



# Growth Spectrum Complexity Dictates Aromatic Intensity in Coriander (*Coriandrum sativum* L.)

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Advancements in availability and specificity of light-emitting diodes (LEDs) have facilitated trait modification of high-value edible herbs and vegetables through the fine manipulation of spectra. Coriander (*Coriandrum sativum* L.) is a culinary herb, known for its fresh, citrusy aroma, and high economic value. Studies into the impact of light intensity and spectrum on *C. sativum* physiology, morphology, and aroma are limited. Using a nasal impact frequency panel, a selection of key compounds associated with the characteristic aroma of coriander was identified. Significant differences ( $P < 0.05$ ) were observed in the concentration of these aromatics between plants grown in a controlled environment chamber under the same photosynthetic photon flux density (PPFD) but custom spectra: red (100%), blue (100%), red + blue (RB, 50% equal contribution), or red + green + blue (RGB, 35.8% red: 26.4% green: 37.8% blue) wavelengths. In general, the concentration of aromatics increased with increasing numbers of wavelengths emitted alongside selective changes, e.g., the greatest increase in coriander-defining E-(2)-decenal occurred under the RGB spectrum. This change in aroma profile was accompanied by significant differences ( $P < 0.05$ ) in light saturated photosynthetic CO<sub>2</sub> assimilation, water-use efficiency ( $W_i$ ), and morphology. While plants grown under red wavelengths achieved the greatest leaf area, RB spectrum plants were shortest and had the highest leaf:shoot ratio. Therefore, this work evidences a trade-off between sellable commercial morphologies with a weaker, less desirable aroma or a less desirable morphology with more intense coriander-like aromas. When supplemental trichromatic LEDs were used in a commercial glasshouse, the majority of compounds, with the exception of linalool, also increased showing that even as a supplement additional wavelength can modify the aromatic profile increasing its complexity. Lower levels of linalool suggest these plants may be more susceptible to biotic stress such as herbivory. Finally, the concentration of coriander-defining aromatics E-(2)-decenal and E-(2)-hexenal was significantly higher in supermarket pre-packaged coriander leaves implying that concentrations of aromatics increase after excision.

In summary, spectra can be used to co-manipulate aroma profile and plant form with increasing spectral complexity leading to greater aromatic complexity and intensity. We suggest that increasing spectral complexity progressively stimulates signaling pathways giving rise to valuable economic traits.

**Keywords:** coriander, vertical farming, aroma, spectrum, light-emitting diodes, photosynthesis

## INTRODUCTION

Light-emitting diodes (LEDs) were introduced in 1962, but have only recently made great progress in revolutionizing the growth of horticultural crops (Davis and Burns, 2016).

LEDs enable growers to maintain profitability in a highly competitive market by reducing the space needed for each plant as well as consuming less energy and having longer lifespans than their traditional counterparts (Massa et al., 2008). While these benefits represent the logistical advantage of LEDs over conventional grow lights (e.g., high-pressure sodium), perhaps their most interesting application lies in the ability of the grower to manipulate crop characteristics through the modification of spectra. Controlling the contribution of key wavelengths allows the grower to manipulate not only the quantity, but also the quality of their crop, for example; the aesthetic appearance (color, flowering time), disease susceptibility, taste, smell, and nutritional content (Dudareva et al., 2006; Samuoliene et al., 2012; Davis and Burns, 2016; Alrifai et al., 2019; Pennisi et al., 2019).

Plants convert or transduce the energy of absorbed photons into biochemical constituents using photosynthetic pigments and photoreceptors (Kong and Okajima, 2016). Utilizing photons from the photosynthetically active radiation (PAR) region of the electromagnetic spectrum (wavelengths between 400 and 700 nm), photosynthetic pigments such as chlorophylls and associated accessory pigments (e.g., carotenoids) generate high energy electrons from water that are ultimately used to fix CO<sub>2</sub> (Demarsy et al., 2018). While greater PPFs and therefore higher rates of CO<sub>2</sub> fixation, leading to greater acquisition of biomass, excessive light can result in damage to components of the photosynthetic system (Takahashi and Badger, 2011). In contrast, photoreceptors determine plant structure and morphology and can operate within and outside of the PPF region—for example, phototropins perceive both blue (400–500 nm) and UV-A (315–400 nm) wavelengths—mediating processes such as phototropism (Briggs and Christie, 2002; Fraser et al., 2016). Three major photoreceptors regulate the development and growth of the plant dependent on the perception of the environment; the phytochromes, cryptochromes, and phototropins (Larner et al., 2008). These receptors respond to red:far-red ratio and blue wavelengths, respectively. No

single receptor has been established for green although the cryptochromes absorb wavelengths in the green region in addition to blue (Smith et al., 2017). Variation in the ratios of these wavelengths affects diverse biological processes, for example, it is well known that photoreceptors have a major role in the determination of desirable morphological features in crops such as leaf area, leaf thickness, and internode length which help construct a canopy for efficient light interception (Crepney and Casal, 2015; Fraser et al., 2016; Smith, 2017). However, different wavelengths are also known to regulate chemical biosynthesis pathways; for example, stimulating the production and subsequent accumulation of carotene (Samuoliene et al., 2012, 2016) and phenolics (Lee et al., 2016) in some species. However, there is less information on the impact of spectral quality on the complex traits of flavor and aroma in horticultural crops such as herbs (despite their high value) with research tending to focus more on lettuce (Zhang et al., 2019), tomato, and bedding plants (Colquhoun et al., 2013).

Coriander is prized globally as a culinary ingredient and for its medicinal properties (Diederichsen, 1996; Sahib et al., 2013). While the seeds are an essential ingredient for products such as curry paste, the leaves and stems are also consumed in sauces and chutneys and added fresh to salads and garnishes due to their attractive green color and fresh citrus aroma and taste. Marketed in small pots or fresh leaves in packaging, coriander is the biggest selling fresh herb in the United Kingdom, with over 1500 hectares cultivated and over 30 million packets sold in 2014 (57 min<sup>-1</sup>, Fraser et al., 2015)—generating an estimated gross market value of £23.7 million. With a large proportion of this crop grown under controlled glasshouse conditions, it lends itself to the application of supplemental LED lighting for improved quality in the light limited northern hemisphere.

The aroma of coriander is critical to its product value. Previous work has shown that corianders distinctive aroma is determined by a combination of volatiles released from its essential oils; most notably the aliphatic aldehydes (Fan and Sokorai, 2002). In the literature, a selection of compounds has also been identified and described, including (but not limited to) 7-dodecenal, dodecanal, decanal (Macleod and Islam, 1976; Curutchet et al., 2014) and linalool. From the literature, E-2-decenal has been reported as the most abundant compound found in coriander leaves (Eyres et al., 2005). These compounds have different odour perception thresholds; abundance does not always imply olfactory impact. The released volatiles from crushed coriander leaves can be characterized based on detection of odour-active compounds with GCO and a human sniffer (Eyres et al., 2005). From the literature, coriander aromatics from many countries have been determined—from Africa (Buthelezi et al., 2016), Fiji (Eyres et al., 2005), and India (Shahwar et al., 2012).

**Abbreviations:** *A*, rate of photosynthetic CO<sub>2</sub> assimilation, μmol m<sup>-2</sup> s<sup>-1</sup>; *A*<sub>sat</sub>, light-saturated rate of photosynthetic CO<sub>2</sub> assimilation, μmol m<sup>-2</sup> s<sup>-1</sup>; GC-MS, gas chromatography mass spectrometry; GC-O, gas chromatography olfactometry; LED, light-emitting diode; NIF, nasal impact frequency; OAV, odour activity value; PFD, photon flux density, μmol m<sup>-2</sup> s<sup>-1</sup>; PPF, photosynthetic photon flux density (400–700 nm only), μmol m<sup>-2</sup> s<sup>-1</sup>; RB, red + blue treatment; RGB, red + green + blue treatment; *W*<sub>i</sub>, water-use efficiency, μmol CO<sub>2</sub> mmol<sup>-1</sup> H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>.

While some publications accurately describe the growing conditions of the sampled coriander (Buthelezi et al., 2016), some do not (Macleod and Islam, 1976; Eyres et al., 2005; Shahwar et al., 2012). It is important to recognize that environmental conditions (e.g., light, temperature, watering regime), origin, and material age all contribute to the final aroma profile of the plant (Dudareva et al., 2006).

Here we investigate the role of growth wavelength on the aroma and morphology of coriander shoots grown in the United Kingdom. The fresh coriander product delivered to the supermarket in packets or pots, consists largely of a bushy, leafy canopy with multiple thin stems, both of which are used in food preparation. The coriander ideotype would be a short plant with high fresh biomass and high leaf:stem ratio, all of which are modulated by growth spectrum. For example, a higher proportion of blue can lead to smaller bushier plants but may increase the thickness of the stems making them less palatable. We hypothesize that growth spectrum will also influence the composition of flavor and aroma compounds and this may be advantageous or detrimental factor for the grower. For example, it may decrease the desirable coriander aroma or flavor. Conversely, using specific-spectra LEDs to grow coriander in the United Kingdom may represent an opportunity to improve quality and marketability if the trade-offs between morphology and aroma/flavor are minimal.

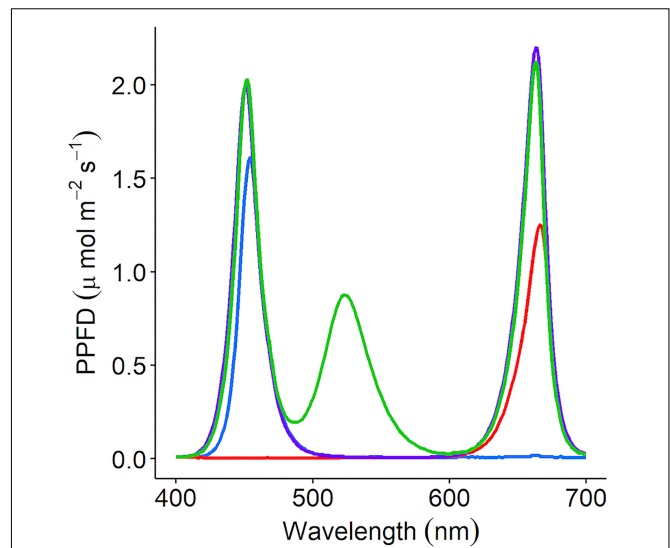
To test this hypothesis, we grew coriander under controlled growth conditions, manipulated the spectra, and determined the content of key aromatic compounds, which had the greatest impact on aroma via gas chromatography (GC) profiles. We also analyzed whole plant physiological traits of the specific-spectra grown plant, such as morphology, biomass, absorbance, and photosynthetic capacity to determine how specific growth spectra would impact the desirable, morphological characteristics of coriander. We show that growth spectrum has a significant impact on the content of desirable aromatic compounds in above-ground material and that there are both potential trade-offs and opportunities for using LEDs to manipulate morphology and quality in this species of herb.

## MATERIALS AND METHODS

### Plant Material

#### Plant Growth Conditions and LED Treatments

*Coriandrum sativum* ("Green Aroma") was grown in a controlled environment chamber at 23/19°C light/dark and 60% relative humidity (RH). The photoperiod was 16/8 h light/dark with a PPF of  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; 20–30 seeds were sown per 250 mL pot with each pot containing compost (Levington's F2S, Everris, Ipswich, United Kingdom). Pots were placed under either monochromatic (red or blue), dichromatic (RB), or trichromatic (35.8% red: 26.4% green: 37.8% blue) wavelengths (Figure 1) and grown for 21 days under well-watered conditions. The LED lamps were designed in-house by electrical engineers at the University of Nottingham. LED components were supplied by Prolight Opto Technology Corporation (Taipei, Taiwan). These were Pk2NThsi series: red



**FIGURE 1** | *C. sativum* was grown under four separate irradiance spectrums using LED lamps; red (peak: 666nm), blue (peak: 454 nm), RB [red (663 nm) + blue (451 nm)], and RGB [red (663 nm) + green (523 nm) + blue (451 nm)]. Each lamp was adjusted to supply  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetic photon flux density (PPFD). The supplemental LED lights used in the commercial glasshouse output the red + green + blue (35.8% red: 26.4% green: 37.8% blue—RGB) spectrum.

(623 nm), green (525 nm), blue (465 nm), and cherry red (far-red) (730 nm).

For GC analysis, samples were pooled per pot; all above-ground tissue was harvested by grinding into a fine powder in liquid nitrogen and stored in  $-80^\circ\text{C}$  until analysis. Analysis was performed on 3 g of the macerated tissue from four independent pot replicates. Concurrently, a second batch of four pots was sown for physiological, morphological, and destructive harvest measurements. Germination success and height were monitored. At day 21, an infra-red gas analyzer (GFS-3000, Heinz-Walz, Germany) was used to measure the response of the leaves to step-changes in light intensity between 0 and  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPF (red with 10% blue provided by LEDs in the GFS-3000). These response curves were adjusted for leaf absorbance (400–700 nm) as determined using an integrating sphere (Li-1800, Licor Biosciences, Lincoln, NE, United States) and spectroradiometer (ASD Handheld, Malvern Panalytical, Cambridge, United Kingdom). The light response curves were fitted in R (RStudio Team, 2015) following the method of Marshall and Biscoe (1980) and Heberling and Fridley (2013). The following light response curve parameters were estimated from fitted non-rectangular hyperbola;  $A_{\text{sat}}$ , ETR (electron transport rate as calculated using the equations of Genty et al., 1989), apparent quantum yield (the linear relationship between number of photos absorbed and  $\mu\text{mol CO}_2$  assimilated),  $R_d$  ( $R_d$ , the daytime dark respiration rate), curve convexity (the efficiency of  $A$  under intermediate light levels), and the LCPT [light compensation point (LCPT)—the light intensity where rates of  $A$  and  $R_d$  are equal]. All plants were harvested and analyzed for fresh and dry weight and leaf to stem ratio.

## Determining the Impact of Supplemental LED Lighting in a Commercial Glasshouse

To determine the impact of supplemental LED lighting on aroma in a commercial setting, *C. sativum* was grown in an automated 1.2 hectare commercially set controlled glasshouse in West Sussex (Langmead Group plc, Chichester, United Kingdom) is a commercial setup producing pot coriander for UK supermarkets. The photoperiod was a 16/8 h light/dark cycle with temperature at 23/19°C. *C. sativum* seeds were sown in 250 mL pots containing a company compost mix and pre-germinated in the 550 m<sup>2</sup> dark germination room for 2 weeks. Once seedlings reached 2 inches tall, the plants were placed either under supplemental LED light at emitting 150 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD trichromatic spectrum (see **Figure 1** for spectrum) positioned approximately 150 cm above the plants or without supplemental lighting. They were grown under well-watered condition. At 35 days old, samples were taken for GC analysis. The material from each pot was pooled for sampling and three separate pots were sampled for the aroma study.

### Supermarket Coriander

To determine differences between fresh (potted) coriander and pre-excised leaf material (packed or bagged), three independent samples were purchased from a local supermarket (Tesco, Long Eaton, United Kingdom). It was assumed that each pot contained between 20 and 26 plants (13 seeds per pot) and that each packaged bunch of coriander was harvested from a single pot when processed. Three pots of coriander were purchased from a supermarket the night before the extraction and well-watered. It was ensured that the use-by date for the plants was < 5 days from the time of purchase. All above ground tissue was harvested for GC-O analysis to determine key aromatics that characterized the scent of coriander.

## Gas Chromatography Mass Spectroscopy (GC-MS)

### GC-MS Sample Preparation

0.5 g frozen ground material and 2.5 g of saturated calcium chloride solution (extraction ratio 1: 5 w/w) was added into 20 mL amber SPME vial. Internal standard (3-heptanone) was also added for relative quantification purpose. Vials were sealed with a septum cap ready for GC-MS analysis.

### GC-MS Analysis

Sample volatiles were analyzed on a Thermo Scientific GC Mass Spectrometer (TRACE 1300 GC, USA, and ISQ series MS).

Headspace volatiles were extracted for 20 min at 50°C, using 50/30 μm DVB/CAR/PDMS SPME Fiber (Supelco, Sigma-Aldrich, United Kingdom), following desorption for 0.2 min at 250°C in splitless mode. ZB-Wax capillary column (length 30 m, inner diameter 0.25 mm, and film thickness 1 μm) (Phenomenex Inc., Macclesfield, United Kingdom) was used with temperature programmed starting at 40°C for 2 min, 8°C/min to 240°C, and held for 5 min.

Helium was used as carrier gas at a constant pressure of 18 PSI and full scan mode scanned from *m/z* 35–300. Identification of volatile compounds by matching retention time of pure chemical

compounds and comparing its mass spectrum against reference libraries (NIST/EPA/NIH Mass Spectral Library, version 2.0, Faircom Corporation, United States).

To determine the impact of the odour of each aromatic compound relative to its concentration the OAV was calculated (Eq. 1) as:

$$OAV = \frac{\text{concentration (ppb)}}{\text{odour threshold}} \quad (1)$$

The odour thresholds for each compound were sourced from the literature (Leffingwell and Associates, 1985).

### GC-Olfactometry Procedure

To assess the impact of each of these compounds and to select the most important components for subsequent analysis, six judges sniffed samples from combined above-ground material from four pots (~13 plants per pot) of *C. sativum* on a GC machine (TRACE 1300 GC, USA, and ISQ series MS) equipped with customized olfactometry detector outlet. The duration of each sniffing session was 32 min with panelists asked to note down when an odour was detected. The six individual aromagrams for the plant material from panelist treatment were added up to one aromagram (**Figure 2**). The NIF was calculated as the percentage of panelists detecting a scent at a particular time. In this way, peak height is not related to relative compound concentration but to frequency of compound detection. Hence, the compounds detected by the highest number of panelists represent the compounds that exert the greatest influence or impact to the overall odour of the coriander sample. The compounds identified from the NIF tests, and associated literature, were used to determine which compounds to be analyzed and quantified in subsequent chromatograms.

Descriptors and odour thresholds for all aromatic compounds determined from Flavornet (Acree and Teranishi, 1993; Acree and Heinrich, 2004; The Good Scents Company [tgsc], 2018; Brown, 2020), and Leffingwell and Associates (Leffingwell and Associates, 1985).

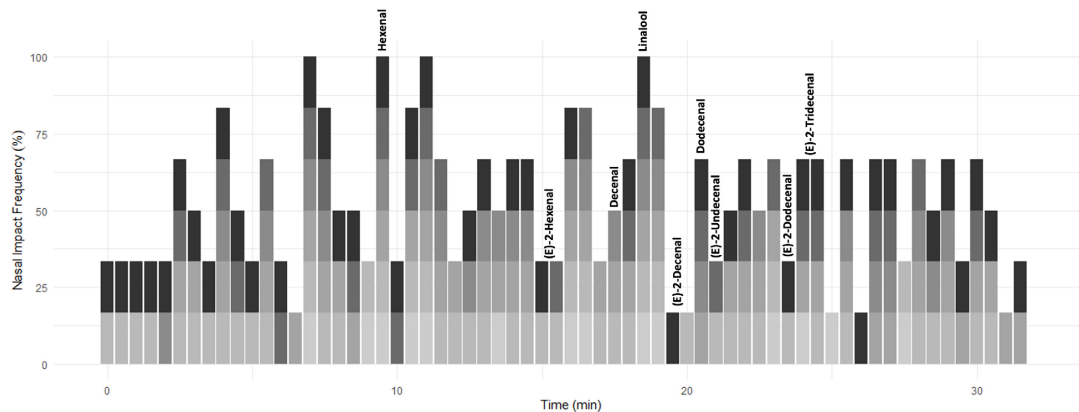
## Statistics and Experimental Design

Statistical analyses were conducted in R<sup>1</sup>. A Shapiro–Wilk test was used to test for normality and a Levene's test of homogeneity was used to determine if samples had equal variance. Single factor differences were analyzed using a one-way ANOVA with a Tukey–Kramer honest significant difference (HSD) test where more than one group existed. The light response curves and derived parameters were determined using R according to the equations of Marshall and Biscoe (1980).

## RESULTS

A NIF aroma gram was determined on potted supermarket coriander (Tesco Ltd., Long Eaton, United Kingdom) samples using a panel of six sniffers and GC-O (**Figure 2** and **Supplementary Figure 1**). The key aromatics of coriander

<sup>1</sup><http://www.r-project.org/>



**FIGURE 2** | A time series depicting the time aromatic compounds were detected in commercially sold *C. sativum* by six panelists (denoted in shades of gray). The scent was assigned a score of 0 (no aroma detected) to 1 (aroma detected) over a period of 32 min and then converted to%. This annotated time series was compared to the GC-MS chromatogram of supermarket-purchased *C. sativum*. Aromatic compounds of interest are annotated.

were selected based on NIF identification and the literature (Table 1) along with their corresponding odour thresholds. The odour threshold is defined as the lowest concentration of a compound that can be detected by the human nose (Van Gemert, 2003). If two compounds have the same concentration in the sample, the compound with the smaller odour threshold will potentially be identified over the compound with the larger threshold.

Of the compounds identified using the GC-O, six were found to significantly differ in relative concentration between plants grown under specific LED spectrums (Figure 3).

**TABLE 1** | Key aromatic compounds associated with the aroma of coriander, the odour threshold at which they are detected (ppb), and the generally accepted descriptor—these compounds were then taken forward for each analysis to determine differences in aroma between *C. sativum* grown under varying environmental conditions.

ID	Aromatic compound	Odour threshold (ppb)	Descriptors
1	Hexanal	4.5	Grass, tallow, fat
2	(Z)-3-Hexenal	0.25	Green, fatty, grassy, weedy, fruity, apple
3	(E)-2-Hexenal	17	Green, banana, aldehydic, fatty, cheesy
4	(E)-2-Hexenol	1	Resin, flower, green
5	Decanal	2	Soap, orange peel, tallow
6	Linalool	7.4	Sweet, floral, citrus
7	Undecanal	5	Sweet
8	(E)-2-Decenal	0.35	Waxy, fatty, earthy, coriander-like, green, mushroom, aldehydic
9	Dodecanal	2	Floral
10	(E)-2-Undecenal	5	Fresh, fruity, citrus, orange peel
11	(E)-2-Dodecanal	1.4	Green, fat, sweet
12	(E)-2-Tridecenal	0.8	Flower, sweet, must

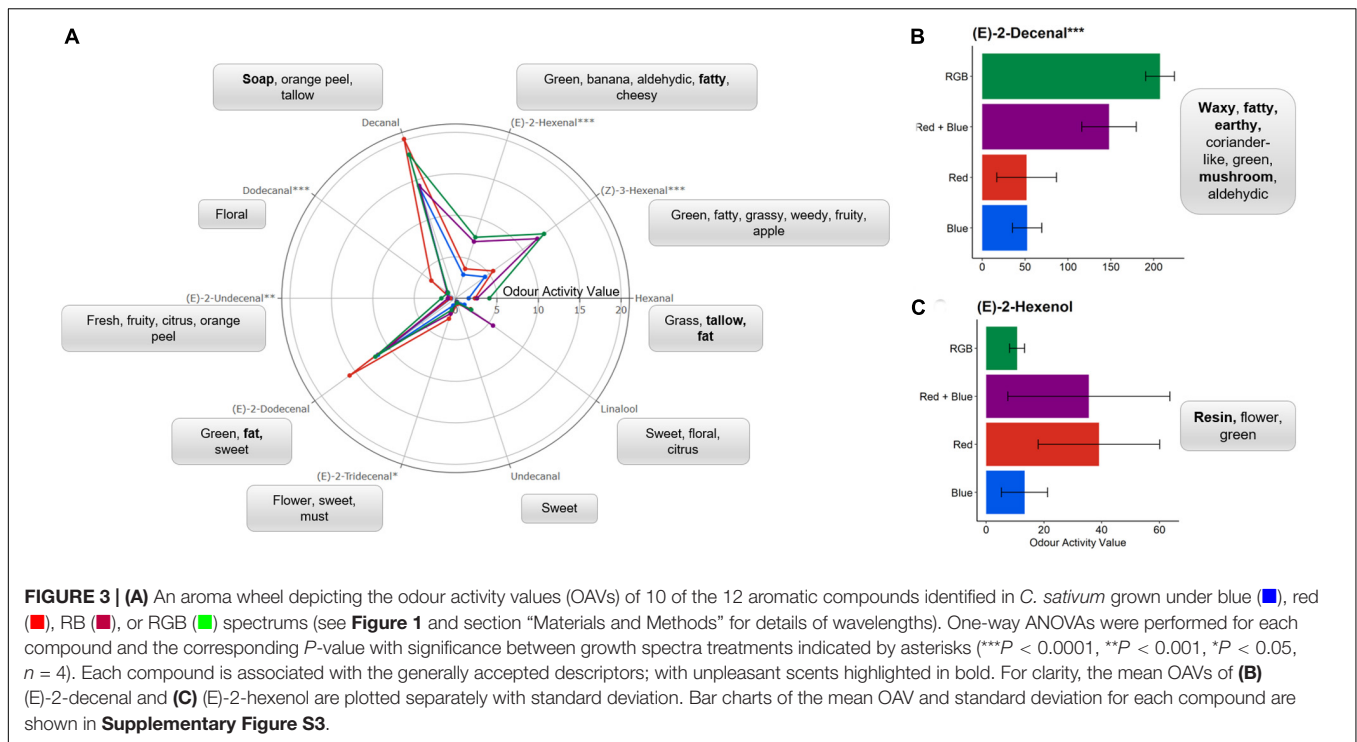
The compounds and their corresponding ID can be identified on the example chromatogram in **Supplementary Figure 1**.

## The Impact of Specific Spectrum on the Aroma and Physiology of *C. sativum*

Light-emitting diode lamps emitting four different spectrums were used to determine the impact of specific wavelengths on the concentration of aromatic compounds in fresh, above-ground *C. sativum* material grown in controlled environment settings (Figure 1 and Supplementary Figure S2). The intensity of the lamps was kept constant during the daytime phase at  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD. In general, the greater the number of wavelengths included in the treatment, the higher the odour activity of the compound; however, there were notable exceptions (Figure 3 and Supplementary Figure S3).

Plants grown under red LEDs demonstrated significant increases in (E)-2-tridecenal and dodecanal when compared to the other LED treatments. For dodecanal, this activity was significantly higher for the plants grown under red light when compared to all other LED treatments ( $P < 0.003$ ) while for (E)-2-tridecenal this increase in activity was only significantly higher than those found in the material grown under blue LEDs ( $P = 0.013$ ). Dodecanal and (E)-2-tridecenal are responsible for the “Soapy, waxy, aldehydic, citrus, orange rind with floral nuances” and “sweet” scents from fresh coriander (Table 1). These long chain aldehydes have the smallest odour thresholds (Table 1) and therefore, at higher concentrations, would have a greater contribution to the overall scent perceived by the sniffer and potentially favor of the fresh material. The compounds with the lowest odour threshold and most associated with the scent of fresh coriander, (E)-2-decenal and (Z)-3-hexenal, were significantly ( $P < 0.01$ ) higher in the RGB and RB treatments when compared with the monochromatic spectrums. With the addition of green wavelengths, the relative concentration of (E)-2-decenal was significantly ( $P = 0.03$ ) higher in the RGB grown plants when compared to the RB treatment.

Overall, the data suggest that plants grown under RB and RGB had increased photosynthetic capacity and  $W_i$  but there are some inconsistencies. Plants grown under the RGB



wavelengths achieved the highest rates of CO<sub>2</sub> assimilation (**A—Figures 4A,B**) and apparent quantum yield (**Figure 4D**) under saturating PPFD conditions, while the plants grown under the single wavelengths showed the lowest. This indicates that RGB could drive higher potential plant growth rate in comparison with other wavelengths. Interestingly, plants grown under RB wavelengths consistently achieved the highest rates of electron transport (ETR—**Figure 4C**). No significant differences for any of photosynthetic parameters were observed between the plants grown under the four different LED treatments (**Figures 4A–G**, *P* > 0.05). The respiration (**Figure 4E**), measure of curve convexity (**Figure 4F**), and LCPT (**Figure 4G**) were highest in the leaves grown under blue LEDs.

Intrinsic *W*<sub>i</sub>—the ratio of CO<sub>2</sub> assimilated to water lost via stomatal conductance—was calculated under each PPFD intensity for each treatment (**Figure 4H**). On average, plants grown under the dichromatic RB spectrum achieved the highest *W*<sub>i</sub> due to significantly lower stomatal conductance (*P* < 0.0001), this was especially clear at the low PPFD intensities (<1000 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD—**Supplementary Figure S4**). Plants grown under the red spectrum demonstrated the lowest *W*<sub>i</sub>, significantly (*P* < 0.0001) lower than plants grown under the blue, RB, and RGB spectrums.

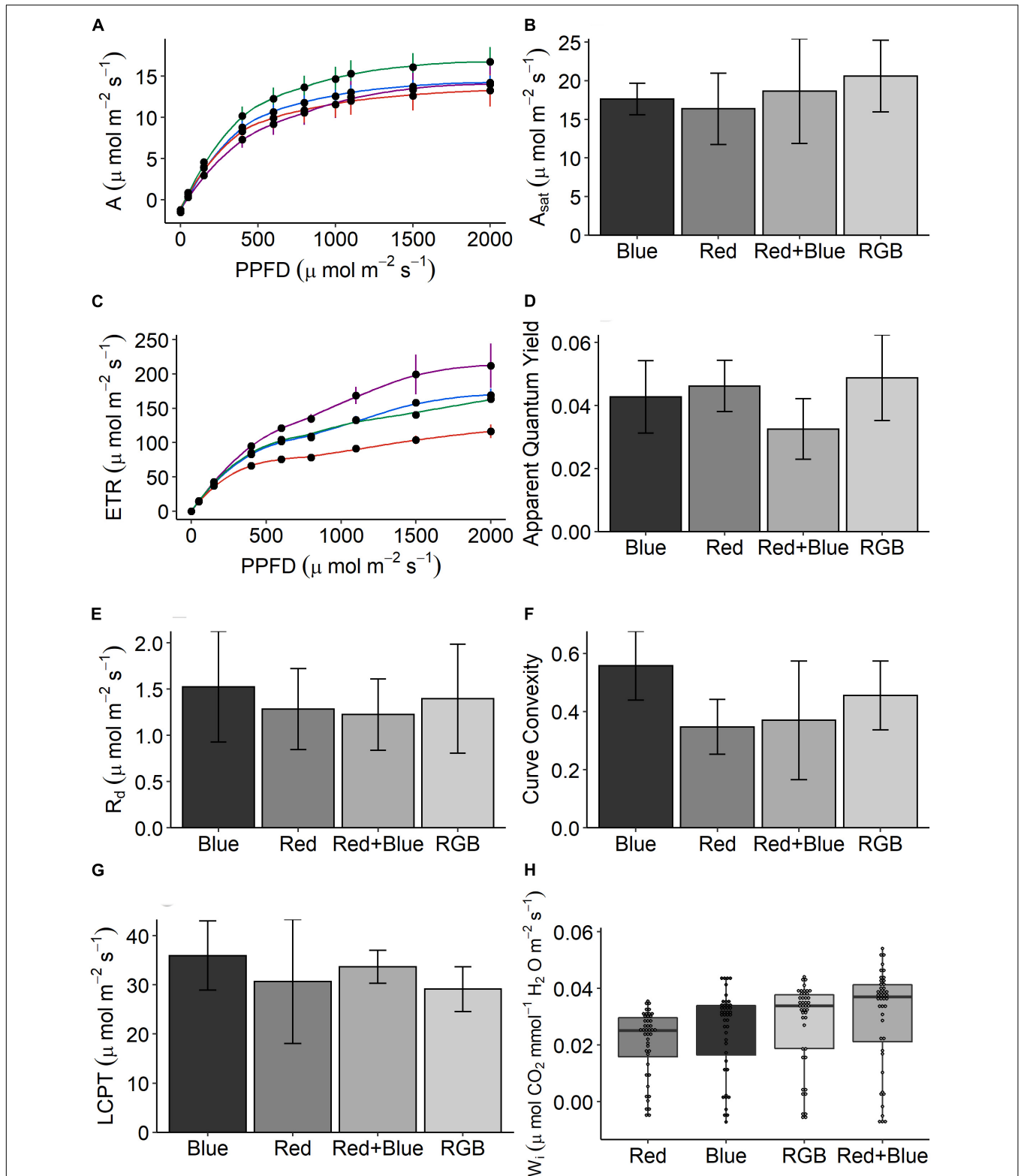
In the production of commercial coriander the grower selects plants with a desirable stem:leaf ratio; while short plants are appealing to the grower for transportation, leafy plants are selected by the consumer for inclusion in recipes. To assess these morphological characteristics, we measured plant features following growth under the four specific LED treatments (**Figure 1**). Although all plants received the same PPFD, significant differences in above ground biomass were determined

between the treatments for all harvest traits (**Figure 5**). Despite low germination rates (**Figure 5A**), plants grown under the red spectrum were the tallest (**Figure 5B**), achieved the highest leaf area (**Figure 5C**) and total biomass (stem and leaf—**Figure 5D**) and dry weight (**Figure 5F**). Interestingly, these plants demonstrated the lowest rates of CO<sub>2</sub> assimilation (**Figure 4A**). Plants grown under the RB and RGB spectrums had the greatest leaf to stem ratios (**Figure 4E**, 1.44 ± 0.19 and 1.28 ± 0.05, respectively) while plants grown under the singular red and blue spectrums had significantly lower leaf:stem ratios (0.58 ± 0.04 and 0.8 ± 0.06, respectively). We conclude that the shorter stature of the RB and RGB treatments tend toward an optimal morphology due to the smaller stem length under these spectra.

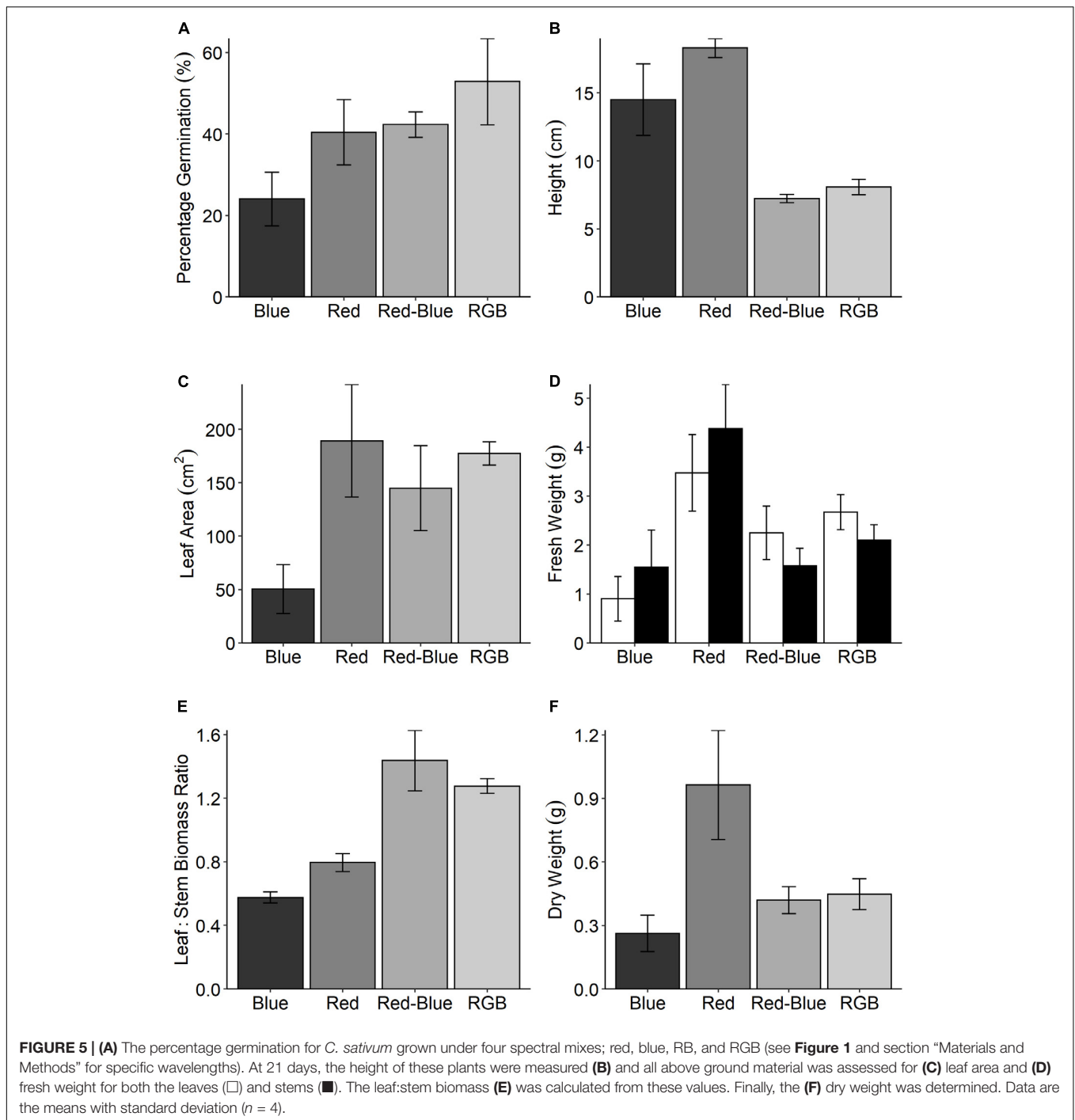
## Coriander Grown in Commercial Glasshouse Settings

Aromatic compounds previously identified as characteristic of the coriander aroma (**Table 1**) were relatively quantified for plant material grown in a commercial glasshouse with no supplemental lighting and for plants grown under LED lamps supplementing approximately equal thirds red, green, and blue wavelengths (35.8% red: 26.4% green: 37.8% blue, respectively) in a commercial glasshouse (**Figure 1**). These results were also compared with two supermarket products; coriander sold in a pot and excised coriander leaves sold in sealed packets (**Figure 6** and **Supplementary Figure S5**).

Significant differences were noted between the treatments for 10 of the 11 aromatic compounds identified (*P* < 0.03).



**FIGURE 4 |** The response of (A) net photosynthetic CO<sub>2</sub> assimilation ( $A$ ) in response to increasing photosynthetic photon flux density (PPFD) for plants grown under the four LED spectrums. From these response curves, (B) light-saturated rates of  $A$  ( $A_{\text{sat}}$ ), (C) the response of electron transport (ETR), (D) apparent quantum yield (mol CO<sub>2</sub>/mol quanta), (E) the rate of respiration ( $R_d$ ), (F) curve convexity, and (G) light compensation point (LCPT) can be estimated. Finally, (H) intrinsic water-use efficiency ( $W_i$ )—the ratio of CO<sub>2</sub> assimilated to water lost via stomatal conductance—is calculated for every replicate under each PPFD intensity. Data are the means with standard deviations ( $n = 4$ ).

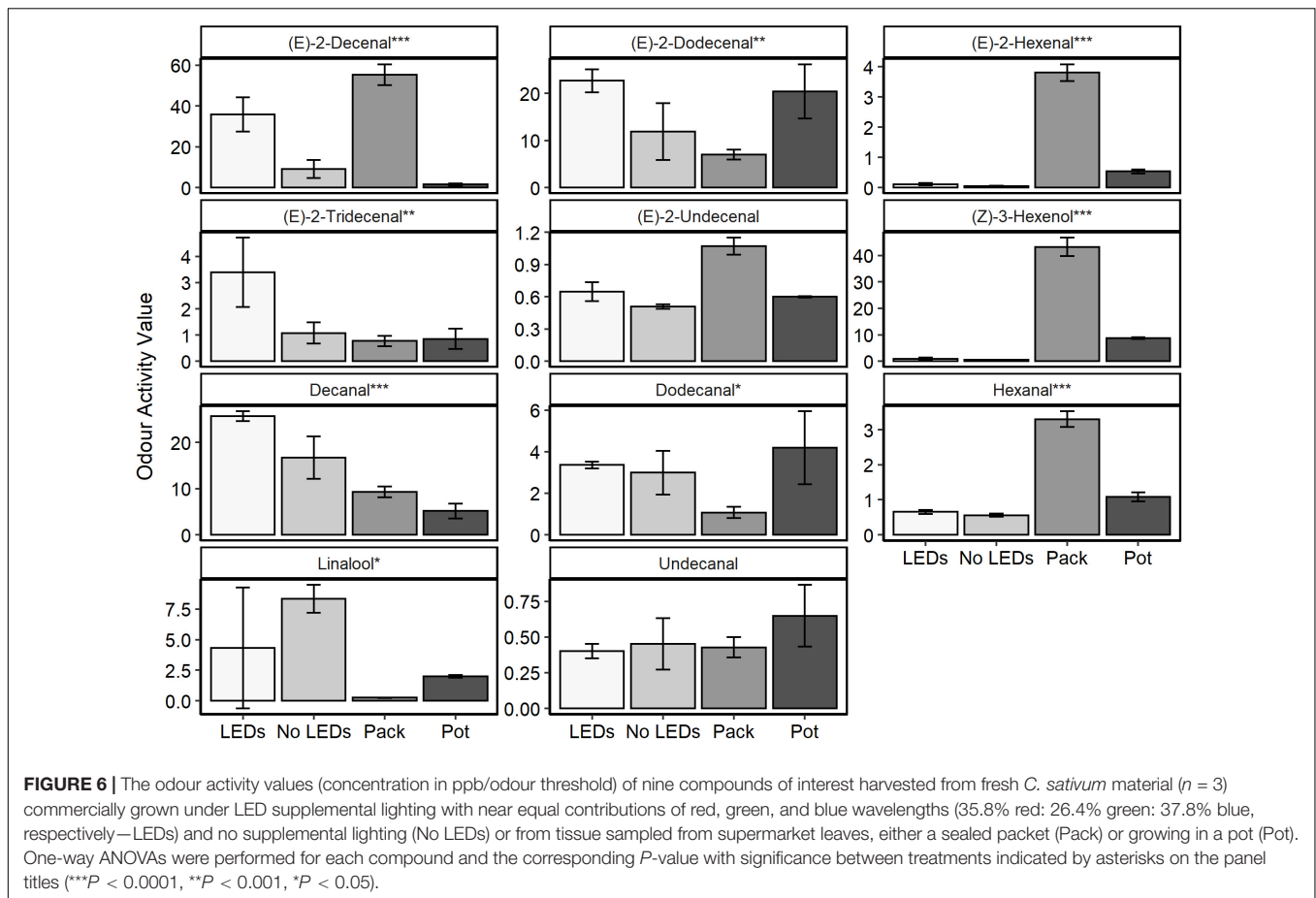


The plants grown under LED lighting demonstrated the highest concentrations of the 11–13 carbon chain aldehydes [(E)-2-dodecanal and (E)-2-tridecanal] and the highest ( $P < 0.0001$ ) concentration of decanal—the compound that characterizes both favorable nuances such as citrus and florals but is also responsible for the soapy undertones of coriander aroma (**Table 1**). Decanal was found to be lowest in material harvested from the purchased, potted coriander, significantly lower than

in the material grown with or without supplemental LED lighting ( $P < 0.003$ ).

The packets of excised coriander purchased from a supermarket showed the highest concentrations of six-carbon aldehydes and alcohols: (E)-2-hexanal, hexanal, and (Z)-3-hexenol. These compounds are associated with the “green” and “grassy” nuances of coriander aroma (**Table 1**). Interestingly, for six out of 11 of the aromatics, concentrations





were higher in the excised, packet coriander than in the potted supermarket coriander.

In general, the plants grown in a commercial glasshouse with no supplemental light were found to have lower concentrations of the aromatic compounds of interest when compared to the material grown under the LEDs. The one exception to this observation was linalool, which was found to be 1.9-fold higher in these plants and over 33-fold higher than measured in the packaged supermarket leaves.

## DISCUSSION

While past studies have focused on differences in the aromatic composition of *C. sativum*, for example, comparing seeds and leaves (Shahwar et al., 2012), wild and domestic varieties (Eyes et al., 2005) or post-harvest treatment (Buthelezi et al., 2016), very few have stated growing conditions of the samples and how these environmental conditions may impact on aroma. Here, we present a study on the combined impact of spectra on the aroma and physiology of commercial *C. sativum*.

Our findings have determined that the majority of *C. sativum* high impact aromatics reported in the literature (Table 1) were also observed for United Kingdom-based, commercially grown coriander as determined using the NIF panel and

GC-O chromatogram (Figure 2 and Supplementary Figure 1). Using these compounds as a gauge, significant differences in concentration (Figure 3) were noted when coriander was grown under distinct LED spectra (Figure 1), emitting the same PPFD, in controlled environment growth rooms. This indicates that the aroma of these plants was modified by wavelength and not total PPFD. This observation has also been noted in the literature for the herbs basil (*Ocimum basilicum*), dill (*Anethum graveolens*), and parsley (*Petroselinum crispum*) (Litvin-Zabal, 2019; Pennisi et al., 2019). For *C. sativum*, while adding greater numbers of narrow band wavelengths generally increased the concentration of most aromatics, significant differences were also observed for plants grown under single wavebands (Figure 3). This suggests that it is possible to manipulate the concentration of particular compounds through the addition or removal of particular wavelengths. For example, to increase the intensity of aromatics most associated with *C. sativum* (e.g., E-2-decenal) for a more desirable stronger scent or decrease compounds that are less desirable (e.g., decanal, dodecanal), which are associated with waxy, soapy nuances (Table 1).

## Growth, Morphology, and Spectrum

Manipulating spectra also generates marked changes in key physiological (Figure 4) and morphological (Figure 5) characteristics. While not significant in this dataset, growing

crops under specific spectrums are known to manipulate photosynthesis and associated processes. All three wavebands (red, blue, and green) are capable of driving photosynthesis with the same quantum efficiency (McCree, 1971; Hogewoning et al., 2012); however, differences in chlorophyll content and leaf/canopy structure (Murchie and Horton, 1997; Terashima et al., 2010) dictate the proportions of each waveband that will reach the chloroplast, depending on position in the leaf and the canopy. Although no anatomical measurements were taken for this paper, this might explain the waveband specific variation in photosynthetic parameters observed in **Figure 4**. It is also possible that at higher growth PPFD, the differences between the photosynthetic responses observed under each spectrum would induce irradiance acclimation responses (Murchie and Horton, 1997) and hence become much greater, as a supplement of  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD is low compared to the daily light received in a glasshouse, depending on latitude and season.

Plants respond to signals derived from light quality and quantity, mediated by an array of photoreceptors such as phytochrome and cryptochrome (Smith et al., 2017). The complex morphological responses observed here, and the associated photosynthetic properties will at least partly be a result of such signaling processes. It is hard to de-convolute these with the current data set and this was not the intention of the study but here we explore possible biological processes at work. Although the plants grown under the red-only spectrum demonstrated some of the lowest rates of photosynthesis per unit leaf area (Schepens et al., 2004), they also demonstrated the highest accumulation of fresh and dry biomass (**Figures 5D,F**). A likely explanation for this is that these plants allocated greater resources to above ground biomass accumulation and leaf area, while  $\text{CO}_2$  assimilation was reduced due to lower amounts of photosynthetic components (such as the enzyme Ribulose biphosphate carboxylase/oxygenase or Rubisco) per unit leaf area (Bugbee and Salisbury, 1988; Kim et al., 2004). In fact, a higher leaf area with lower specific leaf weight (thinner leaves) and increased stem elongation is a common strategy to enhance light capture in low light growing environments (Evans and Poorter, 2001) and explains leaf and stem morphology within the current growth PPFD. A lack of investment in photosynthetic assimilation per unit leaf area would limit plants grown under red wavelengths if the total PPFD exceeded  $350 \mu\text{mol m}^{-2} \text{s}^{-1}$  while those plants grown under RB or RGB mixes would better utilize higher light—potentially accumulating greater biomass more rapidly (**Figure 4A**). Changes in leaf area and stem elongation under low irradiance have been linked to activity of the photoreceptor phytochrome which is determined by the ratio of red to far red light. We suggest such a response is at work here (Franklin and Whitelam, 2005). In contrast, blue light effects are mediated by the photoreceptor cryptochrome (Smith et al., 2017) which, among other effects, is known to regulate leaf specific leaf weight (thickness). Thus addition of blue light can lead to thick leaves with higher amounts of photosynthetic components and a higher photosynthetic capacity but this effect is hard to discern in the current data set. The large differences seen in **Figure 5** between red, blue, and RB are likely to be a result of interactions between these different

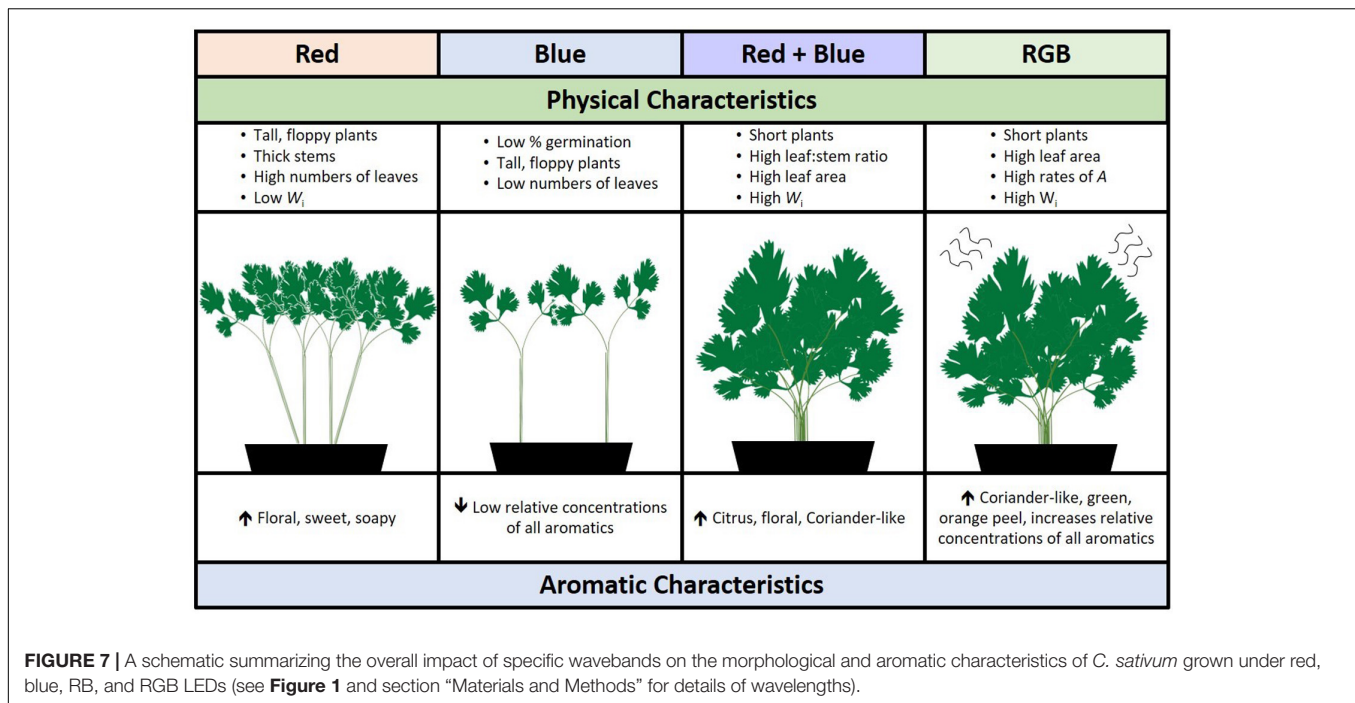
photoreceptor-mediated processes. The particularly high rate of photosynthesis in the RGB plants is hard to explain but may be a result of enhanced Rubisco content per unit leaf area as a result of photoacclimation to red, blue, and green. Green light is known to interact with blue light responses (Smith et al., 2017). This study only includes single measurements at one developmental stage and does not include lifetime measurements of  $\text{CO}_2$  assimilation or dark respiration, which may also explain some of the disparity in biomass acquisition between the treatments.

While green light is known to reverse blue-light stimulated stomatal opening (Frechilla et al., 2000; Smith et al., 2017), the plants grown under RB had the highest mean intrinsic  $W_i$  (**Figure 4H**). It is well known that red and blue wavelengths modulate stomatal behavior (Lawson, 2009), with a small amount of blue on a red background initiating rapid stomatal opening (Shimazaki et al., 2007). For coriander grown under a 50:50 red:blue ratio, this effect seems negated by the concurrent lower stomatal conductance and higher rates of  $\text{CO}_2$  assimilation demonstrating the highest  $W_i$  between the spectrum treatments. In addition to the regulation of  $W_i$ , green light has been implicated for improving  $\text{CO}_2$  uptake in lower levels of the canopy (Smith et al., 2017)—coriander develops a highly dense canopy prior to harvest and the addition of green wavelengths to supplemental lighting may increase growth rates and maintain better canopy structure in packed commercial glasshouse growing conditions.

## Aroma and Growth Spectrum

It is less clear how such mechanisms could influence the flavor and aroma properties, but it seems likely that they are involved too: for example, phytochrome is implicated at all major developmental transitions in plants in addition to environmental signal processing (Schepens et al., 2004). Further, red to far red ratios are known to regulate volatile organic compound emissions such as ethylene, in response to plant to plant competition (Kegge and Pierik, 2010).

In addition to strong aroma, the fresh coriander ideotype for commercial production would have high seed fecundity (i.e., high germination rates), produce large numbers of leaves to stems, and be easy to transport to supermarkets. Interestingly, plants grown under red wavelengths acquired the greatest biomass in the same period of time but were also significantly taller suggesting a leggy, shade-avoidance phenotype (Fraser et al., 2016). Plants grown under red-only wavelengths also produce higher concentrations of unpleasant aromatics decenal and E-(2)-tridecenal (soapy, sweet, and musty aromatic nuances). While greater numbers of wavelengths had a positive impact on germination and leaf area, the RB spectrum improved the leaf:stem ratio while shortening the plants, potentially making them easier to pack or harvest. From these results, we conclude that there is a fine balance between manipulating aroma and maintaining the preferred coriander ideotype; using specific LED supplements may yield the best aroma but not a visually appealing plant (**Figure 7**). This may allow growers to target niche products such as curry pastes, micro-greens, or custom vertical farming, a growing global market



(Vertical farming research predicts industry growth, 2019). Such options are dependent on the ability of growers to invest in lighting infrastructure for industrial scale production, assuming a viable business model.

As well as manipulating the aroma of low odour threshold aromatics in controlled growth room conditions, glasshouse-based supplemental LED lighting was also found to manipulate the odour profile of coriander (**Figure 6**). With the exception of linalool and undecanal, using LEDs to supplement the light of glasshouse-grown coriander increased the concentration of all the aromatics measured when compared to non-supplemented plants. Comparing LED-supplemented material to non-Supplemented Material uncovered significant differences in the quantity of high impact aromatics including decanal and (E)-2-decanal which would potentially make the supplemented coriander smell (and taste) more strongly of coriander. However, increases in decanal, although contributing stronger citrusy undertones to the material, could also discourage some consumers due to increases in a soapy aroma.

The data presented here also suggest that coriander which has been cut and packed for sale has a different aromatic composition to the coriander sold in a pot. Although this could be attributed to the samples originating from different companies or production batches, increases in long-chain aldehydes and alcohols have been linked to the stress response of plants (Holopainen and Gershenzon, 2010). Increases in the concentration of long-chain aldehydes in the cut material could also reflect the material beginning to dry after excision, therefore concentrating the aromatics before our GC-MS analysis (hence higher relative concentrations) and promoting the intensification of the aromatics after purchase in the supermarket for the consumer. This also suggests potential to manipulate aroma

profile of the coriander in post-harvest processing by irradiating the excised material under specific spectrum or by selling excised material grown under specific spectrum.

The highest concentrations of linalool, a volatile monoterpene (Schwab et al., 2008), were determined for the plants grown in a glasshouse without supplemental LED lighting. Linalool is a natural herbivore repellent indirectly defending against herbivory and acting as an attractant to predators of herbivores (Degenhardt et al., 2003). High concentrations of this compound in the leaves of *Arabidopsis thaliana* and potato have been shown to repel aphids and mites through manipulation of the terpenoid biosynthesis pathway (Kappers et al., 2005; Aharoni et al., 2006). The presence of linalool in these particular samples suggests defense against biotic stresses (Holopainen and Gershenzon, 2010) in the glasshouse environment. With less linalool detected in the plants grown under supplemental LEDs, or in the packed or potted supermarket coriander, these data suggest that these plants may be more susceptible to biotic attack within glasshouse or growth room setups. In addition to plant defenses, the terpenoid pathways have also been manipulated in tomato plants to engineer more aromatic and flavorful fruits (Lewinsohn et al., 2001). Metabolic engineering of volatile terpenoids can have negative implications for plant growth and fitness (Aharoni et al., 2003, 2006), leading to lowered potential oil yields in some species (Mahmoud and Croteau, 2001). This suggests that the decrease of linalool in LED grown plants will also lead to a changed perception of *C. sativum* aroma for the consumer, which may or may not be negated by the increase of lower threshold, similar smelling compounds.

To our knowledge, this is the first publication investigating the combined impact of spectra on the physiology, growth and

aroma of *C. sativum* plants. These data highlight the fine balance between actively manipulating the growth and physiology to produce a marketable plant while maintaining or strengthening the aromatics in this popular herb.

## CONCLUSION

The work presented here and, in the literature, suggests that modification of aroma in response to growth spectrum is an adaptive response that is linked to numerous diverse biological roles. The observations that aromatic complexity derives from spectral complexity may appear surprising, but we must recall that the existence of desirable secondary plant compounds is related to defense, competition, and fitness. When we move from a monochromatic source, which the plant is unlikely to experience in nature, to more complex dichromatic and trichromatic spectra we may progressively be activating the signaling pathways that give rise to these measurable economic traits. In this paper, we hypothesize that we have de-convoluted these pathways through the manipulation of growing spectra. The practical application of our observations is that flavor and aroma can be co-manipulated with the form (morphology) of the plant, enabling a grower to produce a combination according to market demand and this principle has a biological basis.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

## AUTHOR CONTRIBUTIONS

EM, IF, JC, and LM conceived this project. DM designed and managed the manufacture of the LED lamps. M-TL performed and analyzed the gas chromatography mass spectrometry and olfactometry data. LM and HS-H grew the plants, performed all the phenotypic experiments in the laboratory, and sampled. UM managed the field experiment at Langmeads Farm and sampled the plants. LM wrote the manuscript. All authors reviewed the final manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2020.00462/full#supplementary-material>

**FIGURE S1** | A representative chromatograms demonstrating the relative abundance of aromatic compounds found in above-ground *C. sativum* material purchased from a commercial retailers ( $n = 3$ ). The numbers above each peak indicate the presence of the aromatic compounds (Table 1 for details), indicated by the NIF test and literature as being a main constituent of the aroma of fresh coriander leaves.

**FIGURE S2** | Representative chromatograms of above-ground *C. sativum* material grown in controlled environment chambers under  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetic photon flux density (PPFD) of either (a) red, (b) blue, (c) RB, or (d) RGB LEDs (see Figure 1 and section "Materials and Methods" for details of wavelengths) ( $n = 4$ ).

**FIGURE S3** | The odour activity values (concentration in ppb/odour threshold) of 12 compounds of interest as determined from fresh *C. sativum* grown under blue, red, RB, or RGB spectrums. Data are the means ( $n = 4$ ) with standard deviation. One-way ANOVAs were performed for each compound and the corresponding  $P$ -value with significance between growth spectra treatments indicated by asterisks (\*\*\* $P < 0.0001$ , \*\* $P < 0.001$ , \* $P < 0.05$ ).

**FIGURE S4** | The relationship between  $\text{CO}_2$  assimilation ( $A$ ) and stomatal conductance ( $g_s$ ) for plants grown under four separate spectrums; red (●), blue (●), RB (●), and RGB (●) (see Figure 1 and section "Materials and Methods" for details of wavelengths) in response to changes in PPFD ( $n = 4$ ).

**FIGURE S5** | Representative chromatograms of *C. sativum* material sampled from four sources; (A) commercially sold *C. sativum* from a pot, (B) commercially sold *C. sativum* leaves, excised and sold in a packet, (C) *C. sativum* grown in a commercial glasshouse under supplemental LEDs, and (D) *C. sativum* grown in a commercial glasshouse with no supplemental LEDs.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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