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Scientia Horticulturae

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

Manuscript Number:	HORTI35051R1
Article Type:	Research Paper
Section/Category:	Greenhouse (cultivation, management, models)
Keywords:	Crop improvement, Light emitting diodes (LEDs), <i>Ocimum basilicum</i> , Plant factories, <i>Solanum lycopersicum</i> .
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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>

Dear Dr. Youssef Rouphael

Re: HORTI35051

Thank you for giving us the opportunity to submit a revised version of the manuscript titled “**Yield, resource use efficiency or flavour: trade-offs of varying blue-to-red lighting ratio in urban plant factories**”. We appreciate you and the reviewers for your precious time spent reviewing our paper and providing valuable comments. We have fully addressed the comments made by the reviewers and believe we have satisfactorily answered their concerns. We’ve incorporated the suggestions made by the reviewers into the revised manuscript as appropriate and made all of the minor technical corrections required.

Changes to the manuscript are listed below:

Lines: 5, 27-28, 49, 112, 125, 138-139, 167, 180, 202, 210, 216, 224, 240, 283, 287, 288, 310, 325, 344, 376-377, 383 have minor technical corrections only.

Lines: 134-135, 150-151, 159, 164-165 clarify aspects of the methodology

Lines: 192-193, 219-222, 227-228, 275-278 and Figure 2 address the issue of the use of Harvest Index

Lines: 141-145, 292-299, and Supplementary Table S1 respond to the reviewers’ queries regarding growing conditions in the facility

Lines: 405 added acknowledgements including funding information.

All of the revisions are highlighted with tracked changes, and all line numbers refer to the revised manuscript. Below we provide point-by-point responses in italics.

Sincerely on behalf of all authors

Hao Zhou,

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Lancaster Environment Centre, Lancaster University, Lancaster, UK

Reviewer #1: The manuscript deals with an interesting subject, where there, despite of a lot of publications published in recent years, still is a lack of knowledge. The manuscript is generally well-written and the methodology used is appropriate. The conclusions drawn from the results are sound. The figures are proper, with some exemptions (see detailed comments). The findings are discussed in relation to relevant literature. The reference list is complete and correct.

Line 27: Please arrange Keywords in alphabetical order. Please note that the scientific name for tomato is now established to be *Solanum lycopersicum*.

We’ve now re-arranged the order of keywords and use the appropriate scientific name of tomato

Line 50: I would suggest to replace "salad" with "lettuce"

We’ve now replaced “salad” with “lettuce”.

Line 136: Were the plants fed with just water or a nutrient solution?

The plants were fed with just water and we’ve now added that clarification.

Please clarify Line 140: Please insert space between “700” and “nm”.

We have inserted the missing space.

Line 174: I think it is now established that “liter” should be abbreviated with a capital “L”.

We have changed “liter” to “L”.

Line 178: I would suggest to start a new sentence from "Following the protocol..."

We disagree with the reviewer as this refers to the use and settings of the GC-MS and not the calibration standards used.

Line 239: Please rephrase as "Energy usage was dependent..."

We've revised the expression accordingly.

Line 313: Please remove redundant period.

We have removed the redundant period.

Line 257: Please check the writing of $\mu\text{mol m}^{-2} \text{s}^{-1}$

We calculated emissions of BVOC compounds in terms of mass per square meter of leaf area per second ($\text{ng m}^{-2} \text{leaf s}^{-1}$), rather than by moles of compound, as is standard for emissions estimates in the atmospheric flux community and previous literature in plant sciences journals.

Figure 1: I myself am not much of a “picture person” but I do not really see the purpose of this figure, so I would suggest to omit it.

Figure 1 illustrates each factor within the assessment framework to indicate the parameters that were measured, and their implications to growers. We think this figure helps non-expert readers to better understand our framework and to choose appropriate measurements for their interests.

Figure 2, legend: Please write "yield" with small letter Figure 5: I would suggest to omit this figure

We have now revised “Yield” to “yield” but prefer to retain Figure 5 as an accessible summary of our results to help readers from the wider community to get useful information easier.

Reviewer #2: This study aimed to introduce a novel assessment framework to optimise light quality accounting for yield, resource use efficiency and favour of sweet basil and tomato in single experimental designs. Sweet basil and tomato were grown under different combinations of red and blue LED lightings. They reported that in both species, 66% and 100% red, respectively optimized water efficiency and energy use. For sweet basil, 100% blue light maximised leaf biomass while 66% red light enhanced leaf flavouring volatiles. In tomato, all LED combinations produced similar fruit biomass, but 100% red light enhanced leaf-level volatile emissions. The findings are interesting and may be useful for the growers who could select the combination of red and blue LED based on the market demands at a cost-effective manner. The manuscript is very written. However, the authors should address the following issues before publishing in "Scientia Horticulturae":

We thank the Reviewer for recognising the novel and important contribution our paper makes, in developing a framework for growers to adapt to specific agronomic and market requirements.

1. Lines 135, why 20°C was used to grow sweet basil? It may be too low for sweet basil as it is a warm-weather crop. Responses of plants to LED spectral quality also depend on other environment factors such as temperature. Are there any indoor farms or plant factories growing sweet basil under such as a chill temperature?

2. Lines 141/142 "The total photon flux density ($115 \pm 2 \mu\text{mol m}^{-2} \text{s}^{-1}$) supply was constant across treatments.". PPFD of $115 \mu\text{mol m}^{-2} \text{s}^{-1}$ was too low for both species although 14 h photoperiod was used. Responses of plants to LED spectral quality also depend on other environment factors such as light intensity and daily light integral (DLI). Are there any indoor farms

or plant factories growing sweet basil and tomato under such as a low PPFD or DLI?

We used the default environmental settings in STC's indoor LED growth facility that have been applied to cultivate a wide range of species and varieties of horticultural and agricultural plants for research or commercial purposes over the past five years, including basil cv. 'Osmin Purple'. Optimum growing temperatures for tomato plants such as the "Microtom" used here are reported to range between 18 and 22°C (Schwarz D, Thompson AJ, Kläring HP. Guidelines to use tomato in experiments with a controlled environment. Front Plant Sci. 2014;5:625. Published 2014 Nov 18. doi:10.3389/fpls.2014.00625) and we wanted to compare basil at the same temperature.

Regarding the PPFD, $115 \mu\text{mol m}^{-2} \text{s}^{-1}$ was the light intensity measured during the leaf level Li-Cor sampling. The actual daily integrated PPFD that plants received is expected to increase with growth and development. We have revised the PPFD from a single value to a range (Line 141) and provided an average vertical light intensity profile in the supplementary document (Table S1a)

3. Line 146, how to measure the plant height for both sweet basil and tomato plants?

Plant height from soil surface to shoot apex was measured with a tape measure (Lines 149-150).

4. Line 151, Harvest index (HI): why root biomass was not included in the calculation as LED spectral quality also affects root growth and development.

7. Lines 218 and 226, I am wondering if the HI for both sweet basil and tomato would be different if the root biomass was included for the calculations.

Since root biomass may respond differently to different LED lighting conditions than aboveground biomass but is unlikely to be of interest to commercial growers of these crops, we calculated HI as leaf/shoot (dry mass) for basil and fruit/shoot (dry mass) for tomato respectively. Nevertheless, we recognise these calculations are of limited value to growers, and have removed them from Fig 2, and the associated main text (Lines 218-221 & 274-5).

5. Line 154, section 2.3 when was leaf-level gas exchange measured, at the beginning of the photoperiod or the middle of photoperiod?

Leaf-level measurements started 3 hours after lights were switched on, continuing to 3 hours before lights were switched off, thus ensuring gas exchange was measured in the middle of the photoperiod

6. Line 163/164 "Leaves insufficiently large to fill 163 the chamber were photographed in-situ and the sampled leaf area subsequently calculated using Image J software ...". Which full expanded leaves are not big enough to cover the leaf chamber, basil leaf or tomato leaf?

Since Micro-Tom is a dwarf tomato variety, some of its leaves were not big enough to cover the whole leaf chamber ($2 \times 3 \text{ cm}^2$). This has now been clarified in the manuscript.

8. Lines 275 to 276 "Blue light generated the greatest yield (Fig. 5a), and therefore direct market value of sweet basil, and would be recommended for growers seeking to maximise harvest.". Fig. 2d shows that HI was the highest for sweet basil under 100% red light. The authors should discuss here that HI may not be a good measure for "Yield".

We agree that HI is not a good proxy for "Yield" in this case, and have removed panels 2d & h.

9. Lines 277 to 286: Based on Figure S4, tomato plants grown under different combined red and blue light may have different light interception area and absorptance which are important factors responsible for the whole plant photosynthetic capability that is associated with leaf growth and shoot/fruit productivity.

We agree that light interception area and absorptance are important for plant growth and productivity, and may change during plant development. Changes in light interception over time are therefore an agronomic reality which our experiment and analyses incorporate. We have added

further discussion of this point in lines 288 – 292.

10. Leaf-level volatile emissions (VOCs) is used to study the favor of both sweet basil and sweet tomato. Would the grower be convinced for the recommendation "Both emission rate and proportion of leaf aromatic volatiles were stimulated by R light in Micro-Tom (Fig. 4b), which is therefore our recommendation (Fig. 5b)."? Leaf-level VOCs could be different from tomato fruit favor.

The reviewer is correct that we use foliar volatile emissions as a convenient proxy for the flavour of the marketable part of both species. We expect emissions of foliar VOCs to indicate plant volatile production rates which may to some extent provide information on flavour. In practice, even directly measuring leaf and fruit volatile content in basil and tomato respectively would not necessarily indicate consumer preference. Taste testing of basil leaves and tomato fruits grown under different blue:red light treatments would be essential for growers targeting markets driven by flavour. This is already discussed in Section 4.3, and particularly Lines 338-340 and 349-363.

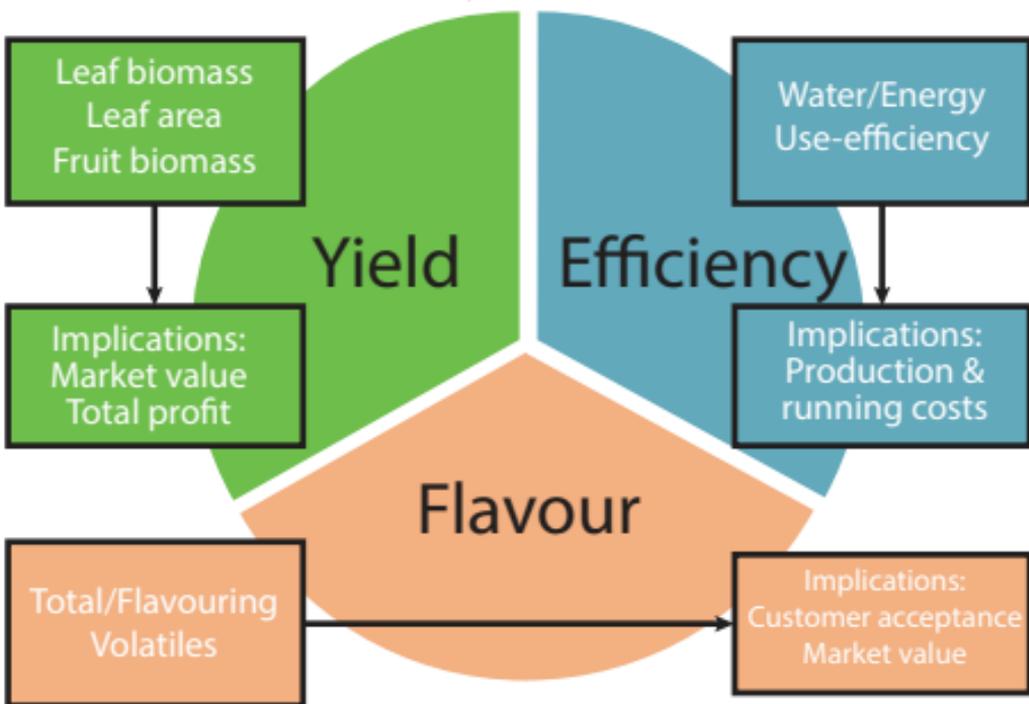
Yield, resource use efficiency or flavour: trade-offs of varying blue-to-red lighting ratio in urban plant factories

Highlights

- An assessment framework for growers to optimise LED light wavelength in urban plant factories;
- Yield, resource use efficiency & flavour require different blue : red light combinations;
- More red light promotes water saving and flavour volatiles in sweet basil & tomato
- More blue light promotes leaf biomass (yield) in sweet basil
- Trade-offs should be considered when customising lighting to meet growers' market demands.

Figure 1.
Illustration of the

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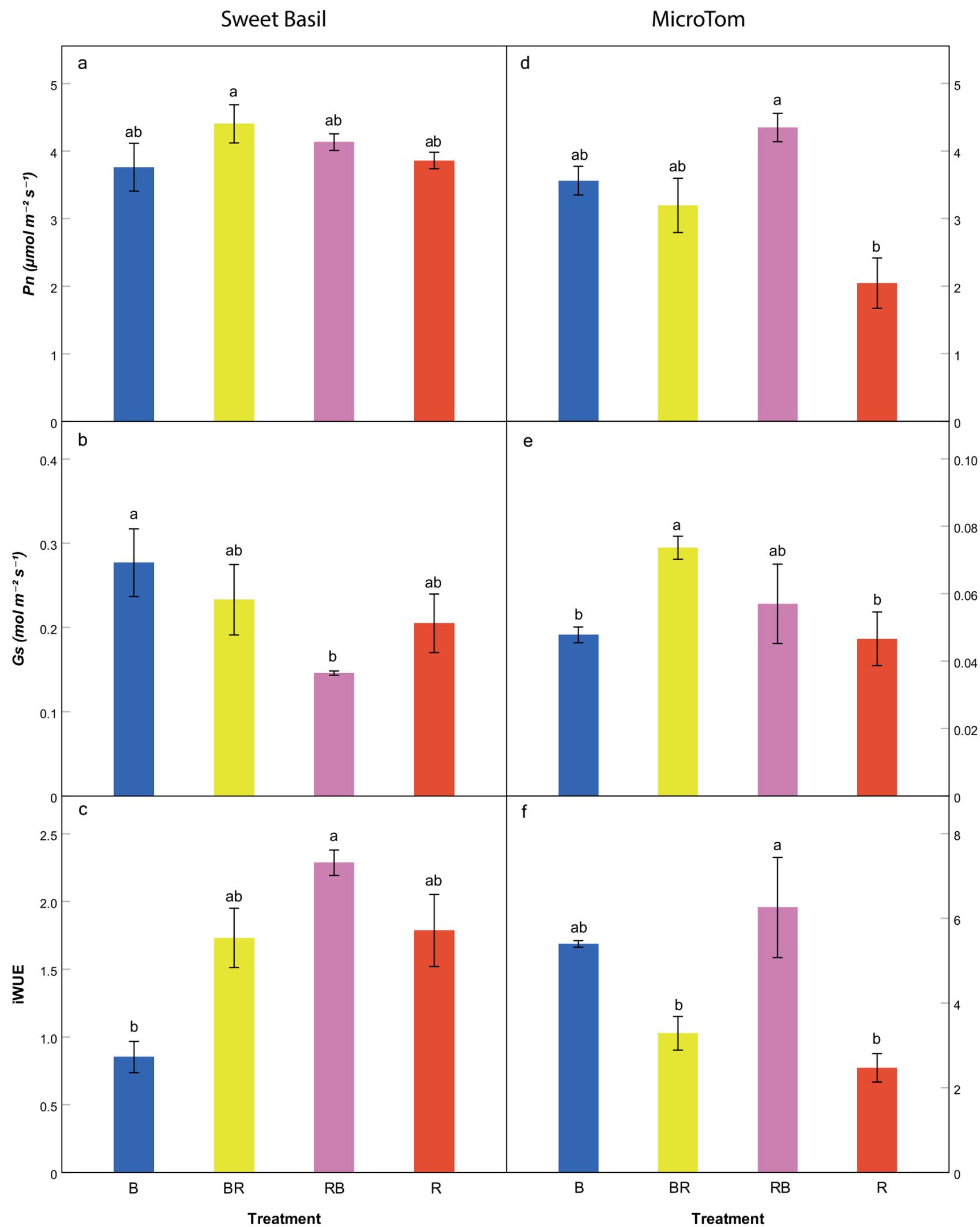
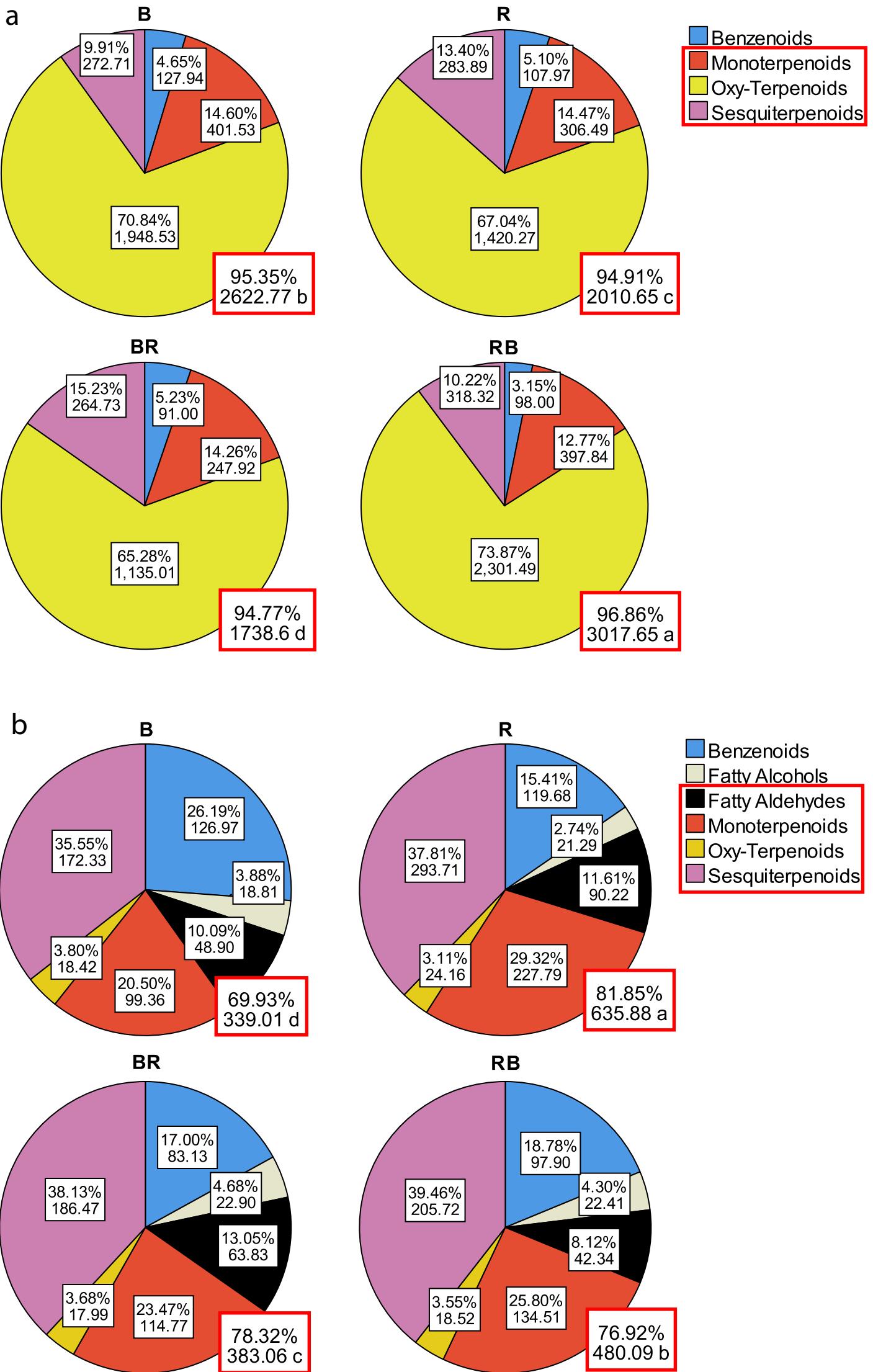


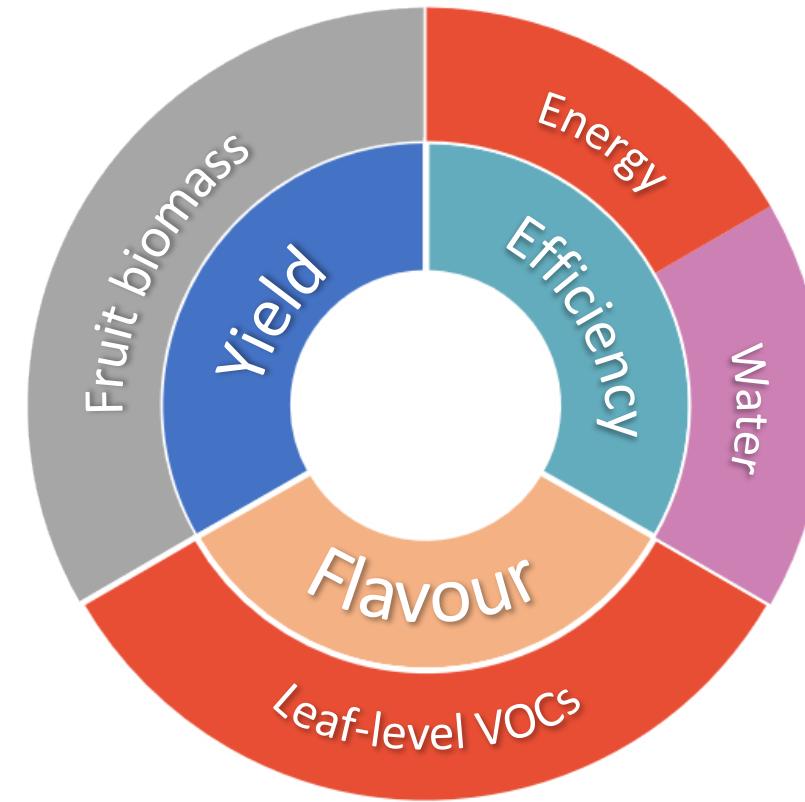
Figure 4. The effect of LED light treatment on volatile emissions from 5-weeks sweet basil (a) and 7-weeks

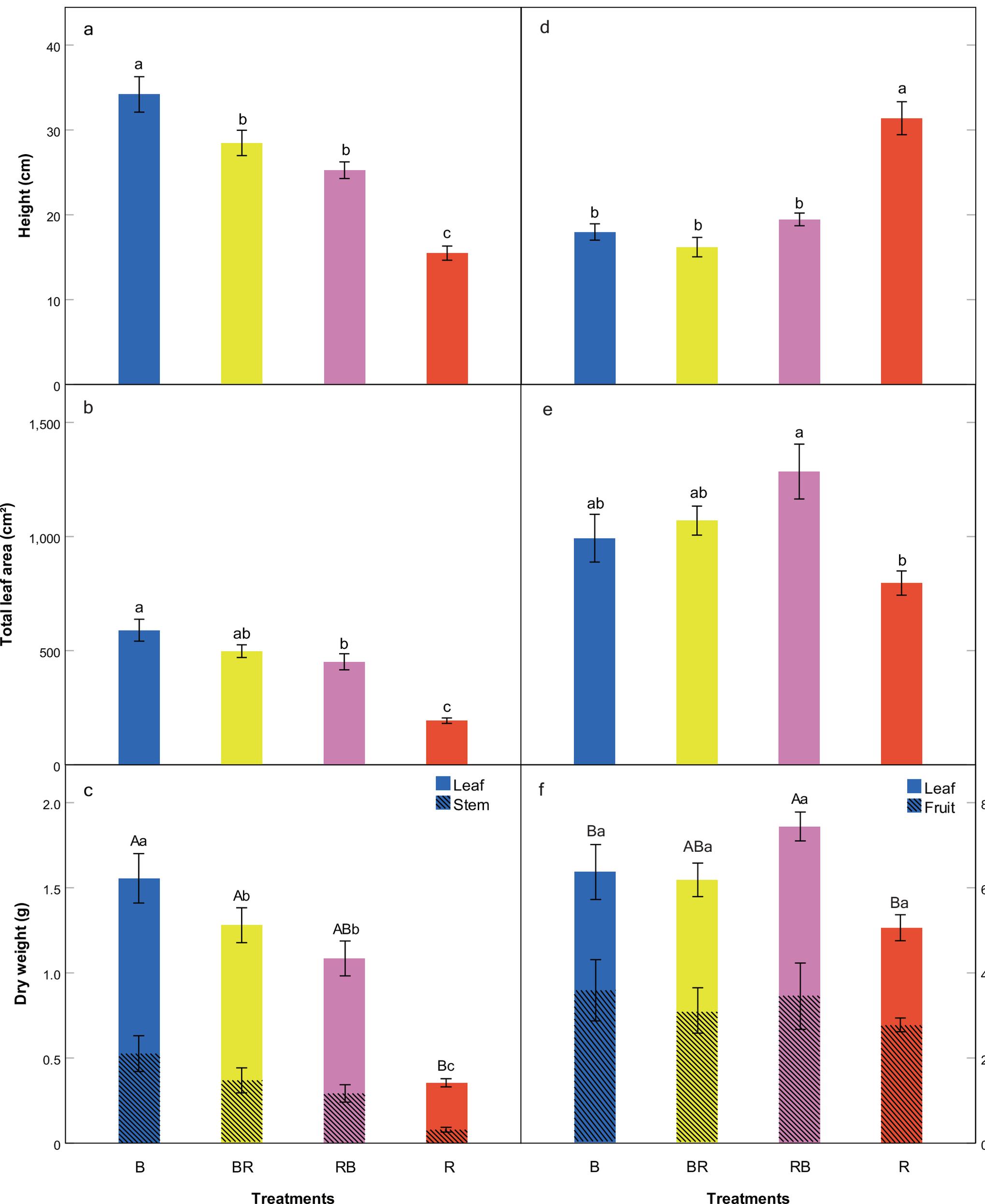


a Sweet basil



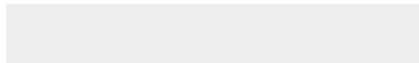
b Micro-Tom







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Supplementary Material

Supplementary Material_unmarked.pdf



Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

AUTHORSHIP STATEMENT

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

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication before its appearance in the *Scientia Horticulturae*.

Authorship contributions

Hao Zhou: Methodology, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization

Rhydian Beynon-Davies: Methodology, Validation, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration

Nicola Carslaw: Validation, Resources, Writing - Review & Editing, Supervision, Project administration

Ian C. Dodd: Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision, Funding acquisition

Kirsti Ashworth: Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision, Funding acquisition

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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**

11 With increasing urbanisation and consumer concerns over food miles, indoor urban plant
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 (Nogueire-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, PPFD), 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-
3
4 56 850 nm) light affect plant growth and development (Higuchi and Hisamatsu, 2016). LEDs of
5
6 57 differing wavelengths can be used to control plant morphogenesis and enhance the production
7
8 58 of secondary metabolites, increasing efficiency and adding value to crops by enhancing nutrient
9
10 59 content and/or taste (Kozai and Zhang, 2016; Lu and Mitchell, 2016). Monochromatic blue and
11
12 60 red light induce specific light signalling responses in plants, significantly affecting
13
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
17
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
21
22 65 (Shimazaki et al., 2007). Red light is absorbed by phytochromes, regulating major
23
24 66 developmental transitions (e.g. germination and flowering) (Smith, 1995), and plant vegetative
25
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
37
38 72 66% blue lighting (Pennisi et al., 2019), while increasing the proportion of blue light enhances
39
40 73 biomass production, stomatal conductance and net photosynthesis rate of other species
41
42 74 (Hogewoning et al., 2010; Matsuda et al., 2004). However, the response to red light appears
43
44 75 less uniform across species. Compared to monochromatic or high percentage blue light, high
45
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
3
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
7
8 86 aroma and flavour (Bertoli et al., 2013; Kim et al., 2014) while the aromatic composition of
9
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.,
15
16 90 2014), and flavour is also dependent on the concentration, emission rate, and composition of
17
18 91 aromatic compounds (Mulder-Krieger et al., 1988). Combinations of blue and red light
19
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).
23
24 94 Basil leaves grown under combined red and blue light had a higher essential oil content than
25
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
29
30 97 (Amaki et al., 2011). Short-term exposure to red light during the fruiting stage altered fruit
31
32 98 volatile profile in tomato (Colquhoun et al., 2013), enhancing the flavour (Tieman et al., 2012).
33
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,
41
42 102 2016). Water and nutrient use efficiency (WUE, NUE) depend on physiological (e.g. stomatal
43
44 103 and metabolic) characteristics , and although relatively high (and constant) across PFALs, can
45
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
49
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.

12 121

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
9
10 141 level height ranged from 115 to 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$ according to leaf distance to the lighting
11
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
15
16 144 consistent in racks and shown in Table S1 together with the average vertical profile.

20 145 **2.2. Morphological measurements**

22 146 Morphological measurements of plant height (H), total leaf area (LA) and fresh/dry weight
23 147 (FW/DW) of leaf and stem (basil, tomato), and fruit (tomato), were recorded following
24 148 destructive harvesting of 9-10 replicates weekly from Week 3 for basil and fortnightly from
25 149 Week 5 for Micro-Tom (reflecting the different growth rates of the two species). Plant height
26 150 was measured from soil surface to shoot apex using a tape measure. Leaf area was determined
27 151 using a LI-3100C Leaf Area Meter (LI-COR, UK). Sampling continued for 6 weeks for basil
28 152 and 13 for tomato.

37 153 38 154 **2.3. Leaf-level gas exchange and resource use efficiency**

39 155 Physiological responses and volatile emissions were sampled in-situ for two consecutive weeks
40 156 in both species (Weeks 4 and 5 for basil, and 6 and 7 for Micro-Tom). The newest fully
41 157 developed leaf from each of 3 randomly selected replicates per treatment was sampled using a
42 158 Li-6400XT (Li-COR Inc., USA), three hours after the lights were switched on. The leaf was
43 159 placed in a 2 x 3 cm clear-top chamber under conditions that closely replicated the growing
44 160 environment (leaf temperature 22°C, relative humidity 50-60%, and CO₂ concentration 400 μL
45 161 L⁻¹). Following a 5-minute period of stabilisation, net photosynthesis (*P_n*), stomatal
46 162 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
19
20 172 were drawn from the Li-6400XT outlet and collected in stainless steel thermal desorption
21
22 173 sorbent tubes (Markes International Ltd, Llantrisant, UK) packed with 0.2 g Tenax® Porous
23
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
41
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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17 198 **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.

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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; Touliatos 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
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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**

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27 307 Instantaneous (photosynthetic) water use efficiency (iWUE), calculated as the leaf-level carbon
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29 308 assimilation rate (CO_2) divided by the water transpiration (H_2O) 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
40
41 314 photosynthesis rate was greatest under BR lights (Fig. 3b, a). Micro-Tom also showed varied
42
43 315 photosynthetic and stomatal responses, with maxima occurring under RB and BR light
44
45 316 respectively (Fig. 3d, e). Therefore commercial growers need to consider the trade-off between
46
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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425 **References**

- Aldarkazali, M., Rihan, H. Z., Carne, D., & Fuller, M. P.,2019. The growth and development of sweet basil (*Ocimum basilicum*) and bush basil (*Ocimum minimum*) grown under three light regimes in a controlled environment. *Agronomy*, 9(11), 743.
doi:10.3390/agronomy9110743
- Amaki, W., Yamazaki, N., Ichimura, M., & Watanabe, H.,2011. Effects of light quality on the growth and essential oil content in sweet basil. *Acta Horticulturae*, 907, 91-94.
doi:10.17660/ActaHortic.2011.907.9
- Bardsley, N., Bland, S., Pattison, L., Pattison, M., Stober, K., Welsh, F., & Yamada, M.,2014. Solid-state lighting research and development: Multi-year program plan. Paper presented at the 2014 DOE SSL R&D Workshop, Tampa, Florida.
- Bertoli, A., Lucchesini, M., Mensuali-Sodi, A., Leonardi, M., Doveri, S., Magnabosco, A., & Pistelli, L.,2013. Aroma characterisation and UV elicitation of purple basil from different plant tissue cultures. *Food Chemistry*, 141(2), 776-787.
doi:10.1016/j.foodchem.2013.02.081
- Brandon, M. F., Lu, N., Yamaguchi, T., Takagaki, M., Maruo, T., Kozai, T., & Yamori, W.,2016. Next evolution of agriculture: A review of innovations in plant factories. In (pp. 723-740).
- Brown, C. S., Schuerger, A. C., & Sager, J. C.,1995. Growth and photomorphogenesis of pepper plants under red light-emitting diodes with supplemental blue or far-red lighting. *120(5)*, 808. doi:10.21273/jashs.120.5.808
- Carvalho, S. D., Schwieterman, M. L., Abrahan, C. E., Colquhoun, T. A., & Folta, K. M.,2016. Light quality dependent changes in morphology, antioxidant capacity, and volatile production in sweet basil (*Ocimum basilicum*). *Frontiers in Plant Science*, 7(1328). doi:10.3389/fpls.2016.01328
- Colquhoun, T. A., Schwieterman, M. L., Gilbert, J. L., Jaworski, E. A., Langer, K. M., Jones, C. R., Rushing, G. V., Hunter, T. M., Olmstead, J., Clark, D. G., & Folta, K. M.,2013. Light modulation of volatile organic compounds from petunia flowers and select fruits. *Postharvest Biology and Technology*, 86, 37-44.
doi:10.1016/j.postharvbio.2013.06.013
- Elevitch, C., & Love, K.,2013. Adding value to locally grown crops in Hawai'i: A guide for small farm enterprise innovation: Permanent Agriculture Resources.
- Fang, W.,2016. Business models for plant factory with artificial lighting (PFAL) in taiwan. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 289-293). Singapore: Springer Singapore.
- Fankhauser, C., & Chory, J.,1997. Light control of plant development. *Annual Review of Cell and Developmental Biology*, 13(1), 203-229. doi:10.1146/annurev.cellbio.13.1.203
- Fisher, P., & Runkle, E.,2004. *Lighting up profits: Understanding greenhouse lighting*: Meister Media Worldwide.

- 1 Fu, X., Chen, Y., Mei, X., Katsuno, T., Kobayashi, E., Dong, F., Watanabe, N., & Yang,
2 Z.,2015. Regulation of formation of volatile compounds of tea (*Camellia sinensis*)
3 leaves by single light wavelength. *Scientific Reports*, 5(1), 16858.
4 doi:10.1038/srep16858
- 5 Gülçin, İ., Elmastaş, M., & Aboul-Enein, H. Y.,2012. Antioxidant activity of clove oil – A
6 powerful antioxidant source. *Arabian Journal of Chemistry*, 5(4), 489-499.
7 doi:10.1016/j.arabjc.2010.09.016
- 8 Harley, P., Otter, L., Guenther, A., & Greenberg, J.,2003. Micrometeorological and leaf-level
9 measurements of isoprene emissions from a southern African savanna. *Journal of*
10 *Geophysical Research: Atmospheres*, 108(D13). doi:10.1029/2002jd002592
- 11 Hayashi, E.,2016. Current status of commercial plant factories with led lighting market in
12 asia, europe, and other regions. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED*
13 *Lighting for Urban Agriculture* (pp. 295-308). Singapore: Springer Singapore.
- 14 Hellén, H., Kuronen, P., & Hakola, H.,2012. Heated stainless steel tube for ozone removal in
15 the ambient air measurements of mono- and sesquiterpenes. *Atmospheric*
16 *Environment*, 57, 35-40. doi:10.1016/j.atmosenv.2012.04.019
- 17 Hernández, R., Eguchi, T., Deveci, M., & Kubota, C.,2016. Tomato seedling physiological
18 responses under different percentages of blue and red photon flux ratios using LEDs
19 and cool white fluorescent lamps. *Scientia Horticulturae*, 213, 270-280.
20 doi:10.1016/j.scienta.2016.11.005
- 21 Higuchi, Y., & Hisamatsu, T.,2016. Light acts as a signal for regulation of growth and
22 development. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for*
23 *Urban Agriculture* (pp. 57-73). Singapore: Springer Singapore.
- 24 Hogewoning, S. W., Trouwborst, G., Maljaars, H., Poorter, H., van Ieperen, W., &
25 Harbinson, J.,2010. Blue light dose–responses of leaf photosynthesis, morphology,
26 and chemical composition of *Cucumis sativus* grown under different combinations of
27 red and blue light. *Journal of Experimental Botany*, 61(11), 3107-3117.
28 doi:10.1093/jxb/erq132
- 29 Ibaraki, Y.,2016. Lighting efficiency in plant production under artificial lighting and plant
30 growth modeling for evaluating the lighting efficiency. In T. Kozai, K. Fujiwara, &
31 E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 151-161). Singapore:
32 Springer Singapore.
- 33 Kim, E.-Y., Park, S.-A., Park, B.-J., Lee, Y., & Oh, M.-M.,2014. Growth and antioxidant
34 phenolic compounds in cherry tomato seedlings grown under monochromatic light-
35 emitting diodes. *Horticulture, Environment, and Biotechnology*, 55(6), 506-513.
36 doi:10.1007/s13580-014-0121-7
- 37 Klee, H. J.,2010. Improving the flavor of fresh fruits: genomics, biochemistry, and
38 biotechnology. *New Phytologist*, 187(1), 44-56. doi:10.1111/j.1469-
39 8137.2010.03281.x
- 40 Klee, H. J., & Tieman, D. M.,2018. The genetics of fruit flavour preferences. *Nature Reviews*
41 *Genetics*, 19(6), 347-356. doi:10.1038/s41576-018-0002-5
- 42 Kozai, T.,2016. Why LED lighting for urban agriculture? In T. Kozai, K. Fujiwara, & E. S.
43 Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 3-18). Singapore: Springer
44 Singapore.

- 1 Kozai, T., & Zhang, G.,2016. Some aspects of the light environment. In T. Kozai, K.
2 Fujiwara, & E. S. Runkle (Eds.), LED Lighting for Urban Agriculture (pp. 49-55).
3 Singapore: Springer Singapore.
- 4 Lanoue, J., Leonardos, E. D., Ma, X., & Grodzinski, B.,2017. The effect of spectral quality on
5 daily patterns of gas exchange, biomass gain, and water-use-efficiency in tomatoes
6 and lisianthus: An assessment of whole plant measurements. *Frontiers in Plant*
7 *Science*, 8(1076). doi:10.3389/fpls.2017.01076
- 8
9
10 Liu, Shirong, G., Taotao, C., Xu, Z., & Tezuka, T.,2012. Regulation of the growth and
11 photosynthesis of cherry tomato seedlings by different light irradiations of light
12 emitting diodes (LED). *African Journal of Biotechnology*, 11.
- 13
14 Liu, X. Y., Chang, T. T., Guo, S. R., Xu, Z. G., & Li, J. (2011). Effect of different light
15 quality of LED on growth and photosynthetic character in cherry tomato seedling.
- 16
17 Lu, N., & Mitchell, C. A.,2016. Supplemental lighting for greenhouse-grown fruiting
18 vegetables. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), LED Lighting for Urban
19 Agriculture (pp. 219-232). Singapore: Springer Singapore.
- 20
21 Matsuda, R., Ohashi-Kaneko, K., Fujiwara, K., Goto, E., & Kurata, K.,2004. Photosynthetic
22 characteristics of rice leaves grown under red light with or without supplemental blue
23 light. *Plant and Cell Physiology*, 45(12), 1870-1874. doi:10.1093/pcp/pch203
- 24
25 Mulder-Krieger, T., Verpoorte, R., Svendsen, A. B., & Scheffer, J. J. C.,1988. Production of
26 essential oils and flavours in plant cell and tissue cultures. A review. *Plant Cell,*
27 *Tissue and Organ Culture*, 13(2), 85-154. doi:10.1007/BF00034451
- 28
29 Naznin, M. T., Lefsrud, M., Gravel, V., & Azad, M. O. K.,2019. Blue light added with red
30 LEDs enhance growth characteristics, pigments content, and antioxidant capacity in
31 lettuce, spinach, kale, basil, and sweet pepper in a controlled environment. *Plants*
32 *(Basel)*, 8(4). doi:10.3390/plants8040093
- 33
34 Nogueire-McRae, T., Ryan, E. P., Jablonski, B. B. R., Carolan, M., Arathi, H. S., Brown, C. S.,
35 Saki, H. H., McKeen, S., Lapansky, E., & Schipanski, M. E.,2018. The role of urban
36 agriculture in a secure, healthy, and sustainable food system. *BioScience*, 68(10),
37 748-759. doi:10.1093/biosci/biy071
- 38
39
40 Olle, M., & Viršile, A.,2013. The effects of light-emitting diode lighting on greenhouse plant
41 growth and quality. *Agricultural and Food Science*, 22(2). doi:10.23986/afsci.7897
- 42
43 Ouzounis, T., Heuvelink, E., Ji, Y., Schouten, H., Visser, R., & Marcelis, L. F. M.,2016. Blue
44 and red LED lighting effects on plant biomass, stomatal conductance, and metabolite
45 content in nine tomato genotypes. *Acta Horticulturae*, 1134, 251-258.
46 doi:10.17660/ActaHortic.2016.1134.34
- 47
48 Papadopoulos, A. P., & Pararajasingham, S.,1997. The influence of plant spacing on light
49 interception and use in greenhouse tomato (*Lycopersicon esculentum* Mill.): A
50 review. *Scientia Horticulturae*, 69(1), 1-29. doi:10.1016/S0304-4238(96)00983-1
- 51
52 Pennisi, G., Blasioli, S., Cellini, A., Maia, L., Crepaldi, A., Braschi, I., Spinelli, F., Nicola, S.,
53 Fernandez, J. A., Stanghellini, C., Marcelis, L. F. M., Orsini, F., & Gianquinto,
54 G.,2019. Unraveling the role of red:Blue LED lights on resource use efficiency and
55 nutritional properties of indoor grown sweet basil. *Frontiers in Plant Science*,
56 10(305). doi:10.3389/fpls.2019.00305
- 57
58
59
60
61
62
63
64
65

- 1 Petro-Turza, M.,1986. Flavor of tomato and tomato products. *Food Reviews International*,
2
3 2(3), 309-351. doi:10.1080/87559128609540802
- 4 Piovene, C., Orsini, F., Bosi, S., Sanoubar, R., Bregola, V., Dinelli, G., & Gianquinto,
5 G.,2015. Optimal red:blue ratio in LED lighting for nutraceutical indoor horticulture.
6 *Scientia Horticulturae*, 193, 202-208. doi:10.1016/j.scienta.2015.07.015
- 7 Royal Philips N.V. (2015). *Tune the light to meet the specific needs of each crop-GreenPower*
8 *LED reserach module*. Retrieved from www.philips.com/horti
- 9
10
11 Ruiz-Hernández, V., Roca, M. J., Egea-Cortines, M., & Weiss, J.,2018. A comparison of
12 semi-quantitative methods suitable for establishing volatile profiles. *Plant Methods*,
13 14, 67-67. doi:10.1186/s13007-018-0335-2
- 14
15 Satterthwaite, D., McGranahan, G., & Tacoli, C.,2010. Urbanization and its implications for
16 food and farming. *Philosophical Transactions of the Royal Society B: Biological*
17 *Sciences*, 365(1554), 2809-2820. doi:10.1098/rstb.2010.0136
- 18
19 Schneider, C. A., Rasband, W. S., & Eliceiri, K. W.,2012. NIH Image to ImageJ: 25 years of
20 image analysis. *Nature Methods*, 9(7), 671-675. doi:10.1038/nmeth.2089
- 21
22 Selli, S., Kelebek, H., Ayseli, M. T., & Tokbas, H.,2014. Characterization of the most aroma-
23 active compounds in cherry tomato by application of the aroma extract dilution
24 analysis. *Food Chemistry*, 165, 540-546. doi:10.1016/j.foodchem.2014.05.147
- 25
26 Shengxin, C., Chunxia, L., Xuyang, Y., Song, C., Xuelei, J., Xiaoying, L., Zhigang, X., &
27 Rongzhan, G.,2016. Morphological, photosynthetic, and physiological responses of
28 rapeseed leaf to different combinations of red and blue lights at the rosette stage.
29 *Frontiers in Plant Science*, 7, 1144-1144. doi:10.3389/fpls.2016.01144
- 30
31 Shimazaki, K.-i., Doi, M., Assmann, S. M., & Kinoshita, T.,2007. Light regulation of
32 stomatal movement. *Annual Review of Plant Biology*, 58(1), 219-247.
33 doi:10.1146/annurev.arplant.57.032905.105434
- 34
35 Shimizu, H.,2016. Effect of light quality on secondary metabolite production in leafy greens
36 and seedlings. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for*
37 *Urban Agriculture* (pp. 239-260). Singapore: Springer Singapore.
- 38
39 Smith, H.,1995. Physiological and ecological function within the phytochrome family.
40 *Annual Review of Plant Physiology and Plant Molecular Biology*, 46(1), 289-315.
41 doi:10.1146/annurev.pp.46.060195.001445
- 42
43 Spadafora, N. D., Cocetta, G., Ferrante, A., Herbert, R. J., Dimitrova, S., Davoli, D.,
44 Fernández, M., Patterson, V., Vozel, T., Amarysti, C., Rogers, H. J., & Müller, C.
45 T.,2019. Short-term post-harvest stress that affects profiles of volatile organic
46 compounds and gene expression in rocket salad during early post-harvest senescence.
47 *Plants (Basel, Switzerland)*, 9(1), 4. doi:10.3390/plants9010004
- 48
49
50
51 Tieman, D., Bliss, P., McIntyre, Lauren M., Blandon-Ubeda, A., Bies, D., Odabasi, Asli Z.,
52 Rodríguez, Gustavo R., van der Knaap, E., Taylor, Mark G., Goulet, C., Mageroy,
53 Melissa H., Snyder, Derek J., Colquhoun, T., Moskowit, H., Clark, David G., Sims,
54 C., Bartoshuk, L., & Klee, Harry J.,2012. The chemical interactions underlying
55 tomato flavor preferences. *Current Biology*, 22(11), 1035-1039.
56 doi:10.1016/j.cub.2012.04.016
- 57
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47
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65
- Tieman, D., Zhu, G., Resende, M. F. R., Lin, T., Nguyen, C., Bies, D., Rambla, J. L., Beltran, K. S. O., Taylor, M., Zhang, B., Ikeda, H., Liu, Z., Fisher, J., Zemach, I., Monforte, A., Zamir, D., Granell, A., Kirst, M., Huang, S., & Klee, H.,2017. A chemical genetic roadmap to improved tomato flavor. *Science*, 355(6323), 391-394.
doi:10.1126/science.aal1556
- Ting, K. C., Lin, T., & Davidson, P. C.,2016. Integrated urban controlled environment agriculture systems. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 19-36). Singapore: Springer Singapore.
- Touliatos, D., Dodd, I. C., & McAinsh, M.,2016. Vertical farming increases lettuce yield per unit area compared to conventional horizontal hydroponics. *Food and energy security*, 5(3), 184-191. doi:10.1002/fes3.83
- Wollaeger, H. M., & Runkle, E. S.,2014. Growth of impatiens, petunia, salvia, and tomato seedlings under blue, green, and red light-emitting diodes. 49(6), 734.
doi:10.21273/hortsci.49.6.734

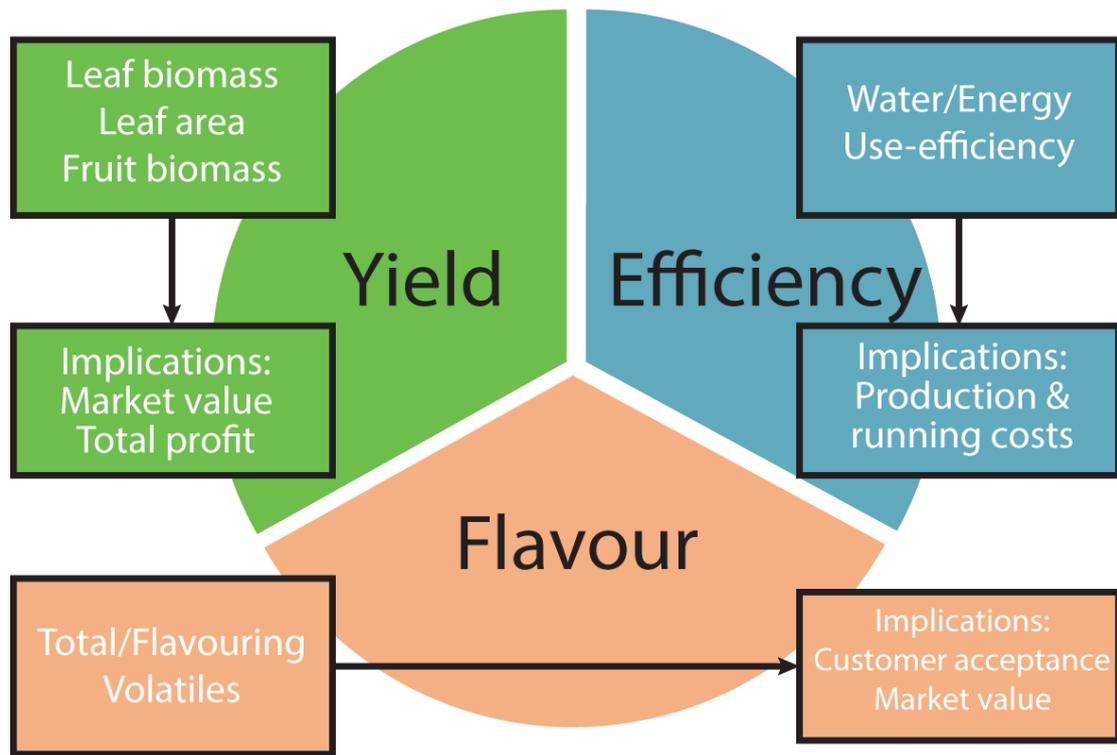
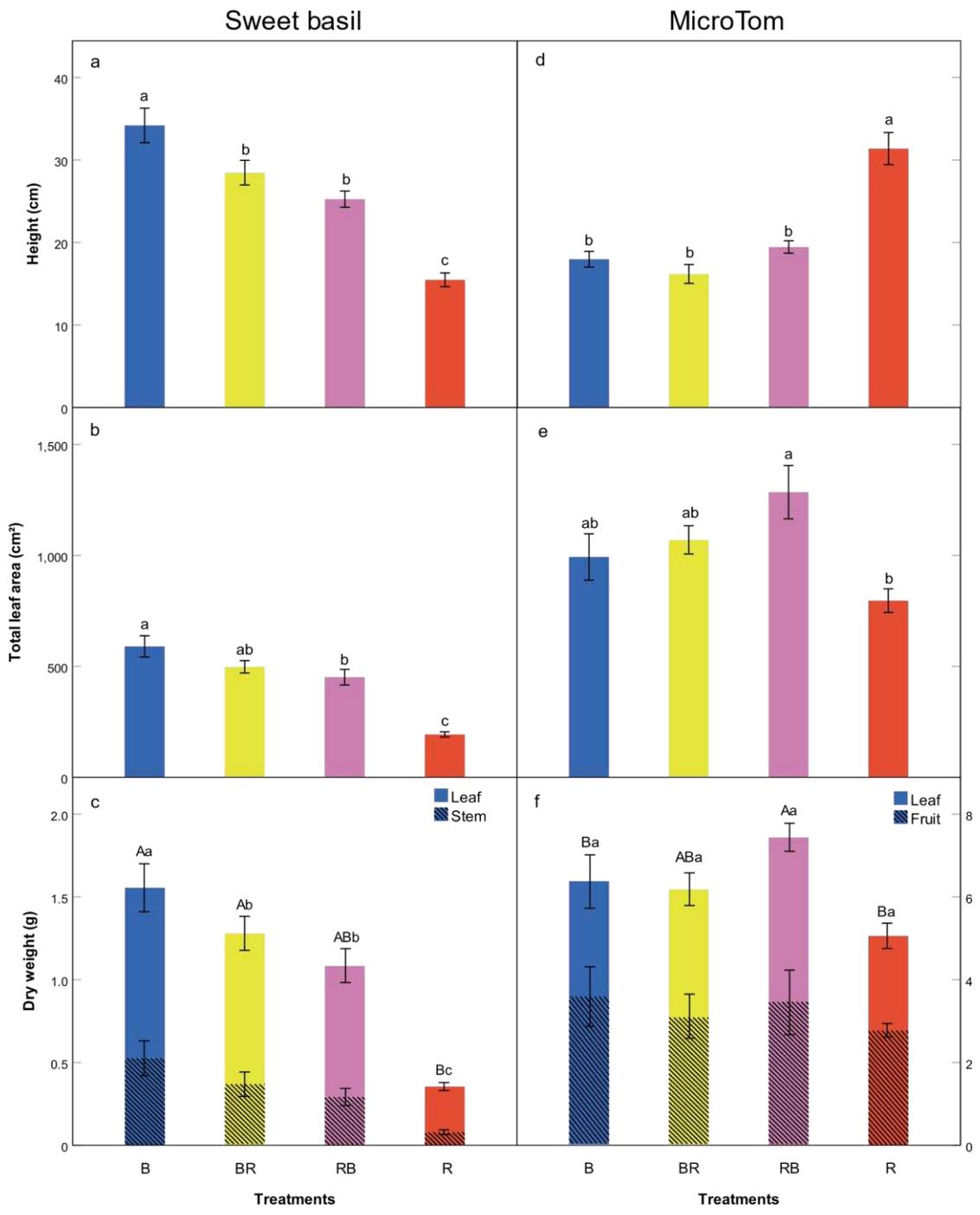


Figure 1. Illustration of the three factors in the assessment framework and specific factors related to each.

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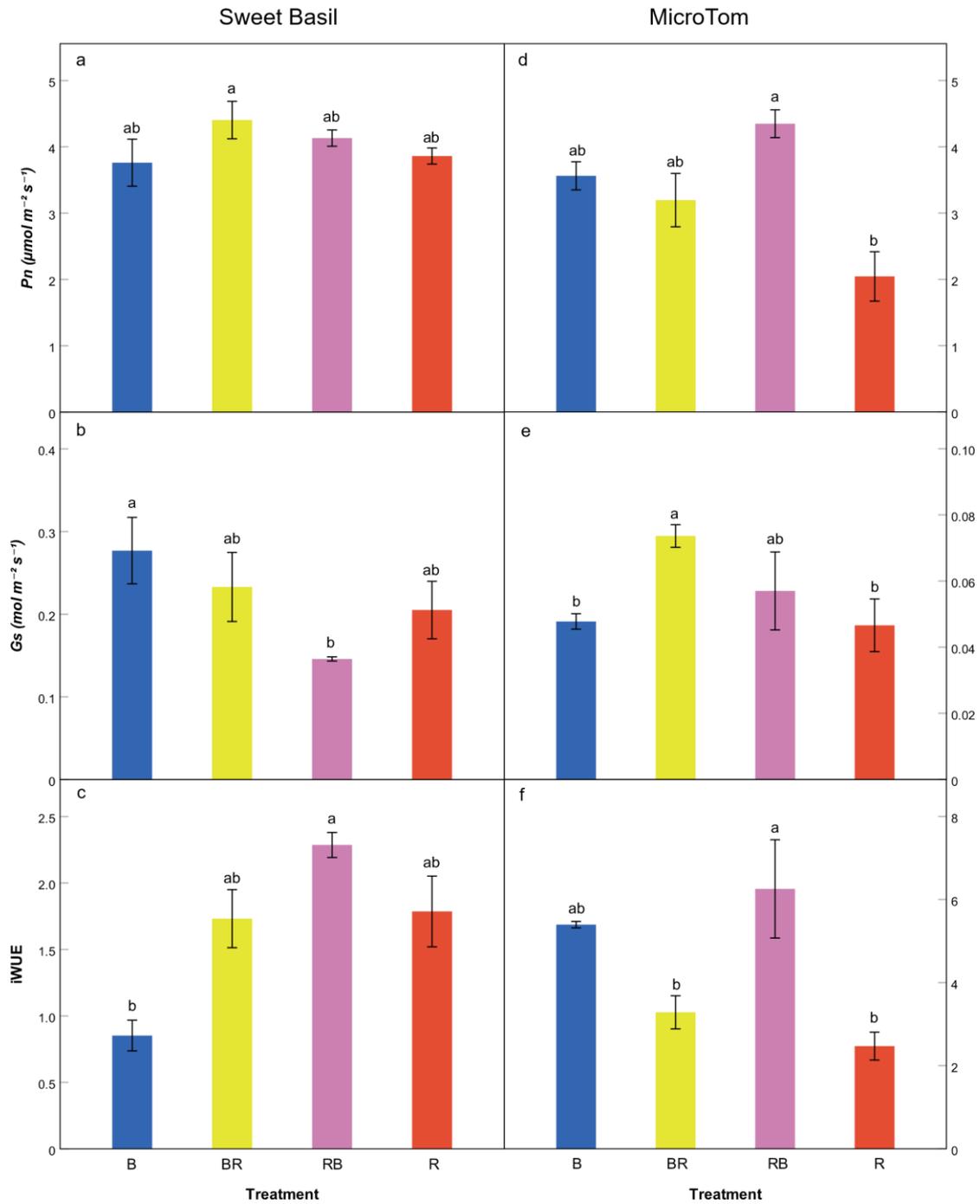


Figure 3. The effect of LED light treatment on net photosynthesis (P_n), stomatal conductance (G_s) and instantaneous water-use-efficiency (iWUE) of sweet basil (left-hand panels) on 5-weeks and MicroTom (right-hand panels) on 7-weeks. Plants grown under B (blue), BR (yellow), RB (purple), R (vermilion)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

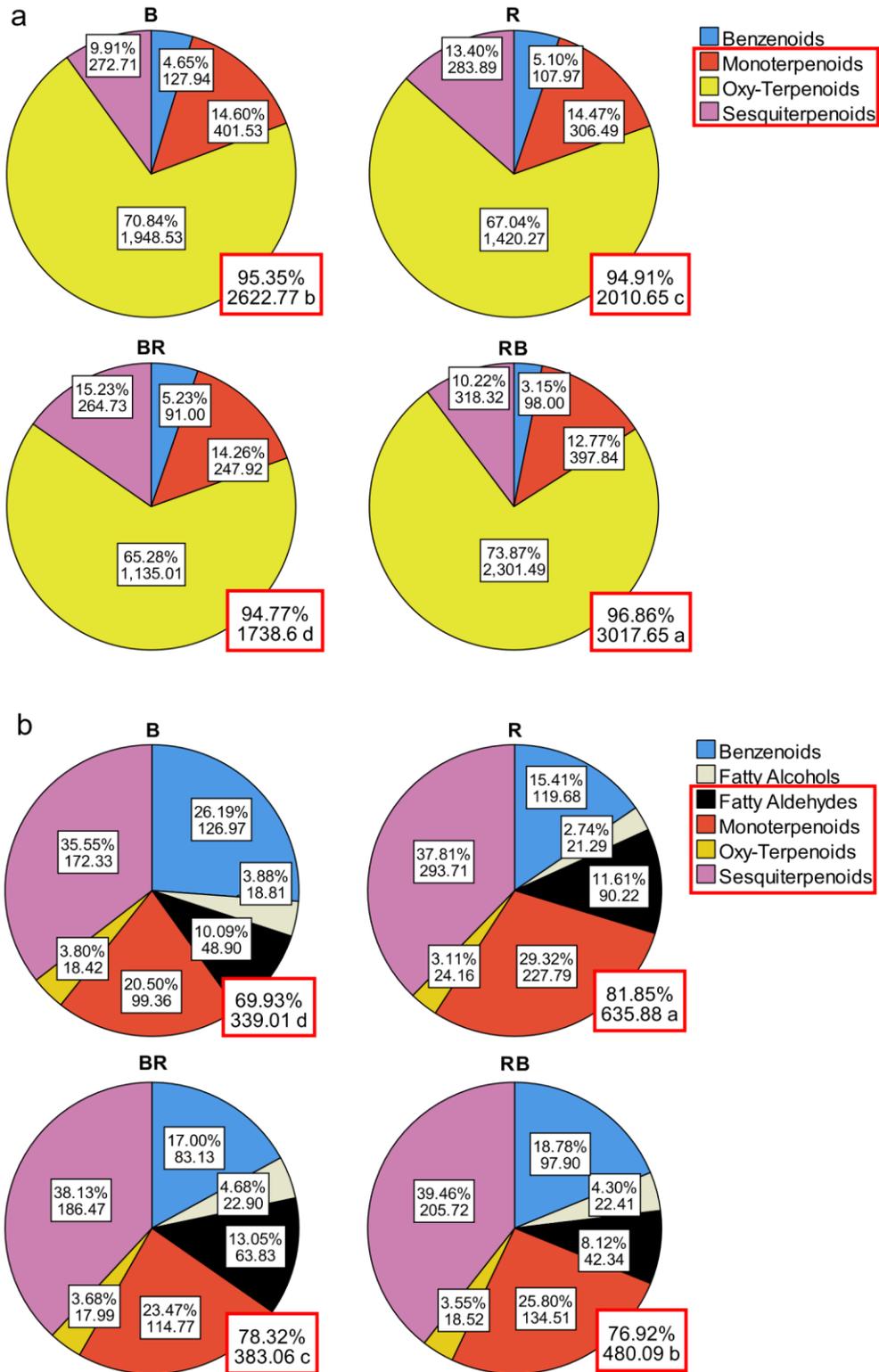
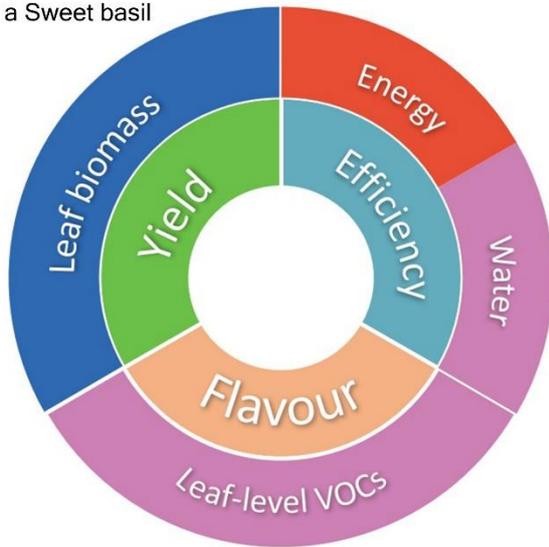


Figure 4. The effect of LED light treatment on volatile emissions from 5-weeks sweet basil (a) and 7-weeks MicroTom (b). Black-framed boxes on each pie indicate the percentage (top) and emission rate (ng m⁻² leaf s⁻¹, bot) of main volatile classes. Red-framed boxes indicate the percentage and emission 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

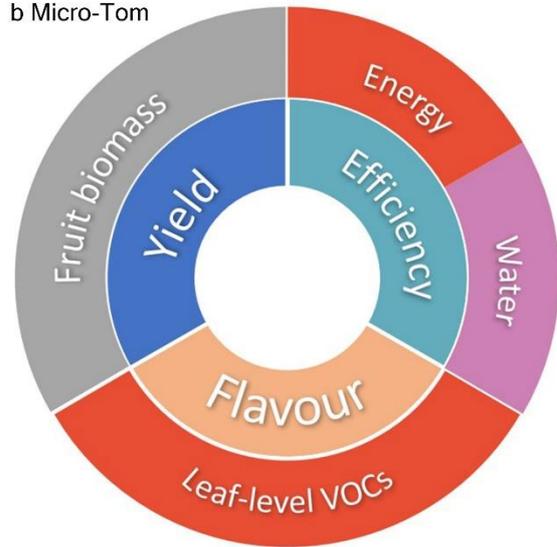


Figure 5. Overall recommendations to optimise production of sweet basil (a) and MicroTom (b). Basil: 100% blue (blue) maximised **yield** (leaf biomass), 66% red (purple) promoted **flavour**; MicroTom: 66% red promoted **yield** (leaf biomass) but fruit biomass was same between treatments (indicated 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

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**

11 With increasing urbanisation and consumer concerns over food miles, indoor urban plant
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.

26

27 **Keywords:** [Crop improvement](#), Light emitting diodes (LEDs), ~~Plant factories, crop~~
28 ~~improvement, *Ocimum basilicum*, Plant factories, *Solanum lycopersicum*, *Lycopersicon*~~

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 (Nogeire-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 salad~~ leaves), but also specific components associated with further
50 financial returns such as essential oils, herbal supplements, soft fruits, and nutritional or
51 pharmaceutical 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

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

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

81 Different wavelengths of light also appear to alter secondary metabolism, associated with crop

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

100 Red-rich LEDs are currently used in most facilities as they have low initial and operating
101 (energy) costs (Kozai and Zhang, 2016) e.g. high photosynthetic photon efficiency (Ibaraki,
102 2016). Water and nutrient use efficiency (WUE, NUE) depend on physiological (e.g. stomatal
103 and metabolic) characteristics, and although relatively high (and constant) across PFALs, can
104 still be improved through lighting choice (Brandon et al., 2016). Increasing energy costs, the
105 location of PFALs in the urban environment with high water costs and consumer demand for
106 low environmental footprint may prompt growers to prioritise the efficiency of their operation.

107 Previous studies of crop responses to different LED lights in indoor controlled environments
108 have generally focused on a single factor (crop productivity, resource use efficiency, and/or
109 quality). Relatively few have simultaneously investigated these factors, and differences in

110 experimental conditions, research facilities and interests have resulted in inconsistent
111 conclusions and recommendations (Carvalho et al., 2016; Lanoue et al., 2017; Pennisi et al.,
112 2019) ~~with~~. While most of the data from plant factories and companies ~~are~~ not publicly
113 accessible. There is a clear need, therefore, for a flexible evaluation framework to assist the
114 grower in optimising light conditions for indoor crop cultivation.

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

121

122 **2. Methods**

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

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

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

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

146 2.2. Morphological measurements

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

155 2.3. Leaf-level gas exchange and resource use efficiency

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

163 conductance (G_s) and transpiration rates (T_r) were logged. The Li-6400XT cuvette remained
164 on the leaf for a further 15 minutes to finish volatile sample collection. ~~Leaves-Any tomato~~
165 ~~leaves~~ insufficiently large to fill the chamber were photographed in-situ and the sampled leaf
166 area subsequently calculated using Image J software (Schneider et al., 2012). Water use
167 efficiency was estimated as instantaneous water-use-efficiency (iWUE) ~~and was~~ defined as the
168 ratio of photosynthesis to transpiration. Energy efficiency was estimated as the relative energy
169 usage based on the power consumption of LED modules from manufacture's product manual
170 (Royal Philips N.V.; 2015).

171 **2.4. Volatile sampling and analysis**

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

189 **2.5. Assessment framework**

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

199 **2.6. Data analysis**

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

205

206 **3. Results**

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

213 **3.1. Yield**

214 Yields strongly depended on the light treatment (e.g. proportion of blue-to-red light) in both

215 crops, but there were species differences. In sweet basil, blue light significantly ($p < 0.05$)
216 enhanced height, leaf area and total biomass, with plants grown under B ~~were~~ more than double
217 the height of those grown under R (Fig. 2a). Total leaf area (Fig. 2b) and leaf and stem dry
218 weight (Fig. 2c) showed similar trends, with leaf area and biomass of plants grown under R
219 only one-third of those grown under B. ~~The harvest index (leaf biomass / shoot biomass) of~~
220 ~~plants under R was significantly higher (by 7-18%) than the other treatments (Fig 2d), but this~~
221 ~~was likely due to the remarkably low stem biomass under R, suggesting this may not be a good~~
222 ~~measure to use for this assessment.~~

223 Micro-Tom grown under R were twice the height of those grown with other treatments (Fig.
224 2de) but had significantly lower (~20-38%) total leaf area (Fig. 2ef) and dry weight (Fig. 2fg).
225 Blue light enhanced both leaf area and dry weight with plants in treatment RB having the
226 greatest values, although not statistically different from those grown under BR and B conditions
227 (Fig. 2ef, fg). Light treatment did not affect ~~either~~ fruit dry weight (Fig. 2fg), ~~or harvest index~~
228 ~~(Fig. 2h), calculated as fruit biomass / shoot biomass. Fruit mass~~which was not correlated with
229 height or dry weight.

230 3.2. Efficiency

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

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

240 Energy usage was dependent on the power consumption of the LED modules. The individual
241 blue and red LED light modules used here provided almost identical light intensity (photon

242 flux). However, the blue LED module consumed nearly 50% more power than the red module
243 (Table. 1), resulting in relatively higher running costs. Hence, increasing the ratio of red light
244 improves energy use regardless of species, minimising running costs.

245 In summary, light treatment RB increased iWUE and R increased relative energy use for both
246 species.

247 **3.3. Flavour**

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

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

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

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268 4. Discussion

269 4.1. Yield

270 For sweet basil, all yield-related parameters (height, leaf area, leaf and stem dry weight)
271 increased as the ratio of blue light increased. Under B light, basil plants were tall (~35cm) with
272 large, well expanded leaves, compared with only ~16cm under R light, which also showed the
273 lowest fresh weight per unit height (“compactness”; see Fig. S2a). This “red light syndrome”
274 of stunted height and small crumpled leaves has been reported previously in basil and other
275 species (Brown et al., 1995; Naznin et al., 2019), and limits production ~~with leaf biomass of~~
276 ~~basil grown under R attaining only 28% of that leaf biomass of B light (Fig. 2c). while~~
277 ~~apparently inflating the harvest index (Fig. 2d), therefore HI is may not be a good measure for~~
278 ~~‘Yield’ in basil under different light treatments.~~The causes of this plant physiological disorder
279 are still under investigation (Hogewoning et al., 2010; Shengxin et al., 2016). Blue light
280 generated the greatest yield (Fig. 5a), and therefore direct market value of sweet basil, and
281 would be recommended for growers seeking to maximise harvest.

282 In Micro-Tom, individual yield parameters responded differently to different light treatments.
283 Red light increased plant height (Fig. 2de) but resulted in a very loose structure (Fig. S2b), as
284 in other tomato cultivars and genotypes (Hernández et al., 2016; X. Y. Liu et al., 2011;
285 Ouzounis et al., 2016), with curling leaves and less total leaf area. All light treatments produced
286 similar fresh and dry fruit (unripe) biomass, indicating similar fruit production efficiency
287 between different light treatments. However, RB light produced the greatest leaf area (Fig. 2ef)
288 and shoot biomass (Fig. 2fg), and we therefore tentatively recommend it (Fig. 5b). While
289 monochromatic red light has been shown to enhance shoot dry biomass and leaf area of tomato
290 (Wollaeger and Runkle, 2014), our results suggest greater leaf biomass production under
291 polychromatic (BR and RB) light treatments, increasing with increasing proportion of red light.
292 ~~This reflects the agronomic reality of commercial crop production in indoor growth facilities.~~
293 ~~In practice, other parameters associated with yield should also be considered. Previous research~~
294 ~~has indicated that plant growth and differences in biomass accumulation may differentially~~

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295 change the light interception and intensity from top to base, thus accelerating differences in
296 total carbon assimilation and distribution across the treatments, and further affecting crop
297 production per unit area in the facility (Papadopoulos and Pararajasingham, 1997; Touliatos et
298 al., 2016). This reflects the agronomic reality of commercial crop production in indoor growth
299 facilities.

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

315 **4.2. Efficiency**

316 Instantaneous (photosynthetic) water use efficiency (iWUE), calculated as the leaf-level carbon
317 assimilation rate (CO₂) divided by the water transpiration (H₂O) rate, was used as an efficiency
318 indicator. RB produced the highest iWUE in both species and is recommended for indoor
319 cultivation (Fig. 5). The least efficient treatments were B in sweet basil (Fig. 3c), R and BR for
320 Micro-Tom (Fig. 3f), consistent with previous studies of both species (Pennisi et al., 2019)
321 (Lanoue et al., 2017). In both species, a combination of blue and red LED light promoted
322 photosynthesis. Although blue light increased stomatal conductance of sweet basil, net

323 photosynthesis rate was greatest under BR lights (Fig. 3b, a). Micro-Tom also showed varied
324 photosynthetic and stomatal responses, with maxima occurring under RB and BR light
325 respectively (Fig. 3d, e). ~~Therefore~~ Commercial growers need ~~therefore to~~ consider the trade-
326 off between total carbon assimilation (yield) and total resource usage. The iWUE is a
327 physiological parameter that we applied in this framework to estimate leaf-level water usage.
328 However, the efficiency of water use in productivity (ratio of biomass to total water use) is
329 frequently used in real growth facilities to calculate overall WUE throughout the growth cycle
330 or season of specific species, and therefore could be more realistic for indoor crop production
331 and specific facilities. Light treatment can (marginally) improve whole plant water usage, but
332 optimising energy efficiency per unit area is much more dependent on the choice of lighting
333 system and likely of more interest to growers since the main costs for PFALs are associated
334 with electricity for lighting, as well as environmental control systems. RB light optimised
335 iWUE of both species, but R treatment delivers the best energy use (Table. 1). Hence R light is
336 recommended for saving costs (Fig. 5). Unit mass WUE and energy use efficiency (EUE) are
337 already generally high in plant factories or vertical farms (Pennisi et al., 2019; Ting et al., 2016).
338 If commercial growers are trying to improve the overall resource use efficiency of PFALs, the
339 trade-off between WUE and EUE would need to be carefully considered, as well as additional
340 indicators such as nutrient use and the costs of environmental regulation such as cooling and
341 dehumidification.

342 **4.3. Flavour**

343 The dominant compounds in plant aroma profiles are mono-, sesqui- and oxygenated terpenoids
344 and fatty aldehydes. Foliar emissions of these were used to assess flavour ~~in this study~~ (Fig. 4)
345 although post-harvest volatile emissions are arguably more relevant than those during
346 cultivation. The constitution of aroma compounds from sweet basil was little affected by light
347 treatment, although RB treatment would be recommended for maximising total emission rates
348 of aromatic volatiles (Fig. 4a, 5). Similarly, low intensity red or high intensity blue light
349 enhanced the concentration of volatiles in basil essential oils and leaf extracts (Amaki et al.,
350 2011; Pennisi et al., 2019). Although total emission rates were lower, red light enhanced

351 production of eugenol, an oxygenated terpenoid and powerful antioxidant, which is an
352 important component of essential oil and therefore flavour (Gülçin et al., 2012). Both emission
353 rate and proportion of leaf aromatic volatiles were stimulated by R light in Micro-Tom (Fig.
354 4b), which is therefore our recommendation (Fig. 5b).

355 Of considerably more importance to the grower, however, is the flavour of the final product
356 (tomato fruits and basil leaves post-harvest), which is highly consumer taste oriented. Long-
357 term post-harvest dynamics related to these treatments are currently unknown, and it is not clear
358 how good a proxy foliar emission during cultivation is. In addition to volatiles, mineral, sugar
359 and acid content (e.g. glutamate, malate) also determine the flavour of fruits or leaves (Petro-
360 Turza, 1986) and these were not measured here. Future trials should therefore adopt fruit or leaf
361 tissue extractions to determine more realistic flavour profiles, and growers seeking to optimise
362 flavour should undertake taste-testing of the final marketable product accounting for its
363 intended use (e.g. whether used raw or cooked, fresh or dried) (Klee and Tieman, 2018).
364 Moreover, the emission rate and composition of volatile contents can be expected to change
365 before and after harvest, and during storage (Spadafora et al., 2019). Greater emissions do not
366 necessarily equate to a better flavour (Mulder-Krieger et al., 1988), rather the relative
367 proportions and concentrations of particular compounds determine the aromatic and flavour
368 characteristics. Hence, flavour changes during production, storage, and distribution, as well as
369 the most appropriate volatile composition profile should also be assessed.

370 This study identified an optimum combination of blue-to-red LED light based on maximising
371 each of **yield**, **efficiency** and **flavour** for an herb (sweet basil) and a model crop (Micro-Tom)
372 grown in indoor plant factory. In so doing, we demonstrated for the first time how each can be
373 selectively enhanced through different wavelengths of light. No light treatment simultaneously
374 optimised all assessment criteria for either species, implying that growers can design bespoke
375 light treatments to optimise the specific attribute that best meets their market requirement.
376 Although a few previous studies (Aldarkazali et al., 2019; Pennisi et al., 2019) have
377 demonstrated the possibility of optimising ~~the performance of~~ light quality for multiple
378 assessment factors in environment-controlled growth facilities, none have demonstrated how

379 this knowledge should be applied by the growers. Hence, we emphasise the practical acquisition
380 of observations required to quantify each factor, and established a systematic, highly flexible
381 framework for all indoor growers and plant factories.

382 **5. Conclusion**

383 We ~~have~~ developed an innovative highly flexible framework that includes ~~for~~ all three key
384 factors (yield, efficiency and flavour) of indoor crop production to assess optimum lighting
385 regimes. The framework is a user-friendly tool that can be universally applied across the indoor
386 agriculture sector. The parameters used to assess each factor can be modified to target the
387 specific demands of the intended market. Individual growers can then identify the optimum
388 trade-off between those three factors based on their final markets and consumers acceptance.
389 Our recommendations are summarised in Fig. 5. Basil “yield” was maximised under 100% blue,
390 while “flavour” was enhanced under 33% blue + 66% red. In Micro-Tom, “yield” was
391 maximised under 33% blue + 66 % red, whereas “flavour” was enhanced under 100% red.
392 Efficiency in both species was optimised under 33% blue + 66% red (water-use-efficiency) and
393 100% red (energy-use-efficiency) lights. Depending on the market requirements, trials with
394 specific cultivars and final consumer taste or acceptability tests may be needed to determine the
395 ideal lighting regime for different indoor growing facilities.

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427 **References**

- Aldarkazali, M., Rihan, H. Z., Carne, D., & Fuller, M. P., 2019. The growth and development of sweet basil (*Ocimum basilicum*) and bush basil (*Ocimum minimum*) grown under three light regimes in a controlled environment. *Agronomy*, 9(11), 743. doi:10.3390/agronomy9110743
- Amaki, W., Yamazaki, N., Ichimura, M., & Watanabe, H., 2011. Effects of light quality on the growth and essential oil content in sweet basil. *Acta Horticulturae*, 907, 91-94. doi:10.17660/ActaHortic.2011.907.9
- Bardsley, N., Bland, S., Pattison, L., Pattison, M., Stober, K., Welsh, F., & Yamada, M., 2014. Solid-state lighting research and development: Multi-year program plan. Paper presented at the 2014 DOE SSL R&D Workshop, Tampa, Florida.
- Bertoli, A., Lucchesini, M., Mensuali-Sodi, A., Leonardi, M., Doveri, S., Magnabosco, A., & Pistelli, L., 2013. Aroma characterisation and UV elicitation of purple basil from different plant tissue cultures. *Food Chemistry*, 141(2), 776-787. doi:10.1016/j.foodchem.2013.02.081
- Brandon, M. F., Lu, N., Yamaguchi, T., Takagaki, M., Maruo, T., Kozai, T., & Yamori, W., 2016. Next evolution of agriculture: A review of innovations in plant factories. In (pp. 723-740).
- Brown, C. S., Schuerger, A. C., & Sager, J. C., 1995. Growth and photomorphogenesis of pepper plants under red light-emitting diodes with supplemental blue or far-red lighting. *120(5)*, 808. doi:10.21273/jashs.120.5.808
- Carvalho, S. D., Schwieterman, M. L., Abraham, C. E., Colquhoun, T. A., & Folta, K. M., 2016. Light quality dependent changes in morphology, antioxidant capacity, and volatile production in sweet basil (*Ocimum basilicum*). *Frontiers in Plant Science*, 7(1328). doi:10.3389/fpls.2016.01328
- Colquhoun, T. A., Schwieterman, M. L., Gilbert, J. L., Jaworski, E. A., Langer, K. M., Jones, C. R., Rushing, G. V., Hunter, T. M., Olmstead, J., Clark, D. G., & Folta, K. M., 2013. Light modulation of volatile organic compounds from petunia flowers and select fruits. *Postharvest Biology and Technology*, 86, 37-44. doi:10.1016/j.postharvbio.2013.06.013
- Elevitch, C., & Love, K., 2013. Adding value to locally grown crops in Hawai'i: A guide for small farm enterprise innovation: Permanent Agriculture Resources.
- Fang, W., 2016. Business models for plant factory with artificial lighting (PFAL) in taiwan. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 289-293). Singapore: Springer Singapore.
- Fankhauser, C., & Chory, J., 1997. Light control of plant development. *Annual Review of Cell and Developmental Biology*, 13(1), 203-229. doi:10.1146/annurev.cellbio.13.1.203
- Fisher, P., & Runkle, E., 2004. *Lighting up profits: Understanding greenhouse lighting*: Meister Media Worldwide.
- Fu, X., Chen, Y., Mei, X., Katsuno, T., Kobayashi, E., Dong, F., Watanabe, N., & Yang, Z., 2015. Regulation of formation of volatile compounds of tea (*Camellia sinensis*) leaves by single light wavelength. *Scientific Reports*, 5(1), 16858. doi:10.1038/srep16858

- Gülçin, İ., Elmastaş, M., & Aboul-Enein, H. Y., 2012. Antioxidant activity of clove oil – A powerful antioxidant source. *Arabian Journal of Chemistry*, 5(4), 489-499. doi:10.1016/j.arabjc.2010.09.016
- Harley, P., Otter, L., Guenther, A., & Greenberg, J., 2003. Micrometeorological and leaf-level measurements of isoprene emissions from a southern African savanna. *Journal of Geophysical Research: Atmospheres*, 108(D13). doi:10.1029/2002jd002592
- Hayashi, E., 2016. Current status of commercial plant factories with led lighting market in asia, europe, and other regions. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 295-308). Singapore: Springer Singapore.
- Hellén, H., Kuronen, P., & Hakola, H., 2012. Heated stainless steel tube for ozone removal in the ambient air measurements of mono- and sesquiterpenes. *Atmospheric Environment*, 57, 35-40. doi:10.1016/j.atmosenv.2012.04.019
- Hernández, R., Eguchi, T., Deveci, M., & Kubota, C., 2016. Tomato seedling physiological responses under different percentages of blue and red photon flux ratios using LEDs and cool white fluorescent lamps. *Scientia Horticulturae*, 213, 270-280. doi:10.1016/j.scienta.2016.11.005
- Higuchi, Y., & Hisamatsu, T., 2016. Light acts as a signal for regulation of growth and development. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 57-73). Singapore: Springer Singapore.
- Hogewoning, S. W., Trouwborst, G., Maljaars, H., Poorter, H., van Ieperen, W., & Harbinson, J., 2010. Blue light dose-responses of leaf photosynthesis, morphology, and chemical composition of *Cucumis sativus* grown under different combinations of red and blue light. *Journal of Experimental Botany*, 61(11), 3107-3117. doi:10.1093/jxb/erq132
- Ibaraki, Y., 2016. Lighting efficiency in plant production under artificial lighting and plant growth modeling for evaluating the lighting efficiency. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 151-161). Singapore: Springer Singapore.
- Kim, E.-Y., Park, S.-A., Park, B.-J., Lee, Y., & Oh, M.-M., 2014. Growth and antioxidant phenolic compounds in cherry tomato seedlings grown under monochromatic light-emitting diodes. *Horticulture, Environment, and Biotechnology*, 55(6), 506-513. doi:10.1007/s13580-014-0121-7
- Klee, H. J., 2010. Improving the flavor of fresh fruits: genomics, biochemistry, and biotechnology. *New Phytologist*, 187(1), 44-56. doi:10.1111/j.1469-8137.2010.03281.x
- Klee, H. J., & Tieman, D. M., 2018. The genetics of fruit flavour preferences. *Nature Reviews Genetics*, 19(6), 347-356. doi:10.1038/s41576-018-0002-5
- Kozai, T., 2016. Why LED lighting for urban agriculture? In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 3-18). Singapore: Springer Singapore.
- Kozai, T., & Zhang, G., 2016. Some aspects of the light environment. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 49-55). Singapore: Springer Singapore.

- Lanoué, J., Leonardos, E. D., Ma, X., & Grodzinski, B., 2017. The effect of spectral quality on daily patterns of gas exchange, biomass gain, and water-use-efficiency in tomatoes and lisianthus: An assessment of whole plant measurements. *Frontiers in Plant Science*, 8(1076). doi:10.3389/fpls.2017.01076
- Liu, Shirong, G., Taotao, C., Xu, Z., & Tezuka, T., 2012. Regulation of the growth and photosynthesis of cherry tomato seedlings by different light irradiations of light emitting diodes (LED). *African Journal of Biotechnology*, 11.
- Liu, X. Y., Chang, T. T., Guo, S. R., Xu, Z. G., & Li, J. (2011). Effect of different light quality of LED on growth and photosynthetic character in cherry tomato seedling.
- Lu, N., & Mitchell, C. A., 2016. Supplemental lighting for greenhouse-grown fruiting vegetables. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 219-232). Singapore: Springer Singapore.
- Matsuda, R., Ohashi-Kaneko, K., Fujiwara, K., Goto, E., & Kurata, K., 2004. Photosynthetic characteristics of rice leaves grown under red light with or without supplemental blue light. *Plant and Cell Physiology*, 45(12), 1870-1874. doi:10.1093/pcp/pch203
- Mulder-Krieger, T., Verpoorte, R., Svendsen, A. B., & Scheffer, J. J. C., 1988. Production of essential oils and flavours in plant cell and tissue cultures. A review. *Plant Cell, Tissue and Organ Culture*, 13(2), 85-154. doi:10.1007/BF00034451
- Naznin, M. T., Lefsrud, M., Gravel, V., & Azad, M. O. K., 2019. Blue light added with red LEDs enhance growth characteristics, pigments content, and antioxidant capacity in lettuce, spinach, kale, basil, and sweet pepper in a controlled environment. *Plants (Basel)*, 8(4). doi:10.3390/plants8040093
- Nogueira-McRae, T., Ryan, E. P., Jablonski, B. B. R., Carolan, M., Arathi, H. S., Brown, C. S., Saki, H. H., McKeen, S., Lapansky, E., & Schipanski, M. E., 2018. The role of urban agriculture in a secure, healthy, and sustainable food system. *BioScience*, 68(10), 748-759. doi:10.1093/biosci/biy071
- Olle, M., & Viršile, A., 2013. The effects of light-emitting diode lighting on greenhouse plant growth and quality. *Agricultural and Food Science*, 22(2). doi:10.23986/afsci.7897
- Ouzounis, T., Heuvelink, E., Ji, Y., Schouten, H., Visser, R., & Marcelis, L. F. M., 2016. Blue and red LED lighting effects on plant biomass, stomatal conductance, and metabolite content in nine tomato genotypes. *Acta Horticulturae*, 1134, 251-258. doi:10.17660/ActaHortic.2016.1134.34
- Papadopoulos, A. P., & Pararajasingham, S., 1997. The influence of plant spacing on light interception and use in greenhouse tomato (*Lycopersicon esculentum* Mill.): A review. *Scientia Horticulturae*, 69(1), 1-29. doi:10.1016/S0304-4238(96)00983-1
- Pennisi, G., Blasioli, S., Cellini, A., Maia, L., Crepaldi, A., Braschi, I., Spinelli, F., Nicola, S., Fernandez, J. A., Stanghellini, C., Marcelis, L. F. M., Orsini, F., & Gianquinto, G., 2019. Unraveling the role of red:Blue LED lights on resource use efficiency and nutritional properties of indoor grown sweet basil. *Frontiers in Plant Science*, 10(305). doi:10.3389/fpls.2019.00305
- Petro-Turza, M., 1986. Flavor of tomato and tomato products. *Food Reviews International*, 2(3), 309-351. doi:10.1080/87559128609540802

- Piovene, C., Orsini, F., Bosi, S., Sanoubar, R., Bregola, V., Dinelli, G., & Gianquinto, G., 2015. Optimal red:blue ratio in LED lighting for nutraceutical indoor horticulture. *Scientia Horticulturae*, 193, 202-208. doi:10.1016/j.scienta.2015.07.015
- Royal Philips N.V. (2015). *Tune the light to meet the specific needs of each crop-GreenPower LED reserach module*. Retrieved from www.philips.com/horti
- Ruiz-Hernández, V., Roca, M. J., Egea-Cortines, M., & Weiss, J., 2018. A comparison of semi-quantitative methods suitable for establishing volatile profiles. *Plant Methods*, 14, 67-67. doi:10.1186/s13007-018-0335-2
- Satterthwaite, D., McGranahan, G., & Tacoli, C., 2010. Urbanization and its implications for food and farming. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1554), 2809-2820. doi:10.1098/rstb.2010.0136
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), 671-675. doi:10.1038/nmeth.2089
- Selli, S., Kelebek, H., Ayseli, M. T., & Tokbas, H., 2014. Characterization of the most aroma-active compounds in cherry tomato by application of the aroma extract dilution analysis. *Food Chemistry*, 165, 540-546. doi:10.1016/j.foodchem.2014.05.147
- Shengxin, C., Chunxia, L., Xuyang, Y., Song, C., Xuelei, J., Xiaoying, L., Zhigang, X., & Rongzhan, G., 2016. Morphological, photosynthetic, and physiological responses of rapeseed leaf to different combinations of red and blue lights at the rosette stage. *Frontiers in Plant Science*, 7, 1144-1144. doi:10.3389/fpls.2016.01144
- Shimazaki, K.-i., Doi, M., Assmann, S. M., & Kinoshita, T., 2007. Light regulation of stomatal movement. *Annual Review of Plant Biology*, 58(1), 219-247. doi:10.1146/annurev.arplant.57.032905.105434
- Shimizu, H., 2016. Effect of light quality on secondary metabolite production in leafy greens and seedlings. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 239-260). Singapore: Springer Singapore.
- Smith, H., 1995. Physiological and ecological function within the phytochrome family. *Annual Review of Plant Physiology and Plant Molecular Biology*, 46(1), 289-315. doi:10.1146/annurev.pp.46.060195.001445
- Spadafora, N. D., Cocetta, G., Ferrante, A., Herbert, R. J., Dimitrova, S., Davoli, D., Fernández, M., Patterson, V., Vozel, T., Amarysti, C., Rogers, H. J., & Müller, C. T., 2019. Short-term post-harvest stress that affects profiles of volatile organic compounds and gene expression in rocket salad during early post-harvest senescence. *Plants (Basel, Switzerland)*, 9(1), 4. doi:10.3390/plants9010004
- Tieman, D., Bliss, P., McIntyre, Lauren M., Blandon-Ubeda, A., Bies, D., Odabasi, Asli Z., Rodríguez, Gustavo R., van der Knaap, E., Taylor, Mark G., Goulet, C., Mageroy, Melissa H., Snyder, Derek J., Colquhoun, T., Moskowitz, H., Clark, David G., Sims, C., Bartoshuk, L., & Klee, Harry J., 2012. The chemical interactions underlying tomato flavor preferences. *Current Biology*, 22(11), 1035-1039. doi:10.1016/j.cub.2012.04.016
- Tieman, D., Zhu, G., Resende, M. F. R., Lin, T., Nguyen, C., Bies, D., Rambla, J. L., Beltran, K. S. O., Taylor, M., Zhang, B., Ikeda, H., Liu, Z., Fisher, J., Zemach, I., Monforte, A., Zamir, D., Granell, A., Kirst, M., Huang, S., & Klee, H., 2017. A chemical genetic

roadmap to improved tomato flavor. *Science*, 355(6323), 391-394.
doi:10.1126/science.aal1556

Ting, K. C., Lin, T., & Davidson, P. C.,2016. Integrated urban controlled environment agriculture systems. In T. Kozai, K. Fujiwara, & E. S. Runkle (Eds.), *LED Lighting for Urban Agriculture* (pp. 19-36). Singapore: Springer Singapore.

Touliatos, D., Dodd, I. C., & McAinsh, M.,2016. Vertical farming increases lettuce yield per unit area compared to conventional horizontal hydroponics. *Food and energy security*, 5(3), 184-191. doi:10.1002/fes3.83

Wollaeger, H. M., & Runkle, E. S.,2014. Growth of impatiens, petunia, salvia, and tomato seedlings under blue, green, and red light-emitting diodes. *49(6)*, 734.
doi:10.21273/hortsci.49.6.734

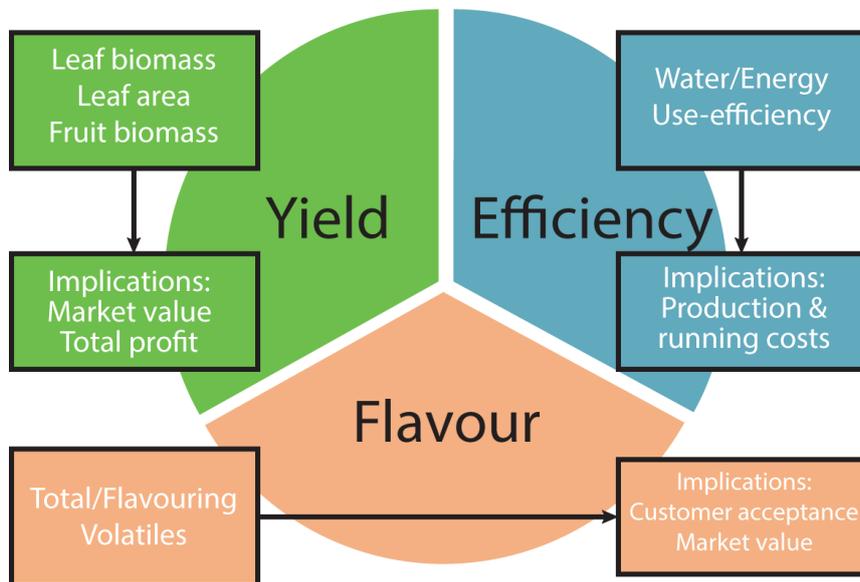
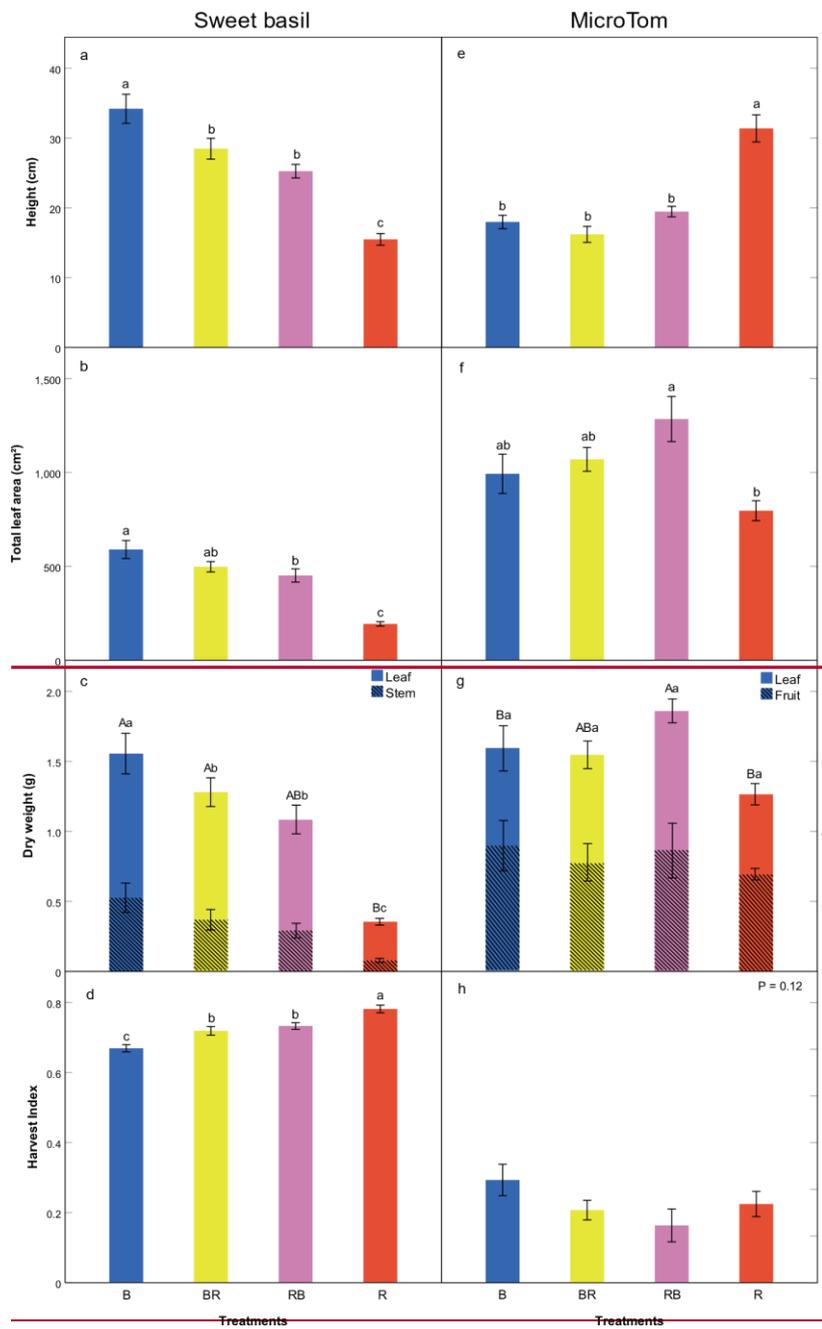


Figure 1. Illustration of the three factors in the assessment framework and specific factors related to each.



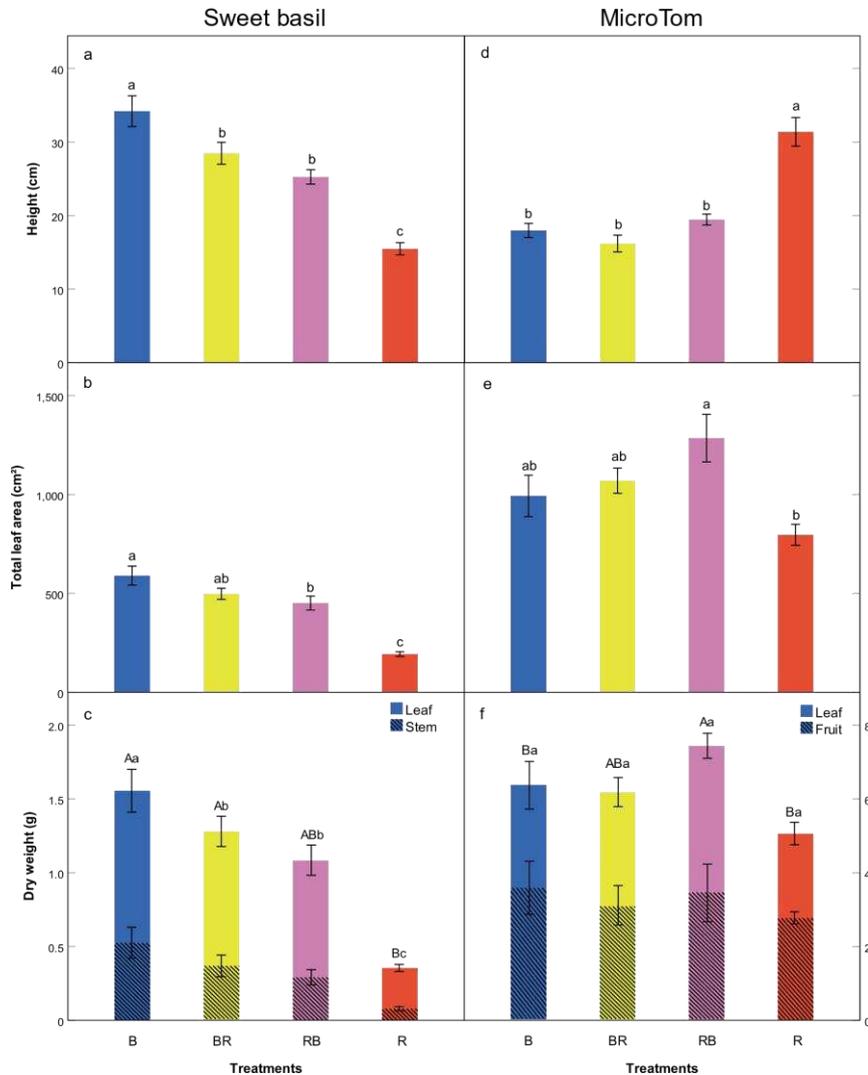


Figure 2. The effect of LED light treatments on yield parameters of sweet basil on 6-weeks (left-hand panels) and MicroTom on 13-weeks (right-hand panel). Quantification of height (a, de), total leaf area (b, ef), leaf/stem dry weight (c), fruit/leaf dry weight (fg)-harvest index (d, h) during the final destructive harvest under B (blue), BR (yellow), RB (purple), R (vermilion) treatments; lower cases indicate significant differences ($p < 0.05$, $n = 9$, \pm SE) between light treatments; in (c, fg), upper and lower cases indicate significant differences of leaf (clear bar) and stem/fruit (shade bar) between treatments, respectively.

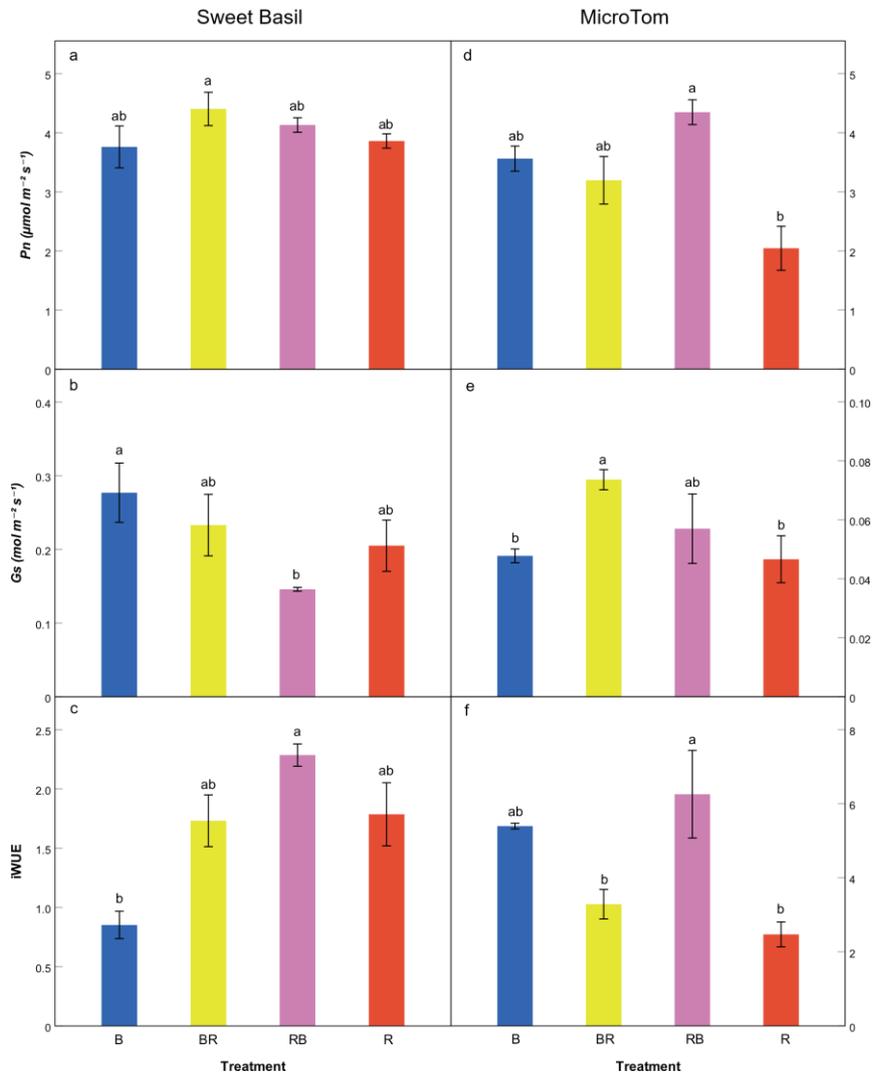


Figure 3. The effect of LED light treatment on net photosynthesis (P_n), stomatal conductance (G_s) and instantaneous water-use-efficiency (iWUE) of sweet basil (left-hand panels) on 5-weeks and MicroTom (right-hand panels) on 7-weeks. Plants grown under B (blue), BR (yellow), RB (purple), R (vermillion)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

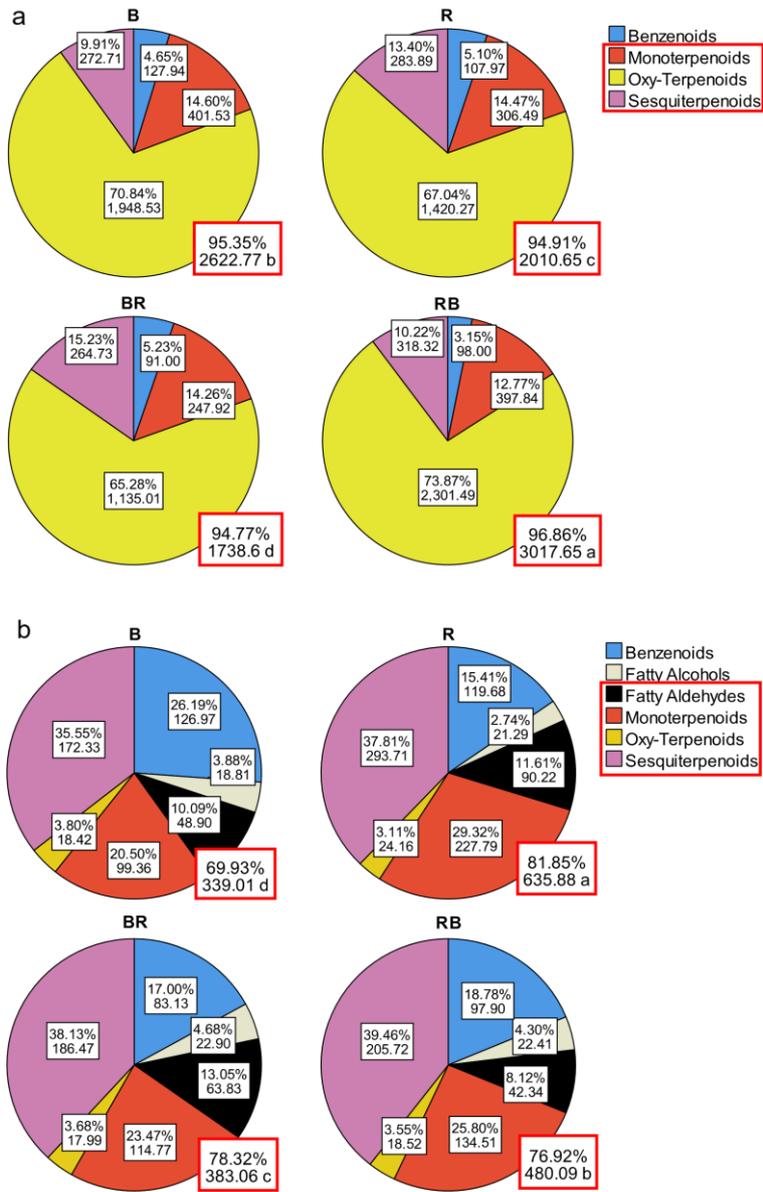


Figure 4. The effect of LED light treatment on volatile emissions from 5-weeks sweet basil (a) and 7-weeks MicroTom (b). Black-framed boxes on each pie indicate the percentage (top) and emission rate ($\text{ng m}^{-2} \text{ leaf s}^{-1}$, bot) of main volatile classes. Red-framed boxes indicate the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

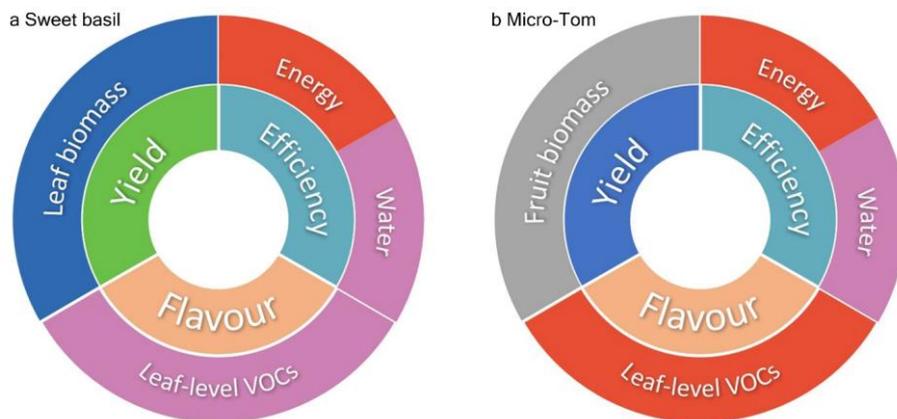


Figure 5. Overall recommendations to optimise production of sweet basil (a) and MicroTom (b). Basil: 100% blue (blue) maximised **yield** (leaf biomass), 66% red (purple) promoted **flavour**; MicroTom: 66% red promoted **yield** (leaf biomass) but fruit biomass was same between treatments (indicated 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
Blue LED	15 $\mu\text{mol/s}$	14 W	BR	1.26
			B	1.4