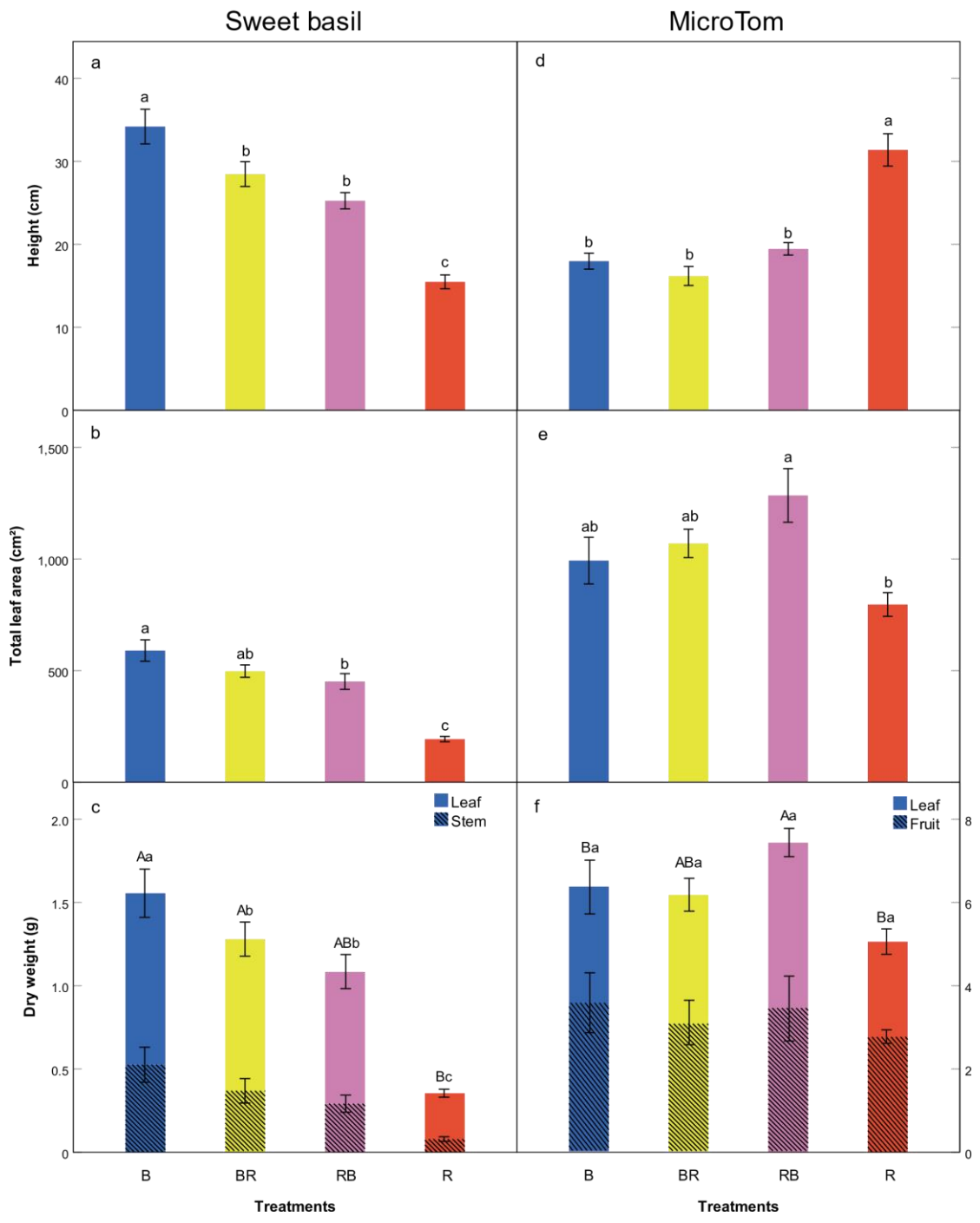


Figure 1. Illustration of the three factors in the assessment framework and specific factors related to each.

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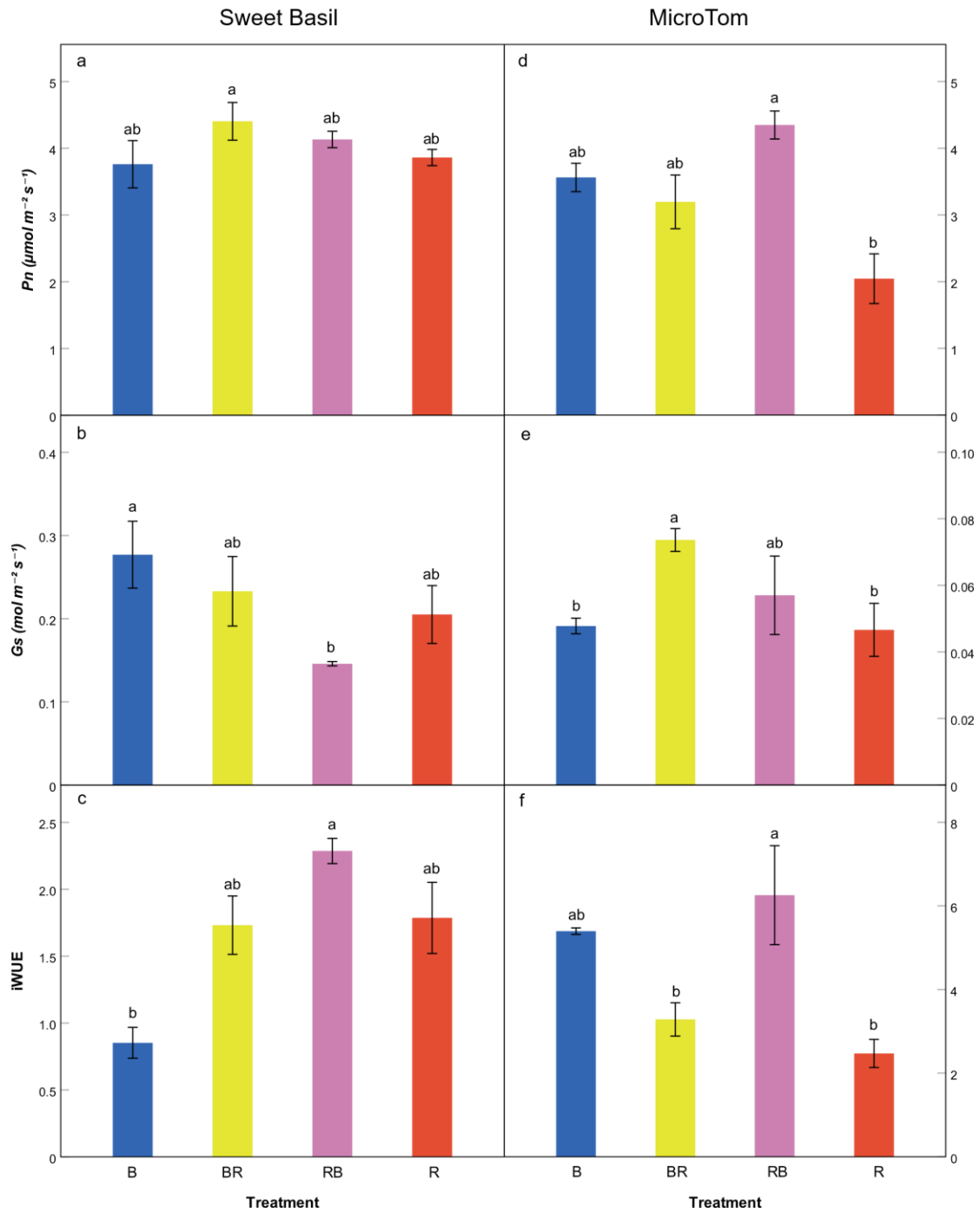


Figure 3. The effect of LED light treatment on net photosynthesis (P_n), stomatal conductance (G_s) and instantaneous water-use-efficiency (iWUE) of sweet basil (left-hand panels) on 5-weeks and MicroTom (right-hand panels) on 7-weeks. Plants grown under B (blue), BR (yellow), RB (purple), R (vermilion) treatments. Lower cases indicate significant differences ($p < 0.05$, $n = 3$, $\pm\text{SE}$) between treatments.

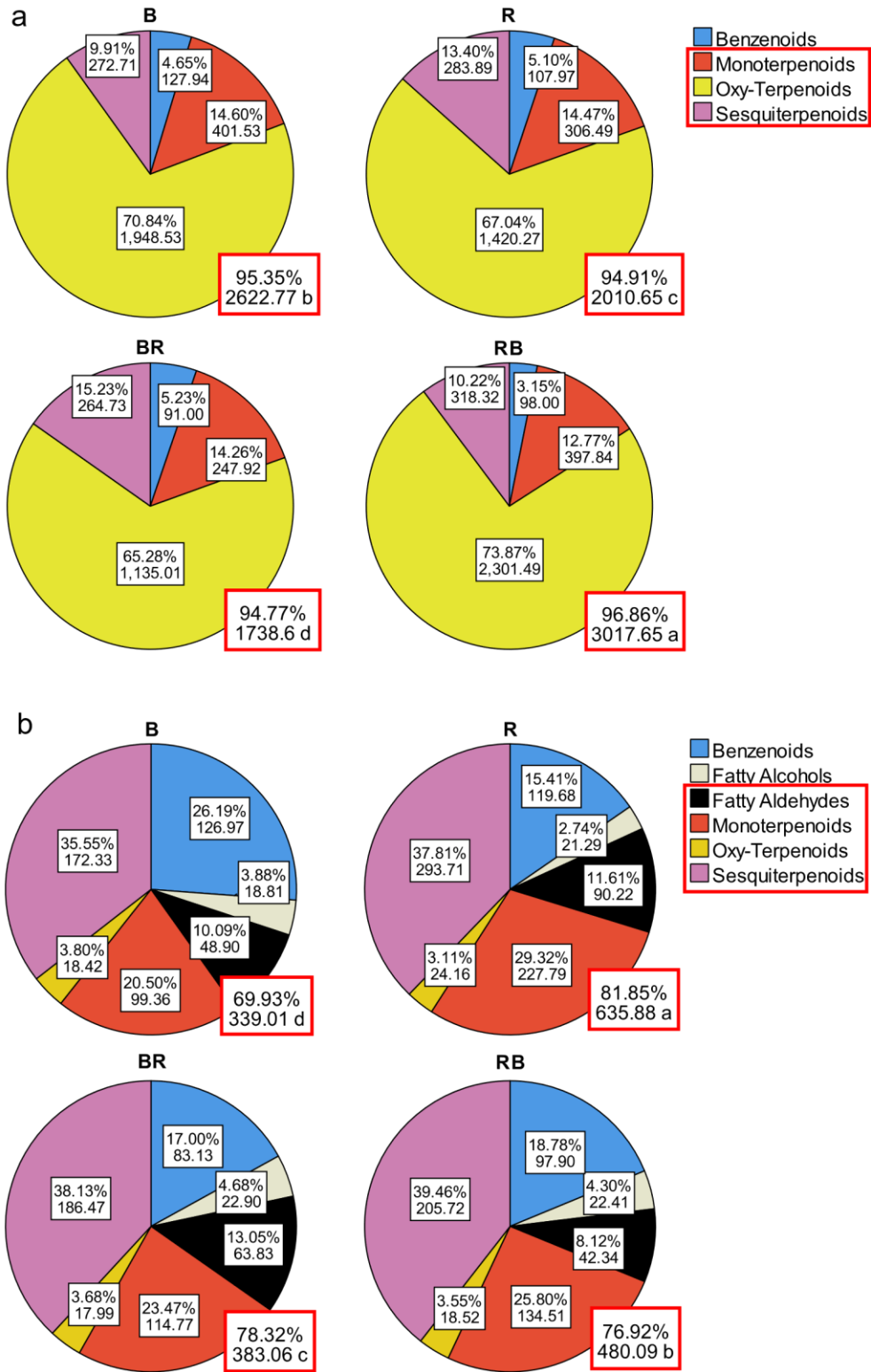
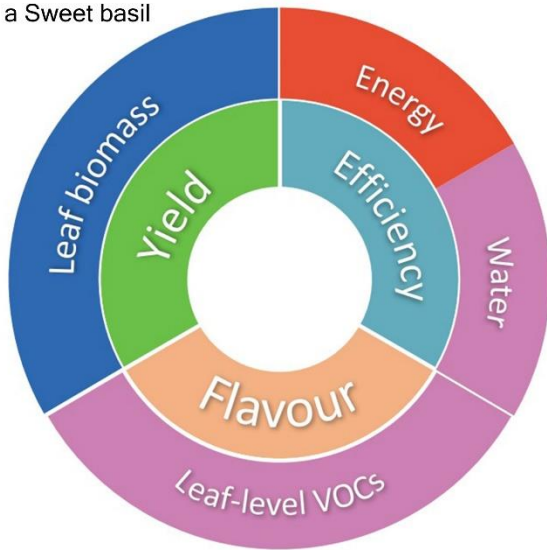


Figure 4. The effect of LED light treatment on volatile emissions from 5-weeks sweet basil (a) and 7-weeks MicroTom (b). Black-framed boxes on each pie indicate the percentage (top) and emission rate (ng m⁻² leaf s⁻¹, bot) of main volatile classes. Red-framed boxes indicate the percentage and emission rate of flavour volatiles (e.g. mono-, sesqui, oxygenated terpenoids, fatty aldehydes). Lower cases indicate significant differences ($p < 0.05$, $n = 3$, \pm SE) between treatments.

a Sweet basil



b Micro-Tom

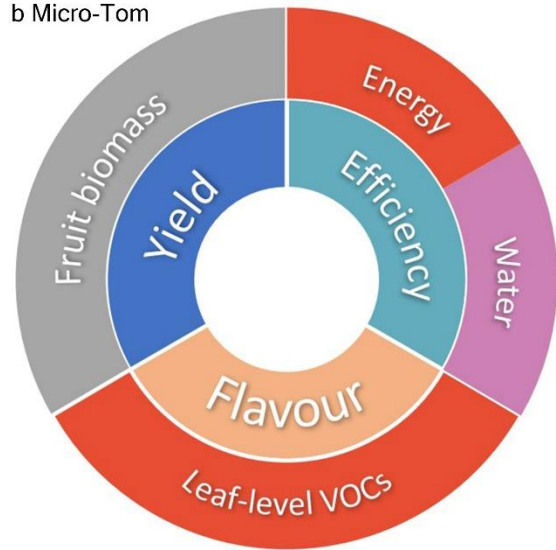


Figure 5. Overall recommendations to optimise production of sweet basil (a) and MicroTom (b). Basil: 100% blue (blue) maximised **yield** (leaf biomass), 66% red (purple) promoted **flavour**; MicroTom: 66% red promoted **yield** (leaf biomass) but fruit biomass was same between treatments (indicated as grey), 100% red (vermillion) for **flavour**. In both species, 66% red and 100% red enhanced water and energy use **efficiency** respectively.

Table 1. Relative energy usage of LED modules. R: 100% red; RB: 66% red, 33% blue; BR: 33% red, 66% blue; B: 100% blue.

Light module	Photon flux	Power	Treatment	Relative usage
Deep red LED	16 $\mu\text{mol/s}$	10 W	R	1
			RB	1.13
			BR	1.26
Blue LED	15 $\mu\text{mol/s}$	14 W	B	1.4