Article:

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

--Manuscript Draft--

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Abstract:	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 (Ocimum basilicum cv. Genovese) and tomato (Solanum lycopersicum 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.

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 µmol m-2 s-1

We calculated emissions of BVOC compounds in terms of mass per square meter of leaf area per second (ng m^{-2} *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 20oC 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 ± 2 µmol m−2 s−1) supply was constant across treatments.". PPFD of 115 µmol m−2 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 μmol m−2 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 begging 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 (2x3 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 basial 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

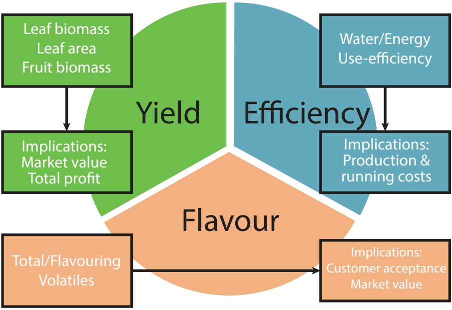


Figure 3. The effect of LED light treatment on net photosynthesis (Pn), stomatal conductance (Gs) and instantaneous water-use-efficiency (iWUE) of sweet basil (left-hand panels) on 5-weeks and MicroTom (right-hand panels) on 7-weeks. Plants

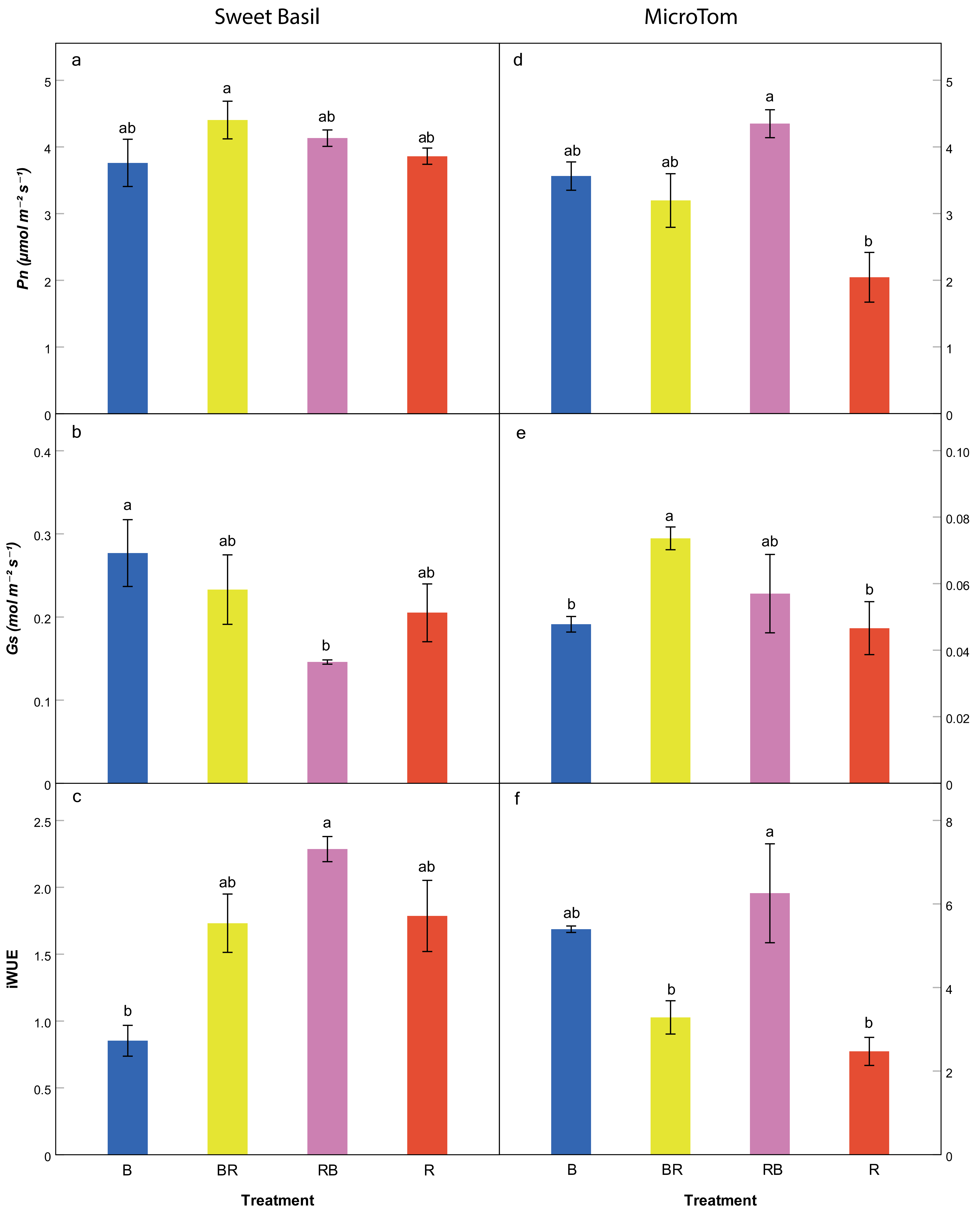


Figure 4. The effect of LED light treatment on volatile emissions from 5-weeks sweet basil (a) and 7-weeks

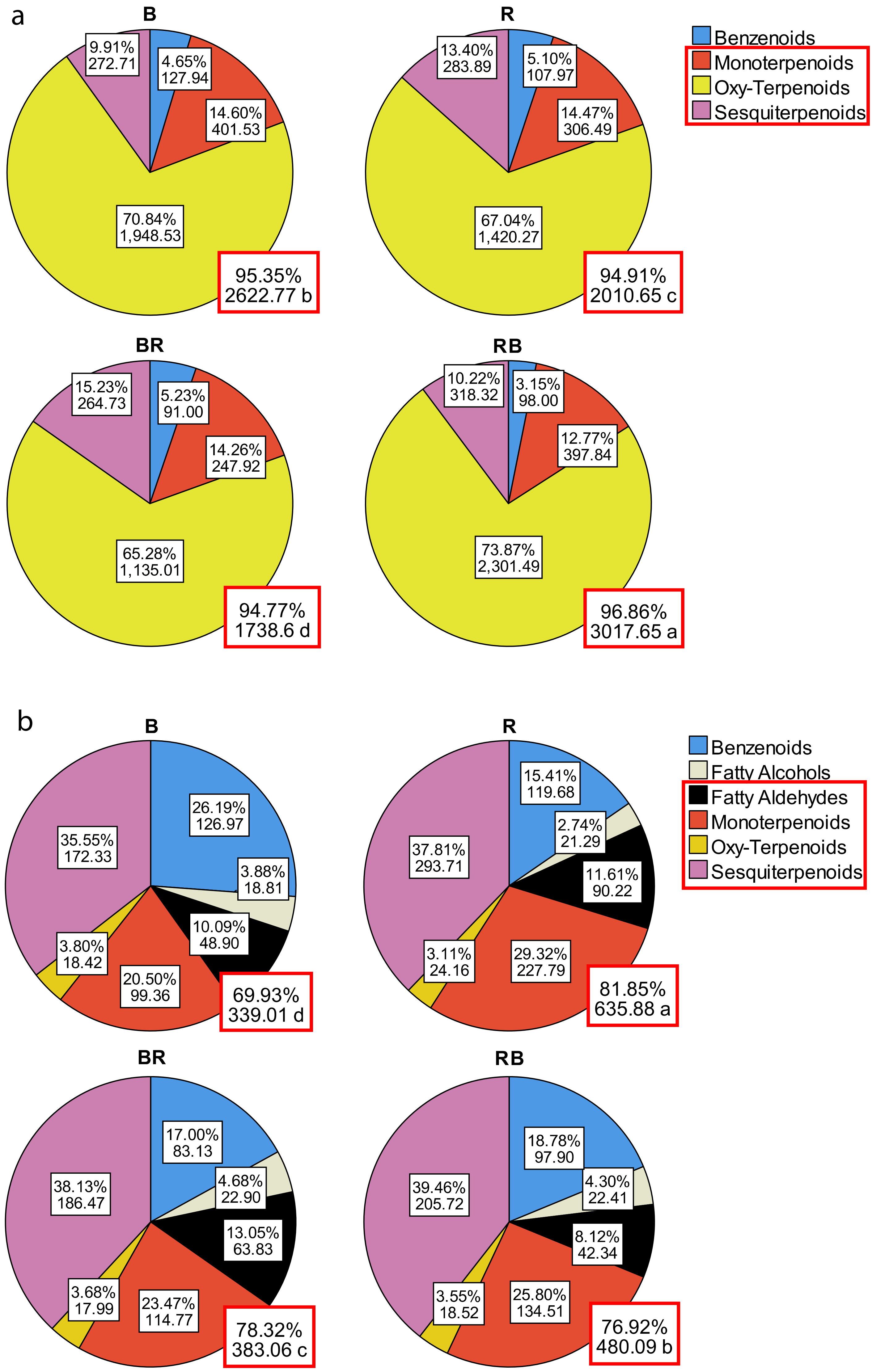


Figure 5. Overall recommendations to optimise production of sweet basil (a) and MicroTom (b). Basil: 100% blue (blue) maximised yield (leaf biomass), 66% red (purple) promoted flavour; MicroTom: 66% red promoted yield (leaf biomass) but

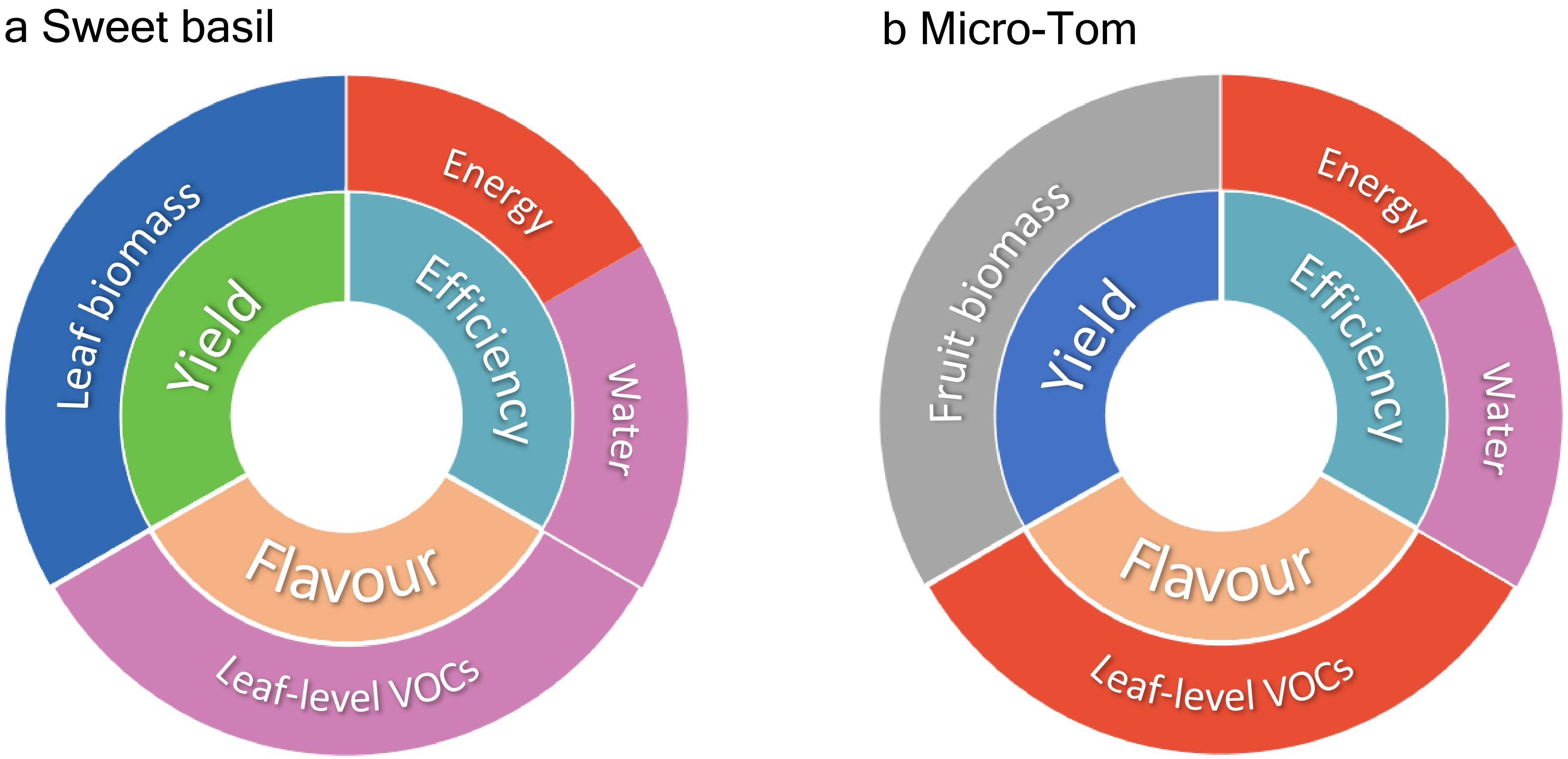
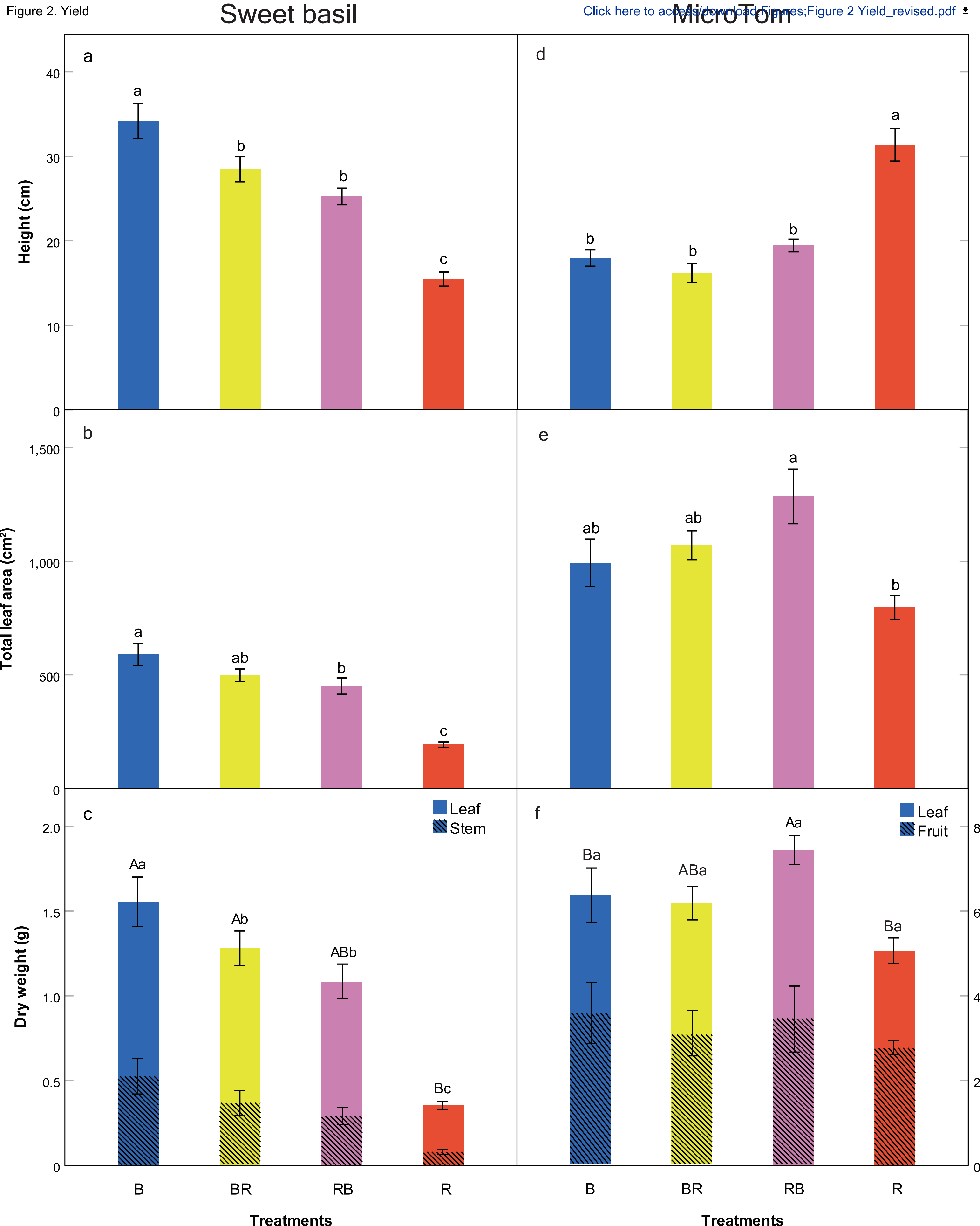


Figure 2. Yield



Supplementary Material

Supplementary Material_unmarked

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

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Abstract

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 (*Ocimum basilicum* cv. Genovese) and tomato (*Solanum lycopersicum* 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.

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

Introduction

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

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

Indoor cultivation of green leafy vegetables and fruiting crops enables control of lighting to optimise yield, resource use efficiency and flavour according to the target market. Both light intensity (the photosynthetic photon flux density, PPFD), and the spectral distribution of UV-B (280-315nm), UV-A (315-400 nm), blue (400-500 nm), red (620-700 nm) and far-red (700-850 nm) light affect plant growth and development (Higuchi and Hisamatsu, 2016). LEDs of differing wavelengths can be used to control plant morphogenesis and enhance the production of secondary metabolites, increasing efficiency and adding value to crops by enhancing nutrient content and/or taste (Kozai and Zhang, 2016; Lu and Mitchell, 2016). Monochromatic blue and red light induce specific light signalling responses in plants, significantly affecting morphological, physiological and biochemical processes through alterations in photosynthetic activities and/or photoreceptors (Higuchi and Hisamatsu, 2016). Blue light is mainly absorbed by phototropins, chloroplasts and cryptochromes causing responses including phototropism, enhanced efficiency of chlorophylls and carotenes (Liu et al., 2012), and stomatal opening (Shimazaki et al., 2007). Red light is absorbed by phytochromes, regulating major developmental transitions (e.g. germination and flowering) (Smith, 1995), and plant vegetative and reproductive growth . Blue and red lights can act synergistically to amplify their individual signalling effects (Fankhauser and Chory, 1997).

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

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

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

Previous studies of crop responses to different LED lights in indoor controlled environments have generally focused on a single factor (crop productivity, resource use efficiency, and/or quality). Relatively few have simultaneously investigated these factors, and differences in experimental conditions, researchfacilities and interests have resulted in inconsistent conclusions and recommendations (Carvalho et al., 2016; Lanoue et al., 2017; Pennisi et al., 2019) with most of the data from plant factories and companies not publicly accessible. There is a clear need, therefore, for a flexible evaluation framework to assist the grower in optimising light conditions for indoor crop cultivation.

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

2. Methods

2.1. Plant materials and growth conditions

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

The hydroponic growth racks were lit with mixed LED lighting and maintained at constant temperature (20±2 ℃) and relative humidity (60±10%). Hydroponic irrigation was initially supplied using an ebb and flow system with tap water every four days, gradually increasing to daily. Plants were rotated every two weeks in racks. Philips GreenPower® LED research module strips (Philips Ltd, UK) were installed on the top of each rack, 40 cm above the bench. Racks were irradiated for 14h from 6:00 a.m. to 8:00 p.m. using combinations of blue (400-500 nm) and red (600-700 nm) LEDs. The four treatments were 100% blue (B), 66% blue + 33% red (BR), 33 % blue + 66% red (RB) and 100% red (R). The total photon flux density at leaf level height ranged from 115 to 180 μmol m^{-2} s^{-1} according to leaf distance to the lighting module, and was constant across treatments. The distribution of quantum energy (Figure S1) was measured using a Jaz spectrometer (Ocean Optics Inc, UK), the spectral distributions are consistent in racks and shown in Table S1 together with the average vertical profile.

2.2. Morphological measurements

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

2.3. Leaf-level gas exchange and resource use efficiency

Physiological responses and volatile emissions were sampled in-situ for two consecutive weeks in both species (Weeks 4 and 5 for basil, and 6 and 7 for Micro-Tom). The newest fully developed leaf from each of 3 randomly selected replicates per treatment was sampled using a Li-6400XT (Li-COR Inc., USA), three hours after the lights were switched on. The leaf was placed in a 2 x 3 cm clear-top chamber under conditions that closely replicated the growing environment (leaf temperature 22℃, relative humidity 50-60%, and CO_2 concentration 400 μL L^{-1}). Following a 5-minute period of stabilisation, net photosynthesis (*Pn*), stomatal conductance (*Gs*) and transpiration rates (*Tr*) were logged. The Li-6400XT cuvette remained on the leaf for a further 15 minutes to finish volatile sample collection. Any tomato leaves insufficiently large to fill the chamber were photographed in-situ and the sampled leaf area subsequently calculated using Image J software (Schneider et al., 2012). Water use efficiency was estimated as instantaneous water-use-efficiency (iWUE) defined as the ratio of photosynthesis to transpiration. Energy efficiency was estimated as the relative energy usage based on the power consumption of LED modules from manufacture's product manual (Royal Philips N.V.; 2015).

2.4. Volatile sampling and analysis

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

2.5. Assessment framework

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

2.6. Data analysis

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

3. Results

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

3.1. Yield

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

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

3.2. Efficiency

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

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

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

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

3.3. Flavour

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

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

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

4. Discussion

4.1. Yield

For sweet basil, all yield-related parameters (height, leaf area, leaf and stem dry weight) increased as the ratio of blue light increased. Under B light, basil plants were tall (~35cm) with large, well expanded leaves, compared with only ~16cm under R light, which also showed the lowest fresh weight per unit height ("compactness"; see Fig. S2a). This "red light syndrome" of stunted height and small crumpled leaves has been reported previously in basil and other species (Brown et al., 1995; Naznin et al., 2019), and limits production with leaf biomass of basil grown under R attaining only 28% of that of B light (Fig. 2c). The causes of this plant physiological disorder are still under investigation (Hogewoning et al., 2010; Shengxin et al., 2016). 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.

In Micro-Tom, individual yield parameters responded differently to different light treatments. Red light increased plant height (Fig. 2d) but resulted in a very loose structure (Fig. S2b), as in other tomato cultivars and genotypes (Hernández et al., 2016; X. Y. Liu et al., 2011; Ouzounis et al., 2016), with curling leaves and less total leaf area. All light treatments produced similar fresh and dry fruit (unripe) biomass, indicating similar fruit production efficiency between different light treatments. However, RB light produced the greatest leaf area (Fig. 2e) and shoot biomass (Fig. 2f), and we therefore tentatively recommend it (Fig. 5b). While monochromatic red light has been shown to enhance shoot dry biomass and leaf area of tomato (Wollaeger and Runkle, 2014), our results suggest greater leaf biomass production under polychromatic (BR and RB) light treatments, increasing with increasing proportion of red light. This reflects the agronomic reality of commertial crop production in indoor growth facilities. In practice, other parameters associated with yield should also be considered. Previous research indicated that plant growth and differences in biomass accumulation may differentially change the light interception and intensity from top to base, thus accelerating differences in total carbon assimilation and distribution across the treatments, and further affecting crop production per unit area in the facility (Papadopoulos and Pararajasingham, 1997; Touliatos et al., 2016). This reflects the agronomic reality of commercial crop production in indoor growth facilities.

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

4.2. Efficiency

Instantaneous (photosynthetic) water use efficiency (iWUE), calculated as the leaf-level carbon assimilation rate (CO_2) divided by the water transpiration (H_2O) rate, was used as an efficiency indicator. RB produced the highest iWUE in both species and is recommended for indoor cultivation (Fig. 5). The least efficient treatments were B in sweet basil (Fig. 3c), R and BR for Micro-Tom (Fig. 3f), consistent with previous studies of both species (Pennisi et al., 2019) (Lanoue et al., 2017). In both species, a combination of blue and red LED light promoted photosynthesis. Although blue light increased stomatal conductance of sweet basil, net photosynthesis rate was greatest under BR lights (Fig. 3b, a). Micro-Tom also showed varied photosynthetic and stomatal responses, with maxima occurring under RB and BR light respectively (Fig. 3d, e). Therefore commercial growers need to consider the trade-off between total carbon assimilation (yield) and total resource usage. The iWUE is a physiological parameter that we applied in this framework to estimate leaf-level water usage. However, the efficiency of water use in productivity (ratio of biomass to total water use) is frequently used in real growth facilities to calculate overall WUE throughout the growth cycle or season of specific species, and therefore could be more realistic for indoor crop production and specific facilities. Light treatment can (marginally) improve whole plant water usage, but optimising energy efficiency per unit area is much more dependent on the choice of lighting system and likely of more interest to growers since the main costs for PFALs are associated with electricity for lighting, as well as environmental control systems. RB light optimised iWUE of both species, but R treatment delivers the best energy use (Table. 1). Hence R light is recommended for saving costs (Fig. 5). Unit mass WUE and energy use efficiency (EUE) are already generally high in plant factories or vertical farms (Pennisi et al., 2019; Ting et al., 2016). If commercial growers are trying to improve the overall resource use efficiency of PFALs, the trade-off between WUE and EUE would need to be carefully considered, as well as additional indicators such as nutrient use and the costs of environmental regulation such as cooling and dehumidification.

4.3. Flavour

The dominant compounds in plant aroma profiles are mono-, sesqui- and oxygenated terpenoids and fatty aldehydes. Foliar emissions of these were used to assess flavour (Fig. 4) although post-harvest volatile emissions are arguably more relevant than those during cultivation. The constitution of aroma compounds from sweet basil was little affected by light treatment, although RB treatment would be recommended for maximising total emission rates of aromatic volatiles (Fig. 4a, 5). Similarly, low intensity red or high intensity blue light enhanced the concentration of volatiles in basil essential oils and leaf extracts (Amaki et al., 2011; Pennisi et al., 2019). Although total emission rates were lower, red light enhanced production of eugenol, an oxygenated terpenoid and powerful antioxidant, which is an important component of essential oil and therefore flavour (Gülçin et al., 2012). 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).

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

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

5. Conclusion

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

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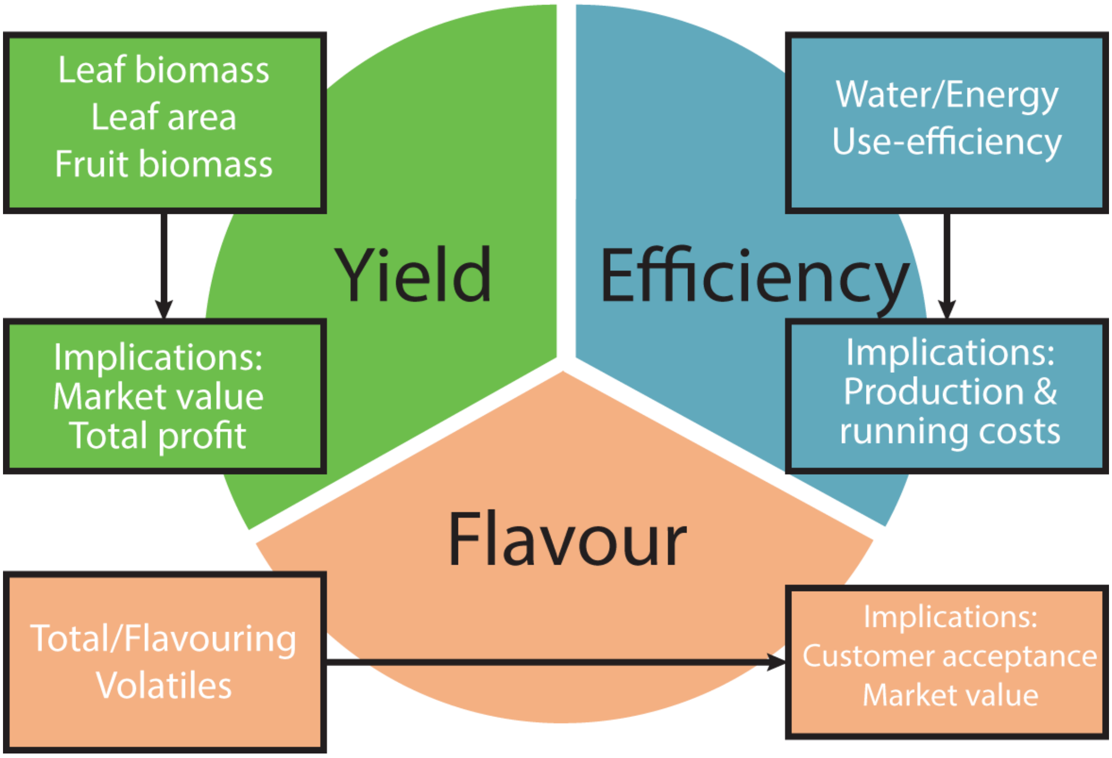
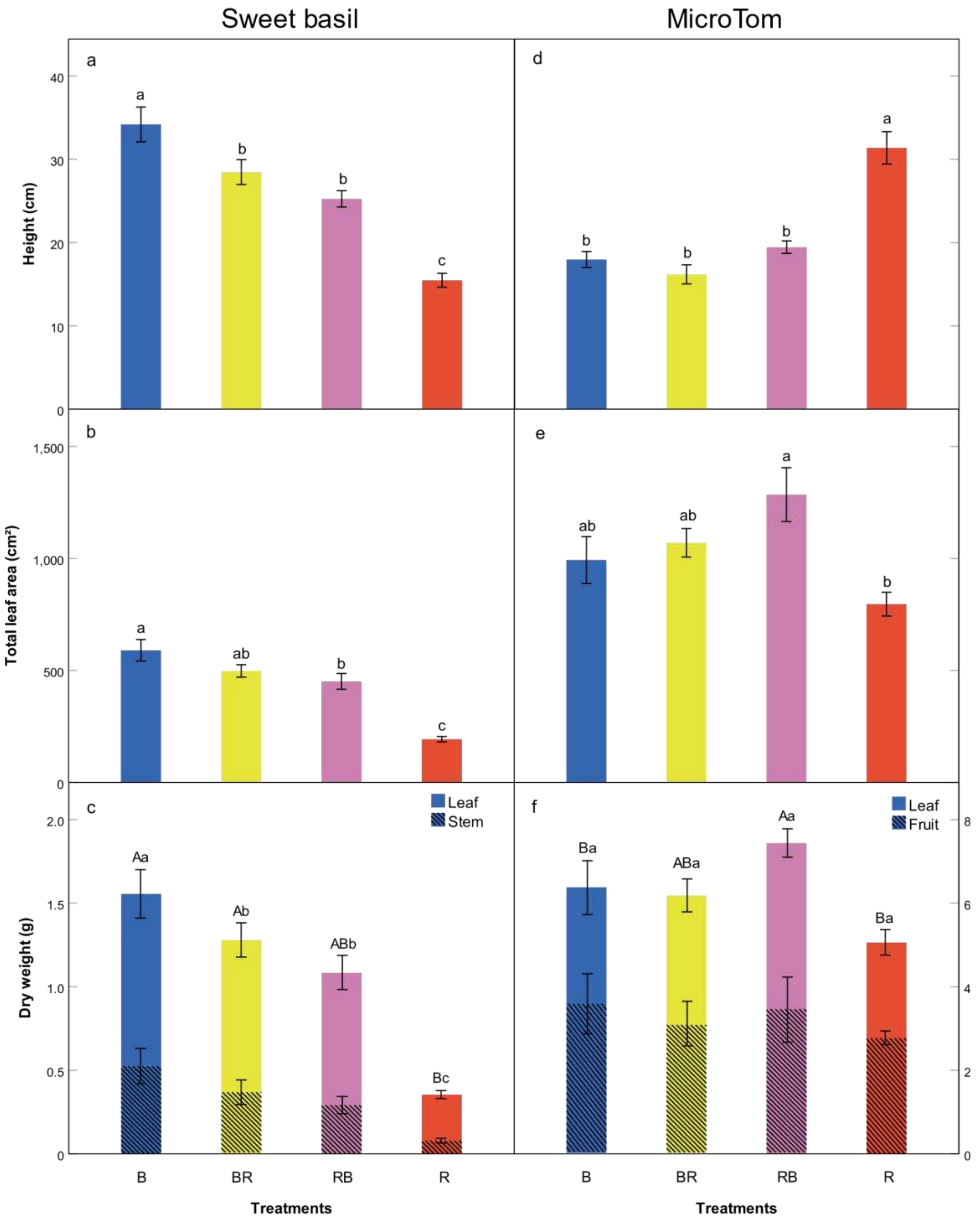


Figure 1. Illustration of the three factors in the assessment framework and specific factors related to each.


Sweet basil
MicroTom
a
d
Height (cm)
0
10
20
30
40
a
b
b
c
b
b
b
a
b
e
Total leaf area (cm²)
0
500
1,000
1,500
a
ab
b
c
ab
ab
a
b
c
f
Dry weight (g)
0
0.5
1.0
1.5
2.0
0
2
4
6
8
Leaf
Stem
Leaf
Fruit
Aa
Ab
ABb
Bc
Ba
ABa
Aa
Ba
B
BR
RB
R
B
BR
RB
R
Treatments
Treatments

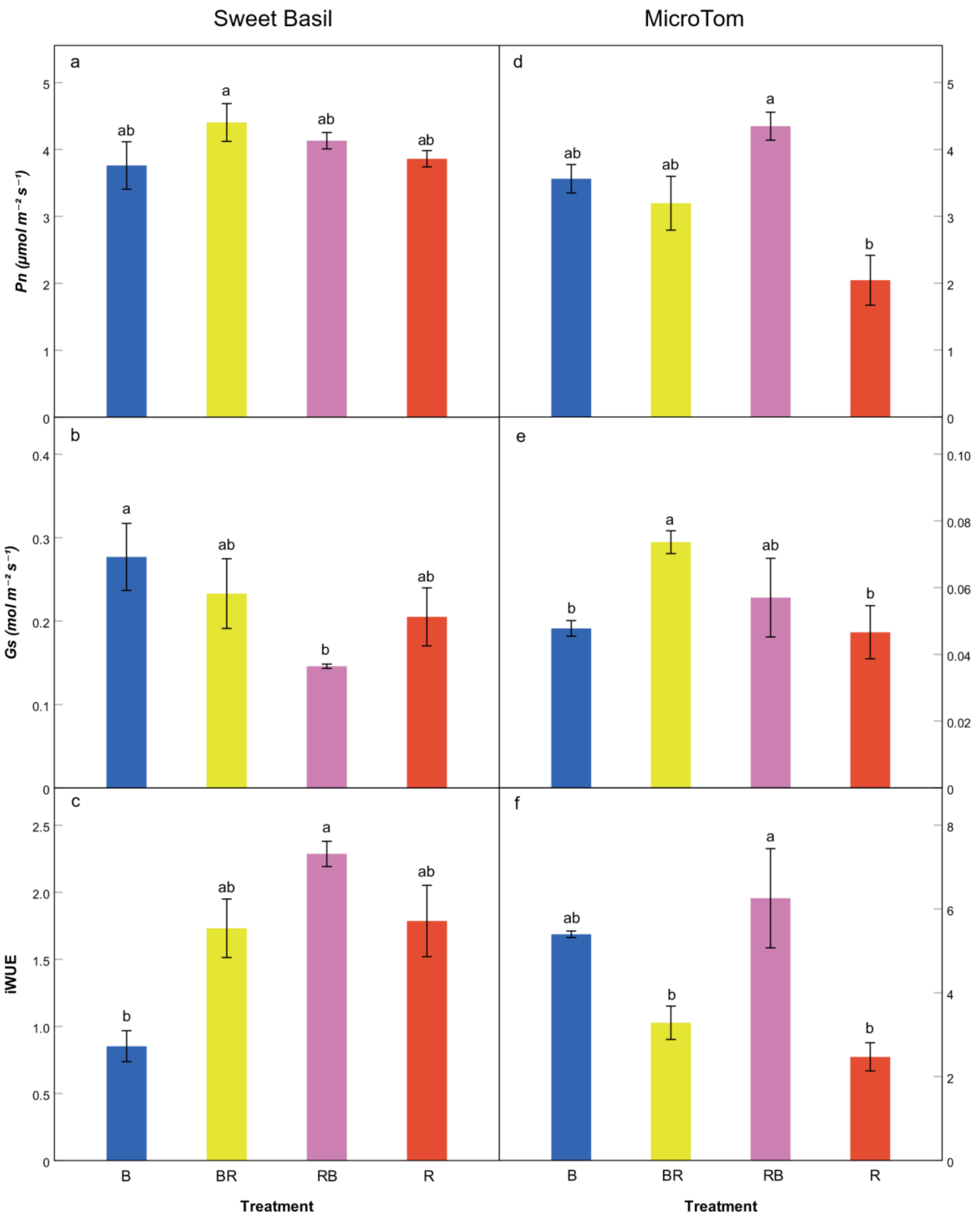


Figure 3. The effect of LED light treatment on net photosynthesis (*Pn*), stomatal conductance (Gs) and instantaneous water-use-efficiency (iWUE) of sweet basil (left-hand panels) on 5-weeks and MicroTom (right-hand panels) on 7-weeks. Plants grown under B (blue), BR (yellow), RB (purple), R (vermilion)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

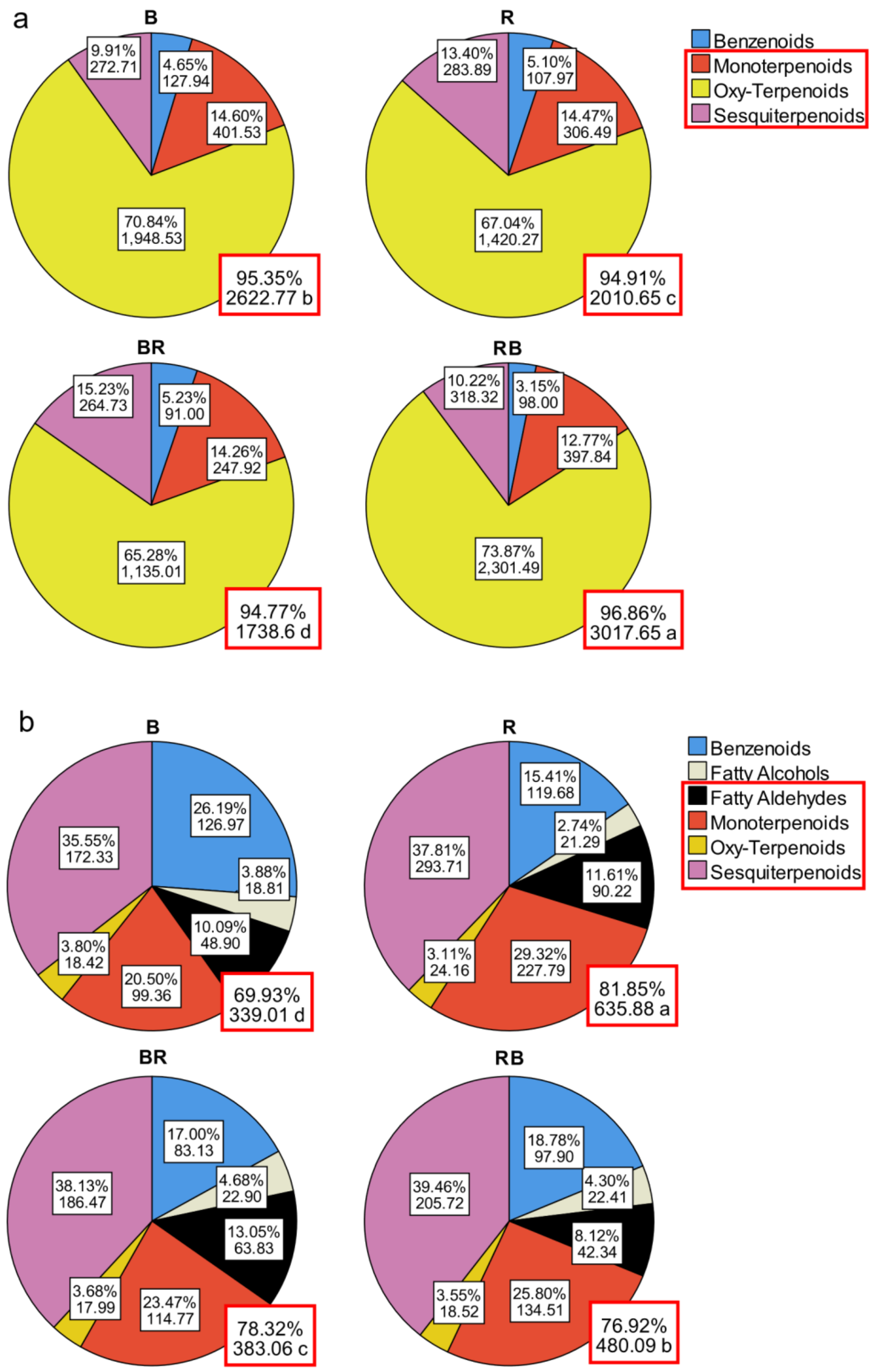


Figure 4. The effect of LED light treatment on volatile emissions from 5-weeks sweet basil (a) and 7-weeks MicroTom (b). Black-framed boxes on each pie indicate the percentage (top) and emission rate (ng m^{-2} leaf s^{-1}, bot) of main volatile classes. Red-framed boxes indicate the percentage and emission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

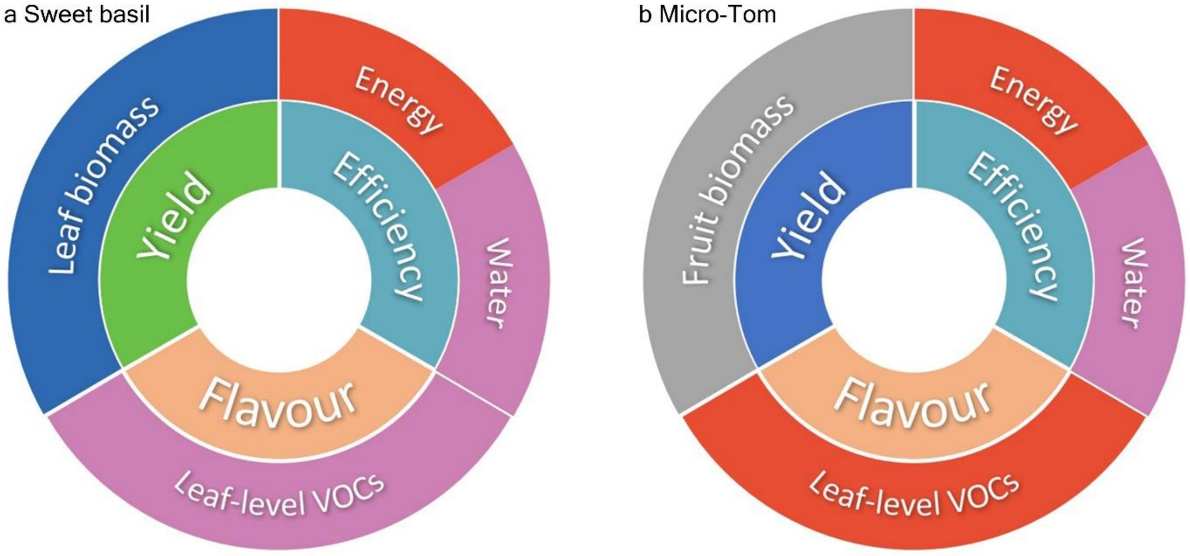


Figure 5. Overall recommendations to optimise production of sweet basil (a) and MicroTom (b). Basil: 100% blue (blue) maximised **yield** (leaf biomass), 66% red (purple) promoted **flavour**; MicroTom: 66% red promoted **yield** (leaf biomass) but fruit biomass was same between treatments (indicated as grey), 100% red (vermilion) 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 µmol/s	10 W	R	1
			RB	1.13
Blue LED	15 µmol/s	14 W	BR	1.26
			B	1.4

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

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Abstract

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 (*Ocimum basilicum* cv. Genovese) and tomato (*Solanum lycopersicum* 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.

Keywords: Crop improvement, Light emitting diodes (LEDs), ~~Plant factories, crop improvement,~~ *Ocimum basilicum*, Plant factories, *Solanum lycopersicum.* ~~*Lycopersicum.*~~

Introduction

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

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

Indoor cultivation of green leafy vegetables and fruiting crops enables control of lighting to optimise yield, resource use efficiency and flavour according to the target market. Both light intensity (the photosynthetic photon flux density, PPFD), and the spectral distribution of UV-B (280-315nm), UV-A (315-400 nm), blue (400-500 nm), red (620-700 nm) and far-red (700-850 nm) light affect plant growth and development (Higuchi and Hisamatsu, 2016). LEDs of differing wavelengths can be used to control plant morphogenesis and enhance the production of secondary metabolites, increasing efficiency and adding value to crops by enhancing nutrient content and/or taste (Kozai and Zhang, 2016; Lu and Mitchell, 2016). Monochromatic blue and red light induce specific light signalling responses in plants, significantly affecting morphological, physiological and biochemical processes through alterations in photosynthetic activities and/or photoreceptors (Higuchi and Hisamatsu, 2016). Blue light is mainly absorbed by phototropins, chloroplasts and cryptochromes causing responses including phototropism, enhanced efficiency of chlorophylls and carotenes (Liu et al., 2012), and stomatal opening (Shimazaki et al., 2007). Red light is absorbed by phytochromes, regulating major developmental transitions (e.g. germination and flowering) (Smith, 1995), and plant vegetative and reproductive growth . Blue and red lights can act synergistically to amplify their individual signalling effects (Fankhauser and Chory, 1997).

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

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

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

Previous studies of crop responses to different LED lights in indoor controlled environments have generally focused on a single factor (crop productivity, resource use efficiency, and/or quality). Relatively few have simultaneously investigated these factors, and differences in experimental conditions, researchfacilities and interests have resulted in inconsistent conclusions and recommendations (Carvalho et al., 2016; Lanoue et al., 2017; Pennisi et al., 2019) with~~. While~~ most of the data from plant factories and companies~~ are~~ not publicly accessible. There is a clear need, therefore, for a flexible evaluation framework to assist the grower in optimising light conditions for indoor crop cultivation.

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

2. Methods

2.1. Plant materials and growth conditions

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

The hydroponic growth racks were lit with mixed LED lighting and maintained at constant temperature (20±2 ℃) and relative humidity (60±10%). Hydroponic irrigation was initially supplied using an ebb and flow system with tap water every four days, gradually increasing to daily. Plants were rotated every two weeks in racks. Philips GreenPower® LED research module strips (Philips Ltd, UK) were installed on the top of each rack, 40 cm above the bench. Racks were irradiated for 14h from 6:00 a.m. to 8:00 p.m. using combinations of blue (400-500 nm~~500nm~~) and red (600-700 nm~~700nm~~) LEDs. The four treatments were 100% blue (B), 66% blue + 33% red (BR), 33 % blue + 66% red (RB) and 100% red (R). The total photon flux density at leaf level height ranged from 115 to 180 ~~(115 ± 2~~ µmol m^{-2} s^{-1}~~) supply~~ according to leaf distance to the lighting module, and was constant across treatments. The distribution of quantum energy (Figure S1) was measured using a Jaz spectrometer (Ocean Optics Inc, UK), ~~and~~ the spectral distributions are consistent in racks and shown in Table S1 together with the average vertical profile.

2.2. Morphological measurements

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

2.3. Leaf-level gas exchange and resource use efficiency

Physiological responses and volatile emissions were sampled in-situ for two consecutive weeks in both species (Weeks 4 and 5 for basil, and 6 and 7 for Micro-Tom). The newest fully developed leaf from each of 3 randomly selected replicates per treatment was sampled using a Li-6400XT (Li-COR Inc., USA), three hours after the lights were switched on.~~).~~ The leaf was placed in a 2 x 3 cm clear-top chamber under conditions that closely replicated the growing environment (leaf temperature 22°C, relative humidity 50-60%, and CO_2 concentration 400 µL L^{-1}). Following a 5-minute period of stabilisation, net photosynthesis (*Pn*), stomatal conductance (*Gs*) and transpiration rates (*Tr*) were logged. The Li-6400XT cuvette remained on the leaf for a further 15 minutes to finish volatile sample collection. ~~Leaves~~ Any tomato leaves insufficiently large to fill the chamber were photographed in-situ and the sampled leaf area subsequently calculated using Image J software (Schneider et al., 2012). Water use efficiency was estimated as instantaneous water-use-efficiency (iWUE) ~~and was~~ defined as the ratio of photosynthesis to transpiration. Energy efficiency was estimated as the relative energy usage based on the power consumption of LED modules from manufacture's product manual (Royal Philips N.V.; 2015).

2.4. Volatile sampling and analysis

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

2.5. Assessment framework

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

2.6. Data analysis

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

3. Results

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

3.1. Yield

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

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

3.2. Efficiency

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

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

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

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

3.3. Flavour

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

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

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

4. Discussion

4.1. Yield

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

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

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

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

4.2. Efficiency

Instantaneous (photosynthetic) water use efficiency (iWUE), calculated as the leaf-level carbon assimilation rate (CO_2) divided by the water transpiration (H_2O) rate, was used as an efficiency indicator. RB produced the highest iWUE in both species and is recommended for indoor cultivation (Fig. 5). The least efficient treatments were B in sweet basil (Fig. 3c), R and BR for Micro-Tom (Fig. 3f), consistent with previous studies of both species (Pennisi et al., 2019) (Lanoue et al., 2017). In both species, a combination of blue and red LED light promoted photosynthesis. Although blue light increased stomatal conductance of sweet basil, net photosynthesis rate was greatest under BR lights (Fig. 3b, a). Micro-Tom also showed varied photosynthetic and stomatal responses, with maxima occurring under RB and BR light respectively (Fig. 3d, e). Therefore ~~C~~commercial growers need ~~therefore~~ to consider the trade-off between total carbon assimilation (yield) and total resource usage. The iWUE is a physiological parameter that we applied in this framework to estimate leaf-level water usage. However, the efficiency of water use in productivity (ratio of biomass to total water use) is frequently used in real growth facilities to calculate overall WUE throughout the growth cycle or season of specific species, and therefore could be more realistic for indoor crop production and specific facilities. Light treatment can (marginally) improve whole plant water usage, but optimising energy efficiency per unit area is much more dependent on the choice of lighting system and likely of more interest to growers since the main costs for PFALs are associated with electricity for lighting, as well as environmental control systems. RB light optimised iWUE of both species, but R treatment delivers the best energy use (Table. 1). Hence R light is recommended for saving costs (Fig. 5). Unit mass WUE and energy use efficiency (EUE) are already generally high in plant factories or vertical farms (Pennisi et al., 2019; Ting et al., 2016). If commercial growers are trying to improve the overall resource use efficiency of PFALs, the trade-off between WUE and EUE would need to be carefully considered, as well as additional indicators such as nutrient use and the costs of environmental regulation such as cooling and dehumidification.

4.3. Flavour

The dominant compounds in plant aroma profiles are mono-, sesqui- and oxygenated terpenoids and fatty aldehydes. Foliar emissions of these were used to assess flavour ~~in this study~~ (Fig. 4) although post-harvest volatile emissions are arguably more relevant than those during cultivation. The constitution of aroma compounds from sweet basil was little affected by light treatment, although RB treatment would be recommended for maximising total emission rates of aromatic volatiles (Fig. 4a, 5). Similarly, low intensity red or high intensity blue light enhanced the concentration of volatiles in basil essential oils and leaf extracts (Amaki et al., 2011; Pennisi et al., 2019). Although total emission rates were lower, red light enhanced production of eugenol, an oxygenated terpenoid and powerful antioxidant, which is an important component of essential oil and therefore flavour (Gülçin et al., 2012). 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).

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

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

5. Conclusion

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

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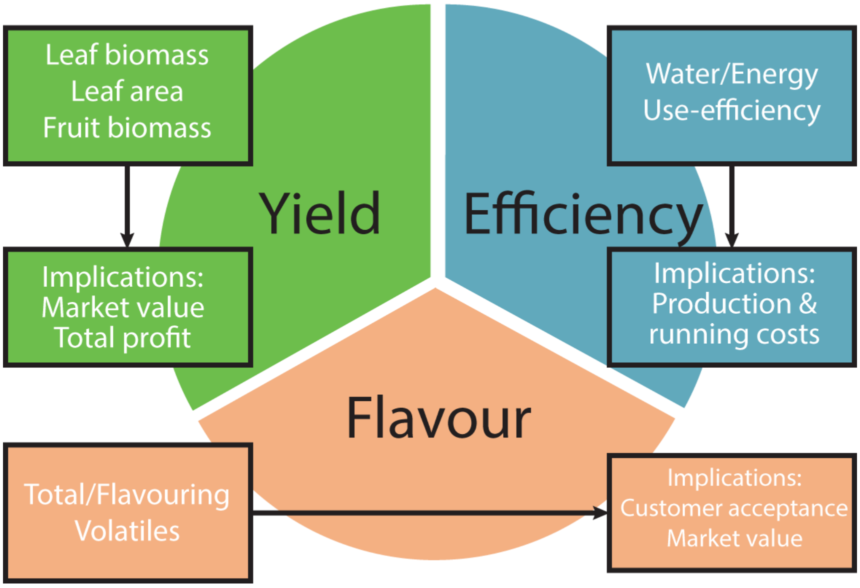
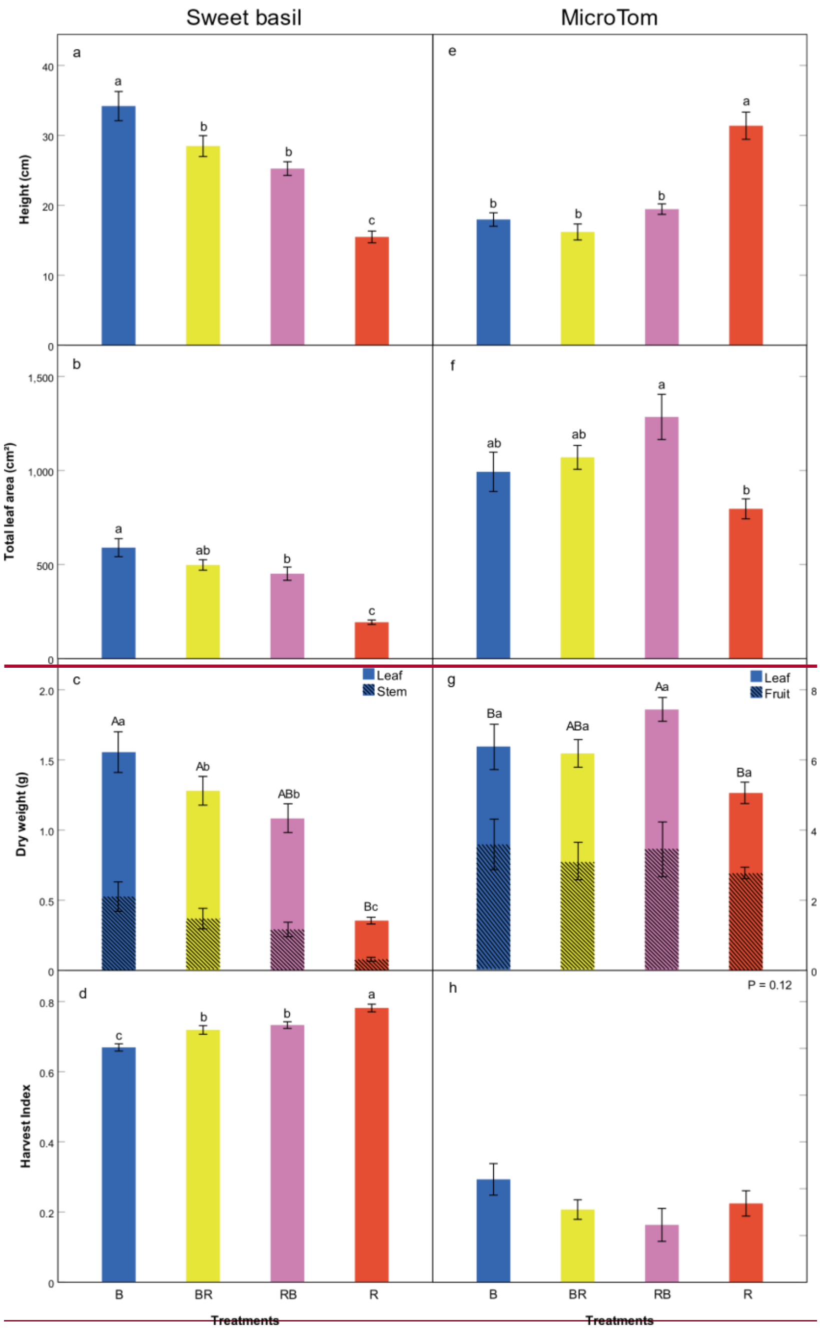


Figure 1. Illustration of the three factors in the assessment framework and specific factors related to each.


Sweet basil
MicroTom
a
e
Height (cm)
40
30
20
10
0
a
b
b
c
b
b
b
a
b
f
Total leaf area (cm²)
1,500
1,000
500
0
a
ab
b
c
ab
ab
a
b
c
g
Leaf
Stem
Leaf
Fruit
Dry weight (g)
2.0
1.5
1.0
0.5
0
8
6
4
2
0
Aa
Ab
ABb
Bc
Ba
ABa
Aa
Ba
d
h
P = 0.12
Harvest Index
0.8
0.6
0.4
0.2
0
c
b
b
a
B
BR
RB
R
B
BR
RB
R
Treatments
Treatments

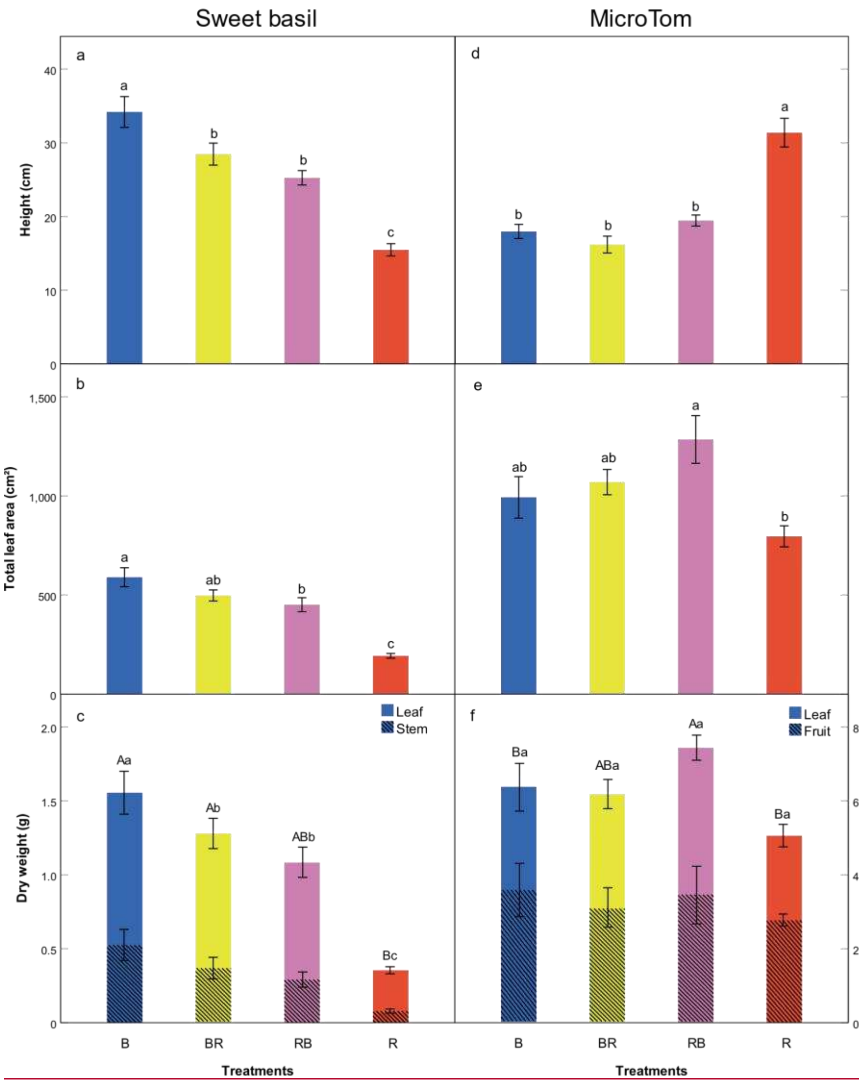


Figure 2. The effect of LED light treatments on yield~~Yield~~ parameters of sweet basil on 6-weeks (left-hand panels) and MicroTom on 13-weeks (right-hand panel). Quantification of height (a, d~~e~~), total leaf area (b, e~~f~~), leaf/stem dry weight (c), fruit/leaf dry weight (f~~g~~)~~, harvest index (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, ±SE) between light treatments; in (c, f~~g~~), upper and lower cases indicate significant differences of leaf (clear bar) and stem/fruit (shade bar) between treatments, respectively.

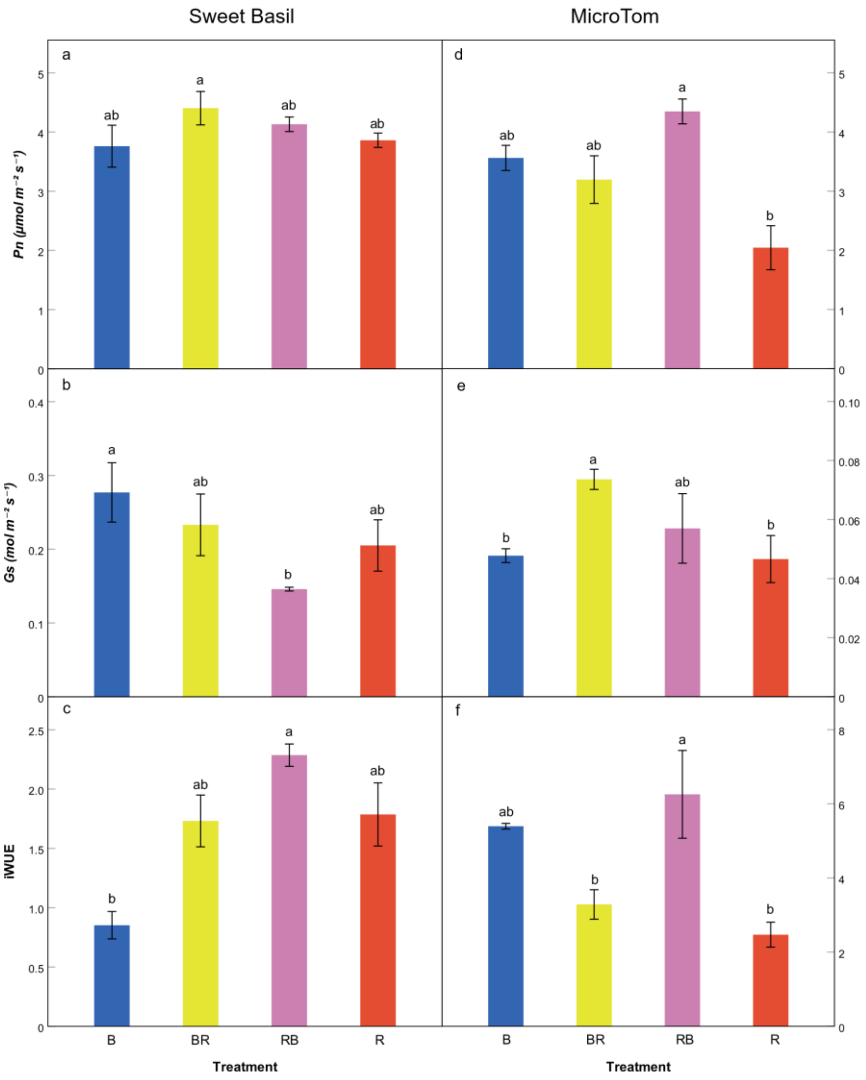


Figure 3. The effect of LED light treatment on net photosynthesis (*Pn*), stomatal conductance (Gs) and instantaneous water-use-efficiency (iWUE) of sweet basil (left-hand panels) on 5-weeks and MicroTom (right-hand panels) on 7-weeks. Plants grown under B (blue), BR (yellow), RB (purple), R (vermilion)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

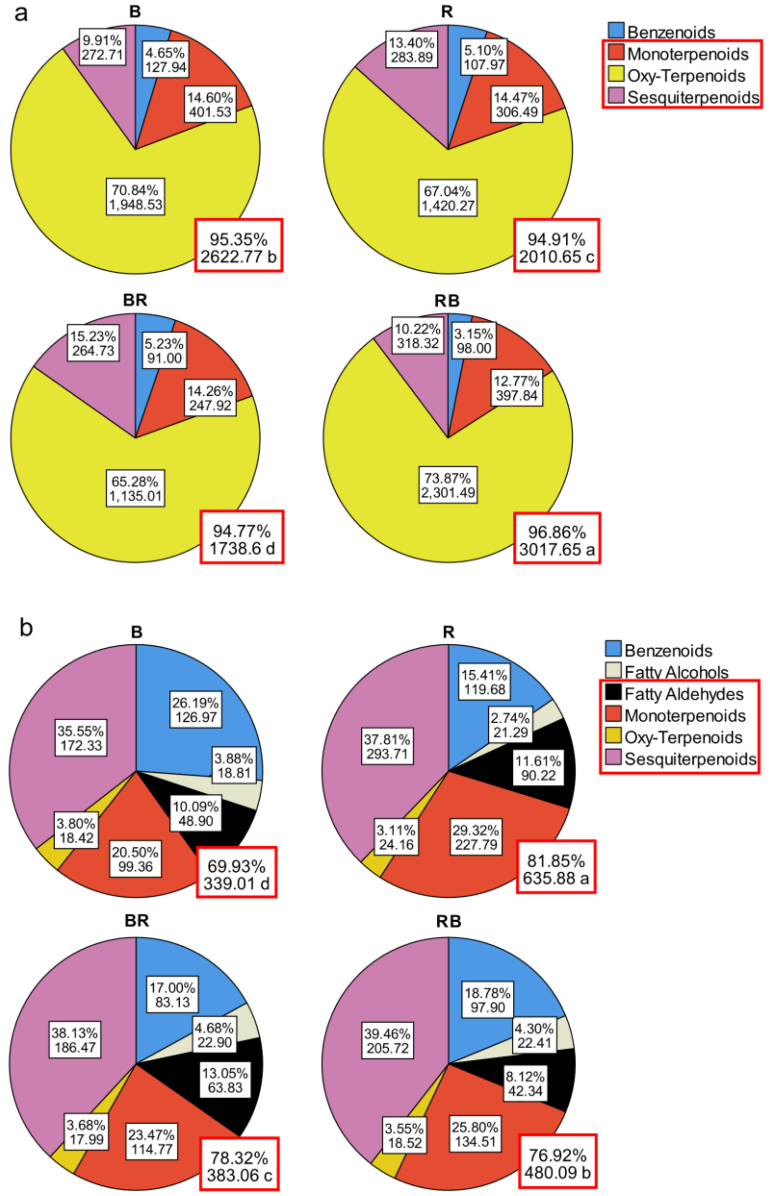


Figure 4. The effect of LED light treatment on volatile emissions from 5-weeks sweet basil (a) and 7-weeks MicroTom (b). Black-framed boxes on each pie indicate the percentage (top) and emission rate (ng m^{-2} leaf s^{-1}, bot) of main volatile classes. Red-framed boxes indicate the percentage and emission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

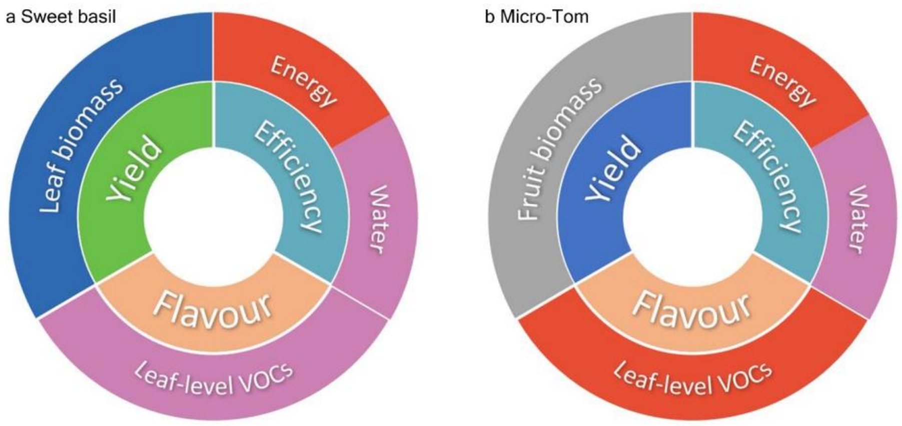


Figure 5. Overall recommendations to optimise production of sweet basil (a) and MicroTom (b). Basil: 100% blue (blue) maximised **yield** (leaf biomass), 66% red (purple) promoted **flavour**; MicroTom: 66% red promoted **yield** (leaf biomass) but fruit biomass was same between treatments (indicated as grey), 100% red (vermilion) 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 µmol/s	10 W	R	1
			RB	1.13
Blue LED	15 µmol/s	14 W	BR	1.26
			B	1.4