



# Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs)

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## ABSTRACT

Light-emitting diode (LED) technology has rapidly advanced the past years and it is nowadays irrevocably linked with controlled-environment agriculture (CEA). We provide here an amalgamation of the recent research achievements in the horticulture and floriculture industry, ranging from greenhouse applications to climate rooms and vertical farming. We hope this overview bestows ample examples for researchers and growers in the selection of the appropriate LED light solution for amending crop yield, phytochemical content, nutritional value, flowering control, transplant success, pre-harvest and postharvest product quality, and production of regeneration material. We leave the reader with some future prospects and directions that need to be taken into account in this ever-growing field.

## 1. Introduction

### 1.1. Review objectives

During the last years, the field of research on light-emitting diodes (LEDs) has yielded technologies that make LED modules more energetically efficient and versatile as lighting systems (Cocetta et al., 2017; Gupta, 2017). Therefore their potential applications in horticulture are constantly expanding. The potential use of LEDs in a) closed systems (growth chambers), b) greenhouses, c) multilayer vertical farming and d) postharvest is discussed. This review focuses on the performance of horticultural species, as they are commonly grown in the aforementioned systems, and the aim is to summarize the effects of LED lights on: (a) plant growth and developmental traits and (b) primary and secondary metabolites. Within each section, responses of plants to monochromatic, dichromatic or continuous spectra are described.

### 1.2. Artificial lamp types

The use of artificial light sources emitting photons over a continuous spectral range from 350 to 750 nm, such as fluorescent (FL), high-pressure sodium (HPS), metal halide, and incandescent (INC) lamps have been long used in tissue culture and growth rooms (Economou and Read, 1987), as well as in greenhouses to supplement natural light (Cathey and Campbell, 1980; Murdoch, 1985; Both et al., 1997; Krizek et al., 1998). Among traditional artificial sources, FL lamps are more commonly utilized in plant-growth applications than INC lamps due to a more efficient energy conversion and due to the higher blue fraction emitted which can reach more than 10% of the total photon emission within the photosynthetically active radiation (PAR), depending on the correlated color temperature (CCT) of the lamp (Simpson, 2003). However, illumination emissions based on traditional artificial lighting is neither spectrally optimal nor energetically efficient for several photoperiodic plant species; especially when lamps are placed in close proximity to the plants, tissue damage from photo-stress is induced (Nelson, 2012; Dutta Gupta and Jatothu, 2013).

*Abbreviations:* CEA, controlled-environment agriculture; LED, light-emitting diode; FL, fluorescent lamp; CWF, cool white fluorescent lamp; HPS, high-pressure sodium lamp; INC, incandescent lamp; PAR, photosynthetically active radiation; UV, ultraviolet light; P, purple light; B, blue light; G, green light; Y, yellow light; R, red light; FR, far-red light; W, white light; phy, phytochrome; cry, cryptochrome; phot, phototropin; UVR8, UV resistance locus 8; F<sub>v</sub>/F<sub>m</sub>, maximum quantum yield of PSII; ΦPSII, quantum efficiency of PSII; LAI, leaf area index; S/R, shoot-to-root ratio

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With the evolving technology in the use of artificial lighting in the 90's, LEDs were first introduced by testing their effects on plant growth for food during space travel at the University of Wisconsin, Purdue University and at NASA's Kennedy Space Center (Massa et al., 2008). According to previous studies, LED lights could provide several unique advantages, among the existing artificial lighting sources, including the ability to control spectral composition, adjustable size, durability, long operating lifetime, relatively cool emitting surfaces and photon output that is linear with electrical input current (Bula et al., 1991; Folta et al., 2005; Bourget, 2008). They could also be characterized as more environmentally friendly and economically favorable, than the conventional lighting, at least for enclosed growth plant facilities, while they have safer handling and disposal procedures (Schultz et al., 2008; Duong and Nguyen, 2010; Shimada and Taniguchi, 2011). Nowadays, LED lights produced are at least as energetically efficient as the traditional light sources (Schubert and Kim, 2005; Pimputkar et al., 2009; Nelson and Bugbee, 2014; Kozai et al., 2016).

Controlled-environment agriculture (CEA) is a subject directly connected to the relying principals of the food system optimization worldwide due to the upcoming population and climate changes scenarios (Food and Agriculture Organization of the United Nations: FAO (2015). The solid-state light sources had been used in CEA such as plant tissue or cuttings, culture rooms and growth chambers, greenhouses and nurseries (Davis and Burns, 2016). LEDs allow wavelengths to be matched to plant photoreceptors in order to have optimal production and influence plant morphology and metabolism (Massa et al., 2008; Yeh and Chung, 2009; Dueck et al., 2012; Hernández and Kubota, 2012; Currey and Lopez, 2013). Concurrently, several studies have been conducted on the effect of spectral quality by employing monochromatic or polychromatic LEDs for a variety of plants on a big range of desired morphological and/or physiological changes in plants (Lee et al., 2007; Shin et al., 2008; Davis and Burns, 2016), such as increasing photosynthesis, modulating plant morphogenesis, controlling flowering time (Mitchell et al., 2015), or enhancing antioxidant activity (Ramalho et al., 2002; Kumar et al., 2016). Notably, blue and red LEDs are commonly used for plant growth as chlorophyll a and b (chl a and chl b, respectively) efficiently absorb blue and red wavelengths; absorbance maxima for chl a are 430 and 663 nm, whereas those of chl b are 453 and 642 nm, respectively (Chory, 2010). Moreover, much research effort has been focused on the effect of different ratios of red to far-red light that could modulate shoot elongation in plants (Gilbert et al., 1995; Von Wettberg and Schmitt, 2005; Casal, 2013) or even more of red, blue and green colors that approved to be beneficial on the growth of edible crops (Kim et al., 2004a; Lin et al., 2013). Also in other studies prior concern was focused on the control of the magnitude of light output to minimize energy consumption (Fujiwara and Toshinari, 2006; Harun et al., 2013).

### 1.3. Photoreceptors

Plant responses are triggered by changes in the light intensity, quality, direction and duration and are governed and conducted by specialized photoreceptors (Kami et al., 2010). Photoreceptor proteins have a small cofactor or chromophore molecule allowing them to sense and respond to specific wavelengths of light over a continuous spectral range (Burgie et al., 2014). Five photosensory systems have been identified up to date; the phytochromes (phys) that absorb maximally in the red (600–700 nm) and far-red (700–750 nm) regions of the spectrum (Chen and Chory, 2011), while blue light (390–500 nm) is mediated by three different classes of photoreceptors: the cryptochromes (crys) (Ahmad and Cashmore, 1993), phototropins (phot) (Christie, 2007) and members of the Zeitlupe family (ztl, fkl1 and lkp2) (Suetsugu and Wada, 2013). In addition, ultraviolet B (UV-B) wavelengths (280–315 nm) are monitored by the UV Resistance locus 8 (UVR8) (Jenkinson, 2014).

Phys are a family of proteins that include two interconvertible

forms, the inactive Pr and the active Pfr, which have their sensitivity peaks in the red at 660 nm and in the far-red at 730 nm, respectively (Smith, 2000; Demotes-Mainard et al., 2016). They govern several processes through the plant life cycle, such as induction of seed germination, seedling de-etiolation, flowering time (Strasser et al., 2010; Casal, 2013), leaf development (Rao et al., 2011), root elongation (Costigan et al., 2011) and tolerance to biotic and abiotic stressors (Ballare et al., 2012). When a germinated seedling emerges and it is exposed to light for the first time, it can survive for a restrictive time period that is highly depended on its seed reserves (etiolated development) (Neff et al., 2000). Thus, it is well known that the seed size effect is predominant regarding the early seedling developmental stages such as germination (Milberg et al., 2000), emergence (Castro, 1999), growth and survival (Baraloto et al., 2005).

Crys are ubiquitous photoreceptors that perceive UV-A and blue radiation (Huché-Thélier et al., 2016). Three crys (cry1, cry2 and cry3) have been identified in Arabidopsis, which are involved photomorphology, photoperiodic flowering (Koornneef et al., 1998; Lin, 2000; Selby and Sancar, 2006; Pokorny et al., 2008; Liu et al., 2011; Gupta, 2017). Crys are also associated with stomatal opening (Sellaro et al., 2010), anthocyanin biosynthesis (Ahmad, 2002), seed dormancy and germination (Barrero et al., 2014), circadian clock (Somers et al., 1998; Devlin and Kay, 2000) and de-etiolation (Ahmad and Cashmore, 1993). Apart from perceiving blue light, crys also sense the blue-to-green ratio (Bouly et al., 2007; Sellaro et al., 2010), and along with an unknown light sensor take part in adaptation to environments enriched in green light (Zhang et al., 2011).

Blue and UV-A light are also perceived by phot photoreceptors. Two phot (phot1 and phot2) have been identified in Arabidopsis. Low-fluence ( $< 1 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) blue light leads to phot1 response. Phot2 along with phot1 mediates the high-fluence response. Phot1 and phot2 usually have overlapping functions and contribute to a number of light mediated developmental responses. Phot1 and phot2 are involved in transient inhibition of hypocotyl elongation and later crucial regulation of plant growth toward a directional light orientation (Folta and Spalding, 2001). They are also associated with chloroplast accumulation, as well as stomatal opening (Ma et al., 2001). The members of the Zeitlupe family (ztl, fkl1 and lkp2) are also triggered by blue wavelengths and affect the regulation of the circadian clock and photoperiodic flowering (Zoltowski and Imaizumi, 2014).

UV-B radiation is mainly perceived by UVR8. Previous research findings on the exploration of gene regulation by UVR8 photoreceptor function in vivo, revealed its importance in UV protection such as the induction of flavonoid biosynthesis, hypocotyl growth suppression (Ulm et al., 2004; Jenkins, 2009) and its regulation role in epidermal cell expansion of wild-type plants (de Veylder et al., 2011), whereas it is possible that UVR8 can also interact with crys in the presence of solar UV radiation (Morales et al., 2013).

Phys and crys essentially control the de-etiolation phase by inhibiting hypocotyl elongation, triggering chloroplast development along with the promotion of cotyledon expansion and leaf growth, so the photosynthetic life of the seedling initiates (Franklin and Quail, 2010). Another overlapping set of responses that takes place among different photoreceptors is the shade avoidance syndrome (SAS), which is regulated by phys, crys, and possibly by phot and UVR8 as the plant perceives, apart from red and far-red light, also blue and UV and the equilibrium between blue and green radiation (Franklin, 2008; Ruberti et al., 2012).

## 2. Impact of LED lighting on development, physiology and primary/secondary metabolism of horticultural species

Natural light drives photosynthesis and also controls plenty of developmental and physiological responses throughout a plant's life cycle. Such responses include seed germination (Bentsink and Koornneef, 2008), apical hook opening (Jiao et al., 2007), shoot elongation (Casal,

2013), root architecture (Sakamoto and Briggs, 2002), leaf expansion (Cookson and Granier, 2006; de Carbonnel et al., 2010), the synthesis of photosynthetic and photo-protective pigments (chlorophylls, carotenoids and anthocyanins) (Reinbothe and Reinbothe, 1996; Brazaityte et al., 2006; Merzlyak et al., 2008; Pizarro and Stange, 2009; Li and Kubota, 2009; Samuoliene et al., 2013; Ouzounis et al., 2014b; Gupta, 2017), flowering (Alvarez-Buylla et al., 2010; Park and Runkle, 2017) and direction of growth (Pedmale et al., 2002). The aforementioned responses are mainly attributed to the effects of blue (B), red (R) and far-red (FR) lights and their ratios. Distinct responses to green (G) light and/or blue/green and red/green ratios have been revealed over the last years (Wang and Folta, 2013). Green light can stimulate photosynthesis deep in the canopy providing to carbon gain, especially within shaded canopies (Smith et al., 2017).

Light is a very critical environmental factor for the production of metabolites in plants (Kopsell and Sams, 2013; Carvalho and Folta, 2014). Plants produce secondary metabolites, which are distinct from primary metabolites such as carbohydrates and amino acids. Phenolic acids and flavonoids (phenolic compound group) are secondary metabolites that assist plants with adapting to biotic and abiotic environmental alterations (Wink, 2010). Phenolic compounds have critical roles in plants as blue and red pigments, as antioxidant compounds and as ultraviolet light screens (Lattanzio et al., 2006). Phenolic acids, such as chlorogenic acid, *p*-coumaric acid, caffeic acid and chicoric acid exert radical scavenging and antioxidant activity, as well as antifungal, antimicrobial and antibacterial action (Lattanzio et al., 2006; Seigler, 1998; Wink, 2010). Flavonoids such as kaempferol glucoside, rutin, quercetin and apigenin glucuronide display radical scavenging and antioxidant activity, have metal ion chelating properties, as well as antimicrobial and antibacterial action (Seigler, 1998). Anthocyanins are related with flower and fruit coloration and serve as insect attractants. They demonstrate antimicrobial activity and also absorb blue or ultraviolet light protecting cells from high light damage (Seigler, 1998).

Carotenoids are terpenoid compounds which serve as orange and yellow accessory pigments (Solovchenko and Merzlyak, 2008). Carotenoids can limit the damage to membranes caused by excess light, since they are free radical scavengers and they can efficiently dissipate excitation energy of chlorophyll. Moreover, they are capable of absorbing light energy, which is in a spectral region where chlorophylls are not sufficiently exploiting, and then transferring it to chlorophylls, thus enhancing plant photosynthetic efficiency (Davies, 2004). The xanthophyll cycle (violaxanthin, zeaxanthin and antheraxanthin are involved) is light regulated and leads to dissipation of excess energy. This process limits reactive oxygen species production (Demmig-Adams and Adams, 1992). In addition, lutein and  $\beta$ -carotene are important carotenoids taking part in the leaf light-harvesting complex.

### 2.1. Application of LED lighting in growth chambers

Plant physiological processes are variably affected by light and the responses are species and cultivar dependent (Ouzounis et al., 2015b). Several combinations of the radiation spectra have been tested in order to study plant growth and development under different light conditions. A vast number of research studies have been conducted using lettuce as a model plant. When cool white fluorescent lamp (CWF) was supplemented with FR LED for lettuce growth, it caused a reduction in anthocyanin, carotenoid and chlorophyll content, while it enhanced fresh and dry weights, stem length, and leaf length and width (Li and Kubota, 2009). The authors also found that R light supplemented to CWF led to increased chlorophyll concentration, whereas supplemental B or ultraviolet (UV) LEDs enhanced anthocyanin concentration but reduced stem length. Red leaf lettuce grown under R supplemented with FR light also exhibited lower anthocyanin concentration and antioxidant potential, whereas R supplemented with B light imposed the exact opposite results (Stutte et al., 2009). Chen et al. (2016) reported that W supplemented with monochromatic LEDs having various emission

peaks differently affected Green oak leaf lettuce. Specifically, supplemental FR light negatively affected fresh weight of shoots, biomass and pigment contents, but increased shoot-to-root (S/R) ratio and ascorbic acid, R and B led to increased fresh weight of shoots, chlorophyll and carotenoid contents, B and G decreased nitrate content but yellow (Y) increased the latter, and G enhanced the accumulation of soluble sugars, while Y suppressed it.

In cucumber, monochromatic R light suppressed fresh and dry mass production compared to various RB and RGB combinations, while B light promoted fresh mass production (Hernández and Kubota, 2016). In addition, the authors found that more B light in different RB combinations led to increased leaf mass per area, chlorophyll content per leaf area, leaf net photosynthetic rate and stomatal conductance, but decreased plant height, hypocotyl and epicotyl length, leaf area, fresh and dry mass. Fan et al. (2013) reported various responses of non-heading Chinese cabbage under the influence of monochromatic and dichromatic LEDs. Particularly, R light increased plant height but induced negative effects on chlorophyll and carotenoid concentration, as well as on four chlorophyll biosynthetic precursors (5-Aminolevulinic acid, Mg-protoporphyrin IX, Protochlorophyllide and Protoporphyrin IX), Y light diminished dry mass production, as well as soluble sugar and protein concentration, G light decreased chl a/b ratio, while B and RB lights promoted the concentration of soluble proteins, chlorophylls and carotenoids but decreased plant height. G light contributes to growth and development of horticultural plants. Snowden et al. (2016) found that G light positively affected leaf area index (LAI) of cucumber, stem length of tomato, petiole length of radish and specific leaf area of pepper at  $500 \mu\text{mol m}^{-2}\text{s}^{-1}$ . However, G light also suppressed chlorophyll concentration of cucumber. Under B light alone, the same authors found suppressed dry mass, LAI, stem and petiole length of tomato, cucumber, pepper and radish. In addition, the authors reported higher net assimilation of cucumber, pepper, radish and lettuce, and greater chlorophyll production of tomato, cucumber, pepper and radish. Mustard, beet and parsley microgreens grown under FR + R supplemented with different B light doses exhibited an increase of several carotenoids ( $\alpha$ - and  $\beta$ -carotene, lutein, zeaxanthin, neoxanthin, violaxanthin) chlorophylls (a and b) and tocopherol under 16%, 25% and 33% B light (Samuoliene et al., 2017). Craver et al. (2017) found that increasing light intensities promoted the carotenoid accumulation in mizuna and mustard microgreens, while a RB (R87:B13) LED increased total integrated chlorophyll of kohlrabi and mustard, and along with a RFRB (R84:FR7:B9) LED promoted the anthocyanin content and total phenolic concentration of Kohlrabi. B LEDs used in combination with R lights showed positive effects on growth, physiological and nutritional characteristics of several horticultural species. In nine tomato genotypes, B supplemented to R light had positive effect on plant biomass, attenuated upward or downward leaf curling and led to increased soluble protein concentration, chlorophyll and carotenoid concentration (Ouzounis et al., 2016). High B ratio combined with small dose of end-of-day (EOD) FR can suppress intumescence injury in tomato (Eguchi et al., 2016). In tomato, monochromatic R light increased fructose and glucose contents, and acid invertase and neutral invertase activities, while RB (3R1B) increased total carbohydrate, starch and sucrose accumulation, and sucrose synthase activity (Li et al., 2017). Moreover, both R and RB increased plant height and stem diameter indicating that these spectra could regulate photosynthesis and plant morphology. W and RB LEDs negatively affected the growth performance of sunflowers, whereas HPS increased top leaf temperature, fungal species abundance compared to natural light (Alsanian et al., 2017). In an experiment involving two basil cultivars grown under light treatments with continuous radiation spectra, Bantis et al. (2016) reported that the most B and UV (1%) containing continuous LED light led to decreased S/R ratio and increased total phenolic content. Two treatments with low R:FR ratio (highest in R and FR; and high in B, R, and FR) had a positive effect on plant shoot height. Moreover, the three aforementioned light treatments enhanced the total biomass

production of basil by more than 40% compared to FL (detailed spectrum percentages in Table 1). In a study purposely comparing cultivation of artichokes under greenhouse conditions or under monochromatic LEDs in a growth chamber, the authors (Rabara et al., 2017) found that R LED increased shoot dry weight and height compared to natural light, even though natural light was three times the total PPFD of R LED. Huang et al. (2017) reported that B led to increased dry biomass of oyster mushrooms, while high intensity of B light enhanced DPPH radical-scavenging effect, Fe-chelating ability, reducing power and soluble sugar content. Urrestarazu et al. (2016) tested the impact of a conventional LED or a LED with “good spectral fit to the maximum photosynthetic response” on lettuce tomato and pepper and reported that the latter LED treatment increased the energetic efficiency of all species.

In roses, several responses have been reported with increased B:R ratio, such as greater leaf biomass, decreased leaf area and shoot biomass, and formation of sun-adapted leaves, while no effect was observed on flowering (Terfa et al., 2013). RB LEDs causes greater photosynthetic rate of chrysanthemum plantlets, compared to monochromatic B or R light, while the R and FR combination led to greater stem length compared to the B and FR combination (Kim et al., 2004b). The same authors reported that B light positively affected the stomata number but decreased their size, whereas the B and R combination decreased the stomata number but increased their size. Orchid (*Oncidium* ‘Gower Ramsey’) plantlets showed greater dry weight under a combination of B and R LEDs compared to fluorescent lamps (Mengxi et al., 2011). Another study with orchids revealed greater leaf expansion and number, chlorophyll content and fresh and dry weight under the influence of R with B and FR compared to monochromatic R and B lights (Chung et al., 2010), while orchid seedlings cultivated under B light exhibited shorter leaf length and width compared to CWF lamps (Lee et al., 2011). Ageratum, marigold and salvia increased their dry weights under FL and BR LED compared to BFR and RFR LEDs, but shoot lengths were negatively affected by BR light compared to RFR and BFR lights. Moreover, the number of floral buds, the occurrence of flower opening and the carbohydrate accumulation were enhanced by BR LED compared to the rest of the treatments (Heo et al., 2006). In two chrysanthemum cultivars treated with night-break, shoot elongation was enhanced under treatments that emitted FR compared to short day treatment and R (peak at 630 nm and 660 nm) containing LED treatments with no FR (Liao et al., 2014). A study with geranium, petunia, snapdragon and impatiens revealed a linear decrease of plant height and total leaf area (only in geranium and snapdragon) as the R:FR increased. Whole-plant net assimilation was increased in geranium, snapdragon and impatiens with additional FR radiation, while FR also promoted flowering of the long-day snapdragon (Park and Runkle, 2017). B and RB lights increased maximum quantum yield ( $F_v/F_m$ ) and quantum efficiency ( $\Phi_{PSII}$ ) of *Cordyline australis*, *Ficus benjamina* and *Sinningia speciosa*, and also increased palisade parenchyma in *S. speciosa* (Zheng and Van Labeke, 2017). Moreover, B light positively affected the stomatal conductance, stomatal index and/or stomatal density of all species, and also leaf thickness and palisade parenchyma of *F. benjamina*.

An overall overview of the effects of different light spectra on plant photomorphogenesis, photosynthesis, and metabolism in closed systems is presented in Table 1.

## 2.2. Application of LED lighting in greenhouses

Supplemental lighting in greenhouses is a common method for nursery growers to increase daily light integral (DLI) perceived by plants in order to enhance seedling production and plant growth. For this purpose several types of artificial lighting sources (in particular HPS, FL and recently LEDs) have already been used (Tinus, 1995; Bourget, 2008). However, the use of LEDs during greenhouse cultivation is rather new and has great potential both from a commercial and

research point of view. LEDs could be used as photoperiodic, supplemental or photomorphogenic lighting for numerous plant species (Morrow, 2008; Mitchell et al., 2012; Kozai et al., 2016). Light intensity was the parameter mainly studied but light quality can also affect growth and development of plants. Until nowadays, not many studies have been published regarding the implementation of LEDs in greenhouses where plants are also influenced by natural light, while most of the studies involve top-lighting applications. When top-lighting is used alone it provides imbalanced light quantity (intensity) and quality distribution along tall plants (Frantz et al., 2000). Intracanalopy lighting, which is the implementation of light within the plant canopy, is also essential for contributing to photosynthesis (Davis and Burns, 2016). However, the reported results are controversial, firstly because different plant species and cultivars are used and second due to various experimental conditions.

When grown in a greenhouse, tomato fresh and dry weights were positively affected by natural light with supplemented W or R LEDs. W light also enhanced the fruit growth rate compared to monochromatic R or B, or no supplemental light following the trend of solar radiation level (Lu et al., 2012). Another study with two tomato cultivars revealed greater harvest period, number of nodes, number of harvested fruits and total fresh weight of fruits when LED (95% R, 5% B) was used for intracanalopy lighting, compared to natural light (Gómez et al., 2013). In a recent study (Lanoue et al., 2017), tomato exhibited greater transpiration rates but lower water use efficiency under natural light supplemented with RB or RW LEDs. Moreover, supplemental FR positively affected the stem length and fruit yield of tomato in the first month of the trial, as well as carotenoid content during the whole experiment (Hao et al., 2016). Trouwborst et al. (2010) working with cucumber found extremely curled leaves, as well as higher leaf mass per area and dry mass allocation, but lower leaf appearance rate and plant length under LED (20% B/80% R) intracanalopy lighting compared to natural light supplemented with HPS. Cucumber cultivated under LED (14% B, 16% G, 53% R, 17% FR) top-lighting and the same LED for intracanalopy lighting showed greater light use efficiency, leaf expansion, stem growth and fruit abortion rate, but decreased number of fruits, yield and flower initiation rate compared to HPS-HPS and HPS-LED top-lighting - intracanalopy lighting combinations (Särkkä et al., 2017). Guo et al. (2016) applied top and bottom vertical LEDs in mini-cucumber production, which resulted in more than 10% fruit yield increase. Moreover, the authors found that plasma light supplemented with vertical B light placed at the top of the canopy reduced leaf size, plant height and subsequently fruit yield in the first month, while vertical FR at the top of the canopy increased fruit yield compared to bottom canopy vertical LEDs. In addition to intracanalopy lighting, Song et al. (2016) tested the impact of different light qualities when applied underneath the plant canopy. The group found that lighting from both directions positively affected the photosynthetic efficiency, reduced the closure of stomata and improved their performance, especially under WRB and WB treatments (compared to RB and WRFR). The authors also reported different mechanisms of photosynthesis improvement, with intracanalopy lighting increasing stomatal conductance, CO<sub>2</sub> supply and thus electron transport activity, while underneath lighting increased CO<sub>2</sub> supply and assimilation efficiency, and excess energy dissipation leading to higher photosynthetic rate. Natural light supplemented with LED light enhanced a number of leaf characteristics in strawberry, including leaf photosynthetic rates, leaf dry mass, leaf area and specific leaf weight. Moreover, average fruit weight, fruit number, marketable yield, fruit soluble solids content were also favored under supplemental LED light (Hidaka et al., 2013). No significant effect in carotenoid concentration of lettuce was found under B and R LED or under HPS lamps (Martineau et al., 2012). However, Ouzounis et al. (2015a) reported greater pigment (chlorophylls and carotenoids) and phenolic (phenolic acids and flavonoids) concentration in green and red leaf lettuce under natural light supplemented with B LED compared to natural light with HPS. Further, they have also recorded increased

**Table 1**  
Spectral effects on horticultural and ornamental species grown in closed systems.

Plant type	Lighting conditions	Species	Effects on plants	Reference
<b>Horticultural species</b>	CWF lamps supplemented with FR (734 nm, $160 \pm 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), R (658 nm, $130 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ),	Lettuce ( <i>Lactuca sativa</i> cv. Red Cross)	FR: Increased fresh and dry weight, stem length, leaf length and width. Reduced anthocyanins, carotenoids, chlorophyll concentration. R: Increased chlorophyll concentration. B: Increased anthocyanins concentration. Decreased stem length and leaf length. UV-A: Increased anthocyanins concentration. Decreased stem length.	Li and Kubota (2009)
	G (526 nm, $130 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), B (476 nm, $130 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) or UV-A (373 nm, $18 \pm 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). In total $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ . R supplemented with FR (RFR, FR:730 nm, $300 + 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LED, B (BR, B:440 nm, $30 + 270 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LED	Red-leaf lettuce ( <i>Lactuca sativa</i> cv. Outeredgeous)	FR: Reduced anthocyanin content and antioxidant potential. B: Increased anthocyanin content and antioxidant potential.	Stutte et al. (2009)
	R (658 nm), Y (590 nm), G (520 nm), B (460 nm) and RB (R:B = 6:1) LEDs, $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Non-heading Chinese cabbage ( <i>Brassica campestris</i> cv. Te'aiqing)	R: Increased plant height. Decreased chlorophyll and carotenoid concentration. Decreased 5-Aminolevulinic acid, Mg-protoporphyrin IX, Protochlorophyllide and Protoporphyrin IX. Y: Decreased dry mass, soluble sugar and protein concentration. (G) Decreased chl <i>a/b</i> . B: Increased soluble sugar concentration and chl <i>a/b</i> . Decreased plant height. RB: Increased soluble protein concentration, chlorophyll and carotenoid concentration. Decreased plant height.	Fan et al. (2013)
	W ( $135 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LED and W ( $105 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LED supplemented with FR (850 nm), R (660 nm), Y (596 nm), G (522 nm), B (450 nm) LEDs emitting $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ each.	Green Oak Leaf Lettuce ( <i>Lactuca sativa</i> cv. crispa)	WFR: Increased S/R ratio and ascorbic acid. Decreased fresh weight of shoots, biomass and pigment contents. WR: Increased fresh weight of shoots, chlorophyll and carotenoid contents WY: Increased nitrate content. Decreased chlorophyll content and soluble sugar accumulation. WG: Decreased nitrate content. Increased soluble sugar accumulation. WB: Increased fresh weight of shoots, chlorophyll and carotenoid contents. Decreased nitrate content.	Chen et al. (2016)
	FL and LEDs with continuous spectra (12% B, 19% G, 61% R, 8% FR; 8% B, 2% G, 65% R, 25% FR; 14% B, 16% G, 53% R, 17% FR; and 1% UV, 20% B, 39% G, 35% R, 5% FR). $200 \pm 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Basil ( <i>Ocimum basilicum</i> cv. Lettuce Leaf and Red Rubin hybrid)	More B and 1% UV increased R:S ratio and total phenolic content.	Bantis et al. (2016)
	Experiment 1: CWF and BR (10% B: 455 nm, 90% R: 661 nm, $69 \pm 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LEDs or BR LEDs supplemented with end-of-day (EOD) FR (743 nm, $66 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LED. Experiment 2: CWF and BR (10% B, 90% R and 75% B, 25% R, $102 \pm 3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LEDs or BR LEDs supplemented with different FR doses (0, 1.1, 2.1, 4.2, 9.4, or $76.0 \text{ mmol m}^{-2} \text{d}^{-1}$ ). BR (B: 445 nm, R: 661 nm. B0:R100%, B10:R90%, B30:R70%, B50:R50%, B75:R25% and B100:R0%) LEDs. In total about $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Tomato rootstock ( <i>Solanum lycopersicum</i> × <i>Solanum habrochaites</i> , cv. Beaufort)	Low R:FR ratio increased shoot height. EOD-FR: Reduced intumescence injury. 75% B/25% R + EOD-FR: Reduced the percent number of leaves exhibiting intumescences and stem elongation.	Eguchi et al. (2016)
	BR (B: 445 nm, R: 661 nm. B0:R100%, B10:R90%, B30:R70%, B50:R50%, B75:R25% and B100:R0%) LEDs. In total about $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Cucumber ( <i>Cucumis sativus</i> cv. Cumlaude)	BR: More B light increased leaf mass per area, chlorophyll content per leaf area, leaf net photosynthetic rate, stomatal conductance and decreased plant height, hypocotyl and epicotyl length, leaf area, and fresh and dry mass. R: Decreased fresh and dry mass. B: Increased fresh mass	Hernández and Kubota (2016)
	RB (R: 662 nm, B: 456 nm. 88R/12B) LED compared to R LED. $150 \pm 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Nine tomato genotypes ( <i>Solanum lycopersicum</i> , <i>S. pimpinellifolium</i> , <i>S. habrochaites</i> )	RB: Increased plant biomass in nine genotypes. Attenuated the upward or downward leaf curling. Increased chlorophyll and flavonol index	Ouzounis et al. (2016)
	Warm, neutral, cool white, R (600–700 nm), G (500–600 nm), B (400–500 nm), RB and RGB LEDs, $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Lettuce ( <i>Lactuca sativa</i> cv. Waldmann's Green), cucumber ( <i>Cucumis sativa</i> cv. Sweet Slice), tomato ( <i>Solanum lycopersicum</i> cv. Early girl), radish	B: Increased net assimilation of cucumber, pepper, radish and lettuce. Increased chlorophyll concentration of tomato, cucumber, pepper and radish. Decreased dry mass, LAI, stem and petiole length of tomato, cucumber, pepper and radish. G: Increased LAI of cucumber, stem length of tomato, petiole length of radish, specific leaf	Snowden et al. (2016)

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Table 1 (continued)

Plant type	Lighting conditions	Species	Effects on plants	Reference
		( <i>Raphanus sativus</i> cv. Cherry Belle) and pepper ( <i>Capsicum annuum</i> cv. California Wonder)	area of pepper at 500 $\mu\text{mol}^{-2}\text{s}^{-1}$ . Decreased chlorophyll concentration of cucumber.	
	RB (87% R/ 13% B), RFRB (84% R/ 7% FR/ 9% B) or RGB (74% R/ 18% G/ 8% B) LEDs at three intensities: 105, 210 and 315 $\mu\text{mol m}^{-2}\text{s}^{-1}$ .	Brassica microgreens: Kohlrabi ( <i>Brassica oleracea</i> cv. gongylodes), mustard ( <i>Brassica juncea</i> cv. Garnet Giant), and mizuna ( <i>Brassica rapa</i> cv. japonica)	Mizuna and mustard: Increasing intensities led to greater carotenoid content. Kohlrabi and mustard: R87:B13 increased total integrated chlorophyll. Kohlrabi: Increasing intensities and R87:B13 or R84:FR7:B9 led to greater anthocyanin content. R84:FR7:B9 increased total phenolic concentration at low light intensity.	Craver et al. (2017)
	Experiment 1: R (625 nm), G (530 nm), B (460 nm) and W (B + R + G) LEDs. 10 $\mu\text{mol m}^{-2}\text{s}^{-1}$ . Experiment 2: B LED in different intensities. 10, 20, 30 and 40 $\mu\text{mol m}^{-2}\text{s}^{-1}$ . LEDs emitting R (657 nm), B (457 nm), P (417 nm), W and RB combinations (R:B = 1:1, and R:B = 3:1). 300 $\pm$ 3 $\mu\text{mol m}^{-2}\text{s}^{-1}$ .	Oyster mushrooms ( <i>Lentinus sajor-caju</i> )	B: Increased dry biomass. Higher B intensity increased DPPH radical-scavenging effect, Fe-chelating ability, reducing power and soluble sugar content.	Huang et al. (2017)
		Tomato ( <i>Solanum lycopersicum</i> cv. SV0313TG)	R: Increased fructose and glucose contents, and acid invertase and neutral invertase activities. RB 3:1: Increased total carbohydrate, starch and sucrose accumulation, sucrose synthase activity R and RB combinations: Increased plant height and stem diameter. P: Reduced seedling growth and Pn, and acid invertase and neutral invertase activities. R and P: Reduced root growth was lower under R and P. R, B and P: Reduced sucrose phosphate synthase activity.	Li et al. (2017)
	Natural light (789 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) compared to R (237 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ), W (21 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) or B (41 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) LEDs. FR (731 nm, 2.5 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) LED, R (660 nm, 170 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) LED, R (638 nm, 130, 105, 80, 55 or 30 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) LEDs and 0, 16, 25 and 33% B (445 nm, 0, 25, 50, or 100 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) LEDs. In total 300 $\pm$ 3 $\mu\text{mol m}^{-2}\text{s}^{-1}$ .	Artichoke (cvs. Green Globe, Cardoon, and Violetto) Microgreens of mustard ( <i>Brassica juncea</i> cv. Red Lion), beet ( <i>Beta vulgaris</i> cv. Bulls Blood) and parsley ( <i>Petroselinum crispum</i> cv. Plain Leaved or French)	R: Increased shoot dry weight and height compared to natural light. W and B: Decreased biomass compared to natural light. Mustard: 16% B increased zeaxanthin, lutein, neoxanthin, violaxanthin and tocopherol, and decreased chlorophyll index.  25% B increased lutein, neoxanthin and violaxanthin. 33% B increased $\alpha$ - and $\beta$ -carotene, chlorophyll b, chlorophyll a and chlorophyll index. Beet: 16% B increased $\alpha$ -carotene, $\beta$ -carotene, lutein, neoxanthin, violaxanthin and tocopherol. 25% B increased violaxanthin. 33% B increased $\beta$ -carotene, zeaxanthin, lutein, violaxanthin, chlorophyll a, carotenoid and tocopherol. Parsley: 16% B increased lutein, neoxanthin, violaxanthin and tocopherol, and decreased chlorophyll index. 25% B increased zeaxanthin, lutein and neoxanthin. 33% B increased $\beta$ -carotene, zeaxanthin and lutein.	Rabara et al. (2017)  Samuoliene et al. (2017)
	Two PPF intensities (L: low, and H: high) from two types of LEDs with continuous spectra: conventional LED (T0) or LED with “good spectral fit to the maximum photosynthetic response” (T1).	Lettuce (cv. Astorga and cv. Cervantes), tomato (cv. Simona), and pepper (cv. Dolce italiano)	T1: Increased energetic efficiency of all species. At both L and H intensities, plant growth was linked to the T1 spectra.	Urrestarazu et al. (2016)
Ornamental species	FL lamps and monochromatic R (650 nm), monochromatic B (440 nm), RB (1:1), RFR (FR: 720 nm, 1:1) and BFR (1:1). In total 50 $\pm$ 5 $\mu\text{mol m}^{-2}\text{s}^{-1}$ .	Chrysanthemum ( <i>Dendranthema grandiflorum</i> cv. Cheonsu)	B: Increased stomata number. Decreased stomata size. RB: Increased photosynthetic rate and stomata size. Decreased stomata number. RFR: Increased stem length.	Kim et al. (2004b)

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Table 1 (continued)

Plant type	Lighting conditions	Species	Effects on plants	Reference
	FL lamps and monochromatic R (660 nm), monochromatic B (455 nm), RB, RFR (FR: 730 nm), BFR and RBFR LEDs. In total $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ . B (10%–30%) and R LEDs.	Orchid ( <i>Oncidium</i> cv. Gower Ramsey)	RBFR: Increased leaf expansion and number, chlorophyll content and fresh and dry weight compared to monochromatic R and B.	Chung et al. (2010)
	WWF, CWF, and R (660 nm), B (450 nm), RB (9:1) and RGB (660:525:450 nm, 8:1:1) LEDs.	Orchid ( <i>Oncidium</i> cv. Gower Ramsey) Orchid ( <i>Paphiopedilum</i> cv. Hsingying Carlos)	BR: Higher dry weight and protein accumulation compared to FL. B: Decreased leaf length compared to CWF.	Mengxi et al. (2011) Lee et al. (2011)
	HPS or RB (80% R: 630 nm, 20% B: 465 nm) LED. $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Rose ( <i>Rosa × hybrida</i> cv. Toril)	RB: Increased leaf biomass. Decreased leaf area and shoot biomass. No effect on flowering	Terfa et al. (2013)
	Incandescent lamp, and five LEDs with emission peak at 630 nm, 660 nm, 690 nm, 735 nm, and a combination of 660 nm and 735 nm.	Chrysanthemum ( <i>Chrysanthemum morifolium</i> cv. Jimba and cv. Iwa no hakusen)	The FR-containing treatments increased shoot elongation compared to non FR-containing treatments, when applied at night-break.	Liao et al. (2014)
	CWF lamps, and BR (1:1), RFR (1:1) and BFR (1:1) LEDs. $90 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Ageratum ( <i>Ageratum houstonianum</i> cv. Blue Field), marigold ( <i>Tagetes erecta</i> cv. Orange Boy), and salvia ( <i>Salvia splendens</i> cv. Red Vista)	FL and BR: Increased dry weights compared to BFR and RFR. RFR and BFR: Increased shoot lengths compared to BR. BR: Increased the number of floral buds, the occurrence of flower opening and the carbohydrate accumulation.	Hao et al. (2016)
	B-R LED and B-R-FR LEDs combinations. DLI of $10 \text{ mol m}^{-2} \text{s}^{-1}$ .	Geranium ( <i>Pelargonium × hortorum</i> ), petunia ( <i>Petunia × hybrida</i> ), snapdragon ( <i>Antirrhinum majus</i> ), and impatiens ( <i>Impatiens walleriana</i> )	All species: Linear decrease of plant height with increasing R:FR. Geranium, snapdragon and impatiens: Increase of whole-plant net assimilation with increasing FR. Geranium and snapdragon: Linear decrease of leaf area with increasing R:FR. Snapdragon: Increased flowering with increasing FR.	Park and Runkle (2017)
	B (460 nm), R (660 nm), W (7% B, 16% G, 75% R, 2% FR) and RB (75% R - 25% B) LEDs. $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	<i>Cordyline australis</i> cv. Red Star, <i>Ficus benjamina</i> cv. Exotica, and <i>Sinningia speciosa</i> cv. Sonata Red	B and RB: Increased $F_v/F_m$ and $\Phi\text{PSII}$ in all species. Moreover, they increased palisade parenchyma in <i>S. speciosa</i> . R: Decreased biomass. B: Increased stomatal conductance, stomatal index and/or stomatal density of all species. Moreover, it increased leaf thickness and palisade parenchyma of <i>F. benjamina</i> .	Zheng and Van Lebeke (2017)

stomatal conductance and increased yield of non-photochemical quenching (NPQ) in green lettuce, while quantum yield of PSII decreased in red lettuce under supplemented B light. B light increased stomatal density but had negative effect on chilling tolerance and shelf life performance of sweet basil compared to natural light (Jensen et al., 2018). In addition, G had positive effects on chilling tolerance, but decreased stomatal density.

Owen and Lopez (2017) reported that the foliage colour of geranium and purple fountain grass was enhanced when plants were grown under a low greenhouse daily light integral ( $\leq 9 \text{ mol m}^{-2} \text{ d}^{-1}$ ), after 14 days of end-of-production supplemental lighting and under  $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$  of 50:50 or 0:100 R:B LED light. Higher B percentage led to greater stomatal conductance, and phenolic acid and flavonoid production in roses, chrysanthemums and campanulas. In addition, monochromatic R LED caused curled leaves and other morphological abnormalities in the three species, while 40% B/60% R led to lower plant height in roses and chrysanthemums, and smaller leaves in campanulas compared to 20% B/80% R, monochromatic R and W LEDs (Ouzounis et al., 2014b). Two *Phalaenopsis* hybrid cultivars (“Vivien” and “Purple Star”) had greater lutein concentration under increasing B light which led to increased G/Y light absorption (Ouzounis et al., 2014a). Moreover, the authors reported greater NPQ, but decreased electron transport rate in “Vivien” hybrid cultivar under 40% B/60% R

light, compared to natural light or natural light supplemented with monochromatic R. In snapdragon and geranium, BGR + FR light led to faster flowering by 7 days on average, and also increased leaf area and plant height of snapdragon (Poel and Runkle, 2017). Meng and Runkle (2014) tested the impact of INC, HPS, and CFL lamps with a LED lamp emitting R + FR + W light on seven ornamental plants, in a commercial greenhouse. The authors practiced night interruption technique and they found that flowering on most species was similar in LED, INC and HPS lamps, revealing that LEDs were at least as effective as the rest of the lamps in controlling flowering.

An overall overview of the effects of different light spectra on plant photomorphogenesis, photosynthesis, and secondary metabolism in greenhouses is presented in Table 2.

### 2.3. Application of LED lighting in vertical farming systems

Vertical farming is a more recent CEA system where electric lamps are solely used for the provision of light to plants. Vertical farming is practiced indoors under controlled conditions (light, heating, ventilation, air-conditioning and CO<sub>2</sub> enrichment) (Kozai et al., 2015; Gupta, 2017). These systems have several benefits for the production of fresh vegetables, such as 1) higher (more than 100 times) annual productivity compared to field agriculture and regardless of season and outdoors

**Table 2**  
Spectral effects on horticultural and ornamental species grown in greenhouses, nurseries and open field.

Plant type	Lighting conditions	Species	Effects on plants	Reference
<b>Horticultural species</b>	Natural light supplemented with HPS ( $221 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), or with HPS ( $139 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and LED (20% B: 465 nm, 80% R: 667 nm) intracanopy lighting ( $82 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).	Cucumber ( <i>Cucumis sativus</i> cv. Samona)	LED: Increased leaf mass per area and dry mass allocation to leaves. Decreased leaf appearance rate and plant length. Leaves were extremely curled.	Trouwborst et al. (2010)
	Natural light supplemented with W, R or B LEDs.	Tomato ( <i>Solanum lycopersicum</i> cv. Momotaro Natsumi)	W: Increased fresh and dry yield. Increased fruit fresh weight per unit photons emitted. Increased fruit growth rate when solar radiation was high, and decreased it when solar radiation was low. R: Increased fresh and dry yield	Lu et al. (2012)
	Natural light supplemented with HPS, LED or regular greenhouse HPS level.	Lettuce ( <i>Lactuca sativa</i> cv. capitata)	No significant difference in concentrations of b-carotene, chlorophyll a, chlorophyll b, neoxanthin, lutein, and antheraxanthin	Martineau et al. (2012)
	Natural light or natural light supplemented with HPS or RB LED (95% R: 627 nm, 5% B: 450 nm) for intracanopy lighting. DLI of $9 \text{ mol m}^{-2} \text{ day}^{-1}$ .	Tomato rootstock ( <i>Solanum lycopersicum</i> × <i>S. habrochaites</i> cv. Maxifort) and scions (cv. Komeett and Success)	LED: Increased the harvest period, number of nodes, number of fruits harvested and fruit fresh weight compared to natural light.	Gómez et al. (2013)
	Natural light supplemented with fluorescent (emission lines at 405, 435 and 545 nm, peaks at 450 and 610 nm) lamp or W (peaks at 450 and 550 nm) LED.	Strawberry ( <i>Fragaria ananassa</i> cv. Fukuoka S6)	LED: Increased leaf photosynthetic rates, leaf dry mass, leaf area, specific leaf weight, average fruit weight, fruit number, marketable yield, fruit soluble solids content	Hidaka et al. (2013)
	Natural light supplemented with HPS emitting $90 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ or B LED emitting 45 or $80 \mu\text{mol m}^{-2} \text{s}^{-1}$ at different time of the day.	Green and red lettuce ( <i>Lactuca sativa</i> cv. Batavia and cv. Lollo Rossa)	Green lettuce – B light: Plants were more compact. Increased stomatal conductance, pigments (chlorophylls and carotenoids), phenolic acids and flavonoids. Red lettuce – B light: Plants were more compact. Increased yield of non-photochemical quenching, pigments, phenolic acids and flavonoids. Decreased quantum yield of PSII.	Ouzounis et al. (2015a)
	Natural light supplemented with top-lighting HPS or plasma lights ( $165 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) and vertical combinations (top and bottom) of FR (725–750 nm, $8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), R (650–670 nm, $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and B (455–485 nm, $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).	Mini-cucumber ( <i>Cucumis sativus</i> )	Vertical LEDs resulted in more than 10% fruit yield increase. Plasma light: Top B reduced leaf size, plant height and fruit yield in the first month. Top FR increased fruit yield compared to bottom canopy.	Guo et al. (2016)
	Natural light supplemented with HPS + FR (725–750 nm, 0, 8, 16 or $24 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LEDs. $165 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR.	Tomato ( <i>Solanum lycopersicum</i> cv. Foronti grafted on rootstock cv. Stallone)	FR: Increased the stem length and fruit yield in the first month of the trial. The increase diminished in the second and third month of fruit harvest. Moreover, FR increased carotenoid content.	Hao et al. (2016)
	Natural light supplemented with RB (3:1), WRB (3:2:1), WRFR (3:2:1) or WB (2:1) LEDs placed either intracanopy or underneath the canopy. $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Tomato ( <i>Lycopersicon esculentum</i> , NS3389)	Underneath canopy: WRB and WB increased health index, development rate and promoted better performance. Moreover, it increased photosynthesis by enhancing the $\text{CO}_2$ supply and $\text{CO}_2$ assimilation efficiency and excessive energy dissipation. Intracanopy: Increased photosynthesis by increasing the stomatal conductance to enhance the $\text{CO}_2$ supply for leaf, thereby promoting photosynthetic electron transport activity. In all treatments, WRB and WB could better stimulate stomatal opening and promote photosynthetic electron transport activity, thus better improving photosynthetic rate.	Song et al. (2016)
	Natural light supplemented with HPS and W or RB (80%R: 660 nm/20%B: 460 nm) LEDs ( $70\text{--}120 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). DLI of $7 \text{ mol m}^{-2} \text{s}^{-1}$ .	Sunflower ( <i>Helianthus annuus</i> cv. Teddy bear)	LED: Reduced growth performance. HPS: Increased top leaf temperature, fungal species abundance.	Alsanius et al. (2017)
	Natural light supplemented with $100 \pm 25 \mu\text{mol m}^{-2} \text{s}^{-1}$ of HPS, RB or RW LEDs.	Tomato ( <i>Solanum lycopersicum</i> cv. Bonny Best)	RB: Increased transpiration rates. Decreased water use efficiency RW: Increased transpiration rates. Decreased water use efficiency	Lanoue et al. (2017)
	Three top-light and intracanopy light combinations with HPS and LED with continuous spectra (14% B, 16% G, 53% R, 17% FR). HPS-HPS ( $290 + 90 \mu\text{mol m}^{-2} \text{s}^{-1}$ ),	Cucumber ( <i>Cucumis sativus</i> cv. Toploader)	LED-LED: Increased light use efficiency, leaf expansion, stem growth, fruit abortion rate. Decreased number of fruits, yield and yield potential, flower initiation rate.	Särkkä et al. (2017)

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Table 2 (continued)

Plant type	Lighting conditions	Species	Effects on plants	Reference
	LED-LED (160 + 125 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), HPS-LED (290 + 125 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Natural light supplemented with RB (80% R: 657 nm – 20% B: 447 nm, and 40% R – 60% B), RB + UV-A (80% R – 20% B + UV-A: 395 nm) or RG (80% R – 20% G: 527 nm) LEDs. 120 increasing up to 190 $\mu\text{mol m}^{-2} \text{s}^{-1}$ due to plants getting taller.	Sweet Basil ( <i>Ocimum basilicum</i> )	HPS-LED: Increased yield, leaf and flower appearance rate. Decreased fruit abortion rate. B: Increased stomatal density but had negative effect on chilling tolerance and shelf life performance. G: positive effects on chilling tolerance, but decreased stomatal density. Abscisic acid (ABA) and ABA glucosylester had positive correlation to stomatal density. ABA- GE/ABA ratio had negative correlation to stomatal density.	Jensen et al. (2018)
<b>Ornamental species</b>	Short days (SD: 9 h of light) and 4 h of night interruption (NI) provided by R + W + FR LED, CFL, HPS or INC lamps.	Ageratum ( <i>Ageratum houstonianum</i> cv. Hawai Blue), calibrachoa ( <i>Calibrachoa</i> × <i>hyb- rid</i> cv. Callie Deep Yellow), dahlia ( <i>Dahlia</i> × <i>hybrid</i> cv. Dahlinoca Texas), dianthus ( <i>Dianthus chinensis</i> cv. Telstar Crimson), petunia ( <i>Petunia</i> × <i>hybrid</i> cvs. Easy Wave Burgundy Star and WPC), snapdragon ( <i>Antirrhinum majus</i> cv. Liberty Classic Yellow), and verbena ( <i>Verbena</i> × <i>hybrid</i> cv. Obsession)	Time to flower and flowering percentage were similar under all light treatments, with few exceptions. Ageratum, dianthus, petunia, snapdragon, and verbena flowered earlier under NI than under SD. For most species, plant height and visible flower bud or inflorescence number at flowering were similar under LED and INC.	Meng and Runkle (2014)
	Natural light or B/W (32% B), R or 40% B/ 60% R LEDs. LEDs emitted 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ . DLI was 11.4 ± 0.9 $\text{mol m}^{-2} \text{day}^{-1}$ .	Two <i>Phalaenopsis</i> hybrids (cv. Vivien and cv. Purple Star)	40% B/60% R: Increased non-photochemical quenching and decreased electron transport rate in cv. Vivien. Increasing B led to increased lutein concentration and greater absorption of the green/yellow part of the spectra.	Ouzounis et al. (2014a)
	W, R (650–670 nm), 40% B/60% R (B: 450–485 nm) and 20% B/80% R LEDs.  LEDs emitted 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ . DLI was 11.52 $\text{mol m}^{-2} \text{day}^{-1}$ .	Rose ( <i>Rosa hybrida</i> cv. Scarlet), chrysanthemum ( <i>Chrysanthemum morifolium</i> cv. Coral Charm) and campanula ( <i>Campanula portenschlagiana</i> cv. BluOne)	B: Higher percentage increased stomatal conductance, and phenolic acid and flavonoid production. R: Curled leaves and other morphological abnormalities. (40% B/60% R) Decreased plant height in roses and chrysanthemums, and leaves in campanulas compared to 20% B/80% R.	Ouzounis et al. (2014b)
	Two HPS lamps (90 or 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and four LEDs (90 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ): 10% B (453 nm)/90% R (660 nm), 45% B/ 55% R, 10% B/5% G (500–600 nm)/85% R and 12% B/10% G/68% R + FR (737 nm, 12 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).	Geranium ( <i>Pelargonium</i> × <i>hort- orum</i> cv. Pinto Premium Salmon), pepper cv. Long Red Slim Cayenne, petunia ( <i>Petunia</i> × <i>hybrida</i> cv. Single Dreams White), snapdragon cv. Montego Yellow, and tomato cv. Supersweet.	Snapdragon: B12G20R68 + FR increased leaf area and plant height, and led to faster flowering by 7 days on average. Geranium: B45R55 and B12G20R68 + FR flowered 7 to 9 days earlier. HPS 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ : Reduced dry weight and took longer to flower.	Poel and Runkle (2017)
	Natural and day-extension light (W LED) and natural light supplemented with HPS, monochromatic B (460 nm) LED, monochromatic R (660 nm) LED, or a combination of R and B (R:B = 87:13 or 50:50) LEDs.	Geranium ( <i>Pelargonium</i> × <i>hort- orum</i> cv. Black Velvet) and purple fountain grass ( <i>Pennisetum</i> × <i>adve- na</i> )	50:50 R:B and B: Increased the foliage colour 14 days after end-of-production, when greenhouse DLI was low (9 $\text{mol m}^{-2} \text{d}^{-1}$ ).	Owen and Lopez (2017)

**Table 3**  
Spectral effects on horticultural species grown in vertical farming systems.

Plant type	Lighting conditions	Species	Effects on plants	Reference
Horticultural species	RGB (11–4.3 chips) LED supplemented with UV-A (352 nm, 3.7 W), UV-B (306 nm, 4.2 W) or UV-C (253.7 nm 7.5 W) LEDs.	Red-leaf lettuce ( <i>Lactuca sativa</i> cv. Hongyeom)	UV-A: Increased fresh and dry weights of shoots up to day-6, total phenolic concentration, antioxidant capacity and PAL activity at day-3, total anthocyanin concentration up to day-4, and PAL gene expression after day-4. UV-B: Decreased $F_v/F_m$ , shoot fresh and dry weights. Increased total phenolic concentration, antioxidant capacity at day-2, and PAL activity at day-3. UV-C: Decreased $F_v/F_m$ , shoot fresh and dry weights.	Lee et al. (2014)
	Eight combinations of R (625 nm), B (465 nm, 0, 10, 20 and 30%) and G (525 nm, 0 and 10%) LEDs. $150 \pm 15 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Lettuce ( <i>Lactuca sativa</i> cv. green-skirt)	80% R/20% B: Increased photosynthetic rate. Photosynthetic rate decreased with additional G or absence of B. Higher B decreased leaf size and plant growth. Shade avoidance response in the absence of B.	Kang et al. (2016)
	R (660 nm, $200 \pm 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and B (450 nm, $100 \pm 3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) LEDs in four alternating light patterns (16 h photoperiod with alteration every 1, 2, 4 or 8 h) or no alterations (8 or 16 h photoperiod).	Green oak leaf lettuce ( <i>Lactuca sativa</i> cv. crispa)	No alteration, 8 h: Sparse plants. No alteration, 16 h: Compact plants. Increased biomass and crude fiber content, but decreased soluble sugar content R/B 8 h: Increased plant height/width and leaf length/width R/B 4 h and 2 h: Increased ascorbic acid content and decreased nitrate content. R/B 8 h and 1 h: Increased yield and nitrate content. Decreased ascorbic acid content	Chen et al. (2017)
	Continuous spectrum LED light and continuous spectrum LED light lacking G (480–560 nm). $95\text{--}105 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Lettuce ( <i>Lactuca sativa</i> cv. youmaicai)	W lacking G: Reduced shoot and root dry weight, chlorophyll a, b, and carotenoid contents, net photosynthetic rate, dark respiration.	Liu et al. (2017)
	R (655 nm), B (456 nm), and different RB ratios combined with three LEDs (R9B1, R8B2, and R6B4). Treatments were applied for 4 weeks as follows: control (continuous irradiation of each light), monochromatic (changing from R to B at 1, 2, or 3 weeks), and combined (changing from R9B1 to R8B2 or R6B4 at 2 or 3 weeks). $151 \pm 4 \mu\text{mol m}^{-2} \text{s}^{-1}$ .	Red-leaf lettuce ( <i>Lactuca sativa</i> cv. Sunmang)	Higher R increased growth and photosynthetic rates but decreased chlorophyll and antioxidant phenolic content. Changing light from R to B rapidly reduced transcript levels of phenylalanine ammonia-lyase (PAL) and chalcone synthase (CHS) genes.	Son et al. (2017)

environmental conditions, 2) reduced distance between production areas and consumption sites, which results in less fuel consumption, less food cooling, losses and transportation time, and therefore potentially lower prices for the consumers, and 3) establishment near (and even inside) the cities in almost any empty space offering job opportunities to a wide range of people, and making it easier to process waste (water, products, heat,  $\text{CO}_2$ ) produced and reuse them (Kozai et al., 2015).

Not all plants can fit in these multilayer systems due to high stature. Plants grown with vertical farming systems should have certain characteristics including compactness (about 30 cm or less), fast growth (10–30 days of cultivation in the system) and production of high-value crops that can be manipulated with environmental control (Kozai et al., 2015). Therefore, lettuce is the main plant species cultivated with vertical farming systems. In a recent publication with lettuce (Liu et al., 2017), W lacking G light (compared to W light) led to reduced shoot and root dry weight, less chlorophyll a, b, and carotenoid contents, as well as reduced net photosynthetic rate and dark respiration. Kang et al. (2016) reported lower photosynthetic rate of lettuce with addition of 10% G or the absence of B light, compared to 80% R/20% B treatment, while greater B portion caused a reduction of leaf size and plant growth. Higher R portion positively affected growth and photosynthetic rates but decreased chlorophyll and antioxidant phenolic content of red-leaf lettuce, while changing light from R to B rapidly reduced transcript levels of phenylalanine ammonia-lyase (PAL) and chalcone synthase (CHS) genes (Son et al., 2017). In a lettuce cultivation experiment with

alternating R and B light, Chen et al. (2017) found that alterations every 8 h resulted in greater plant height/width and leaf length/width, and higher nitrate but lower ascorbic acid content along with alterations every 1 h. Moreover, alterations every 2 or 4 h led to increased ascorbic acid content and decreased nitrate content, while no alterations resulted in compact plants with increased biomass and crude fiber content, but decreased soluble sugar content (16 h photoperiod) or sparse plants (8 h photoperiod). UV light seems to enhance the accumulation of phytochemicals in plants. In red leaf lettuce, small amount of supplemental UV-A light led to increased anthocyanin and total phenolic production, antioxidant capacity, PAL gene expression and activity, and fresh and dry weights of shoots (Lee et al., 2014). Supplemental UV-B caused greater total phenolic concentration, antioxidant capacity and PAL activity. UV-B and UV-C quickly stressed the plants (decreased  $F_v/F_m$ ) and negatively affected shoot fresh and dry weights (Lee et al., 2014).

An overall overview of the effects of different light spectra on plant photomorphogenesis, photosynthesis, and secondary metabolism in vertical farming practices is presented in Table 3.

#### 2.4. Application of LED lighting for maintaining postharvest quality of fruits and vegetables

The storage potential for the majority of horticultural products is limited from some days to a few weeks. Main causes for postharvest loss

are weight loss, senescence, firmness loss, over ripening, softening, decay and specific physiological disorders. The use of LED lighting during storage could very well be an alternative solution for reducing postharvest losses and maintaining product quality due to their advantages of long life, convenience (small and compact) as well as their low heat emission that allow their use in cold storage rooms and refrigerator trucks with low requirements of refrigeration load. Moreover, LEDs used in cold storage are effective as bactericides (Hasan et al., 2017). These advantages allow the application of LED light in all steps of the supply chain from precooling and packaging, to refrigerated transport and market display. At the retail market the use of LED could have the disadvantage of misleading the consumer by altering their appearance, e.g. green tissue under R light (Ma et al., 2014b).

Tomato is a vegetable that is usually harvested at an immature stage and the ripening process takes place during storage and distribution of the product. Storage of mature green tomato fruit for 7 days in darkness or under R and B LED light, 85.72 and 102.70  $\mu$  Einstein  $m^{-2} s^{-1}$  respectively, had an effect on the fruit ripening (Chomchalow et al., 2002). Tomato fruits exposed to R and a combination of R and UV radiation required five days less than non-treated fruits to reach the same maturity level, while R + UV also raised lycopene,  $\beta$ -carotene, total flavonoids and phenolics concentrations (Panjai et al., 2017). An effect on fruit ripening was observed when fruit from the same LED light treatments were stored in darkness (Dhakal and Baek, 2014). In particular, storage in darkness had the best result for lycopene accumulation and development of red color while application of B light for a 7 days period led to a delay in lycopene accumulation, redness and consequently ripening, indicating that this inhibition of the ripening process is a potential way to extend long-term postharvest storage (Dhakal and Baek, 2014). In a similar fashion, green mature tomato fruit stored in 263  $\mu$ mol  $m^{-2} s^{-1}$  of white light for 13 days contained 32% more ascorbate compared to fruit kept to lower irradiances and darkness (Ntagkas et al., 2016). The positive effect of postharvest lighting on vitamin C is evident also in fresh cut lettuce. Witkowska (2013) increased by means of postharvest lighting the levels of vitamin C as well soluble carbohydrates (via enhancement of gluconeogenesis) in fresh cut lettuce. That has been hypothesized to be the reason for the observed improved visual appearance and eventually prolonged shelf life. The upregulation of vitamin C caused by light is evident for both leaves and fruit as it is mediated through both respiration and photosynthesis (Ntagkas et al., 2017). Senescence and especially yellowing is a major postharvest problem for green tissues. Application of R LED light delays yellowing and decreases ethylene production of broccoli inflorescences while B LED light had no effect (Ma et al., 2014b). The use of LED G light (12–13  $\mu$ mol  $s^{-1} m^{-2}$ ) effectively extend shelf-life of broccoli florets about three times than florets stored in dark (Jin et al., 2014). Broccoli florets storage under G LED light resulted higher phenolics and antioxidant activity but without affecting sulforaphane and total glucosinolates content, main phytochemicals compounds of *Brassica* vegetables (Jin et al., 2014). Moreover, R LED light had positive effect on ascorbic acid content during the first two days storage with regulation at the transcriptional level (Ma et al., 2014b). Also, the use of artificial lighting of white and B light LED of 20  $\mu$ mol  $m^{-2} s^{-1}$  during storage of Brussels sprouts controlled yellowing and maintained the green color both of the outer and inner leaves (Hasperu  et al., 2016). The outer leaves of the sprouts exposed to the above LED lighting had higher flavonoids content and higher antioxidant activity than those sprouts stored in the dark. Spectra beyond visible radiation were also found to affect the content of pigments in plants. Tomato fruit treated during postharvest storage with UV-C light was found to have higher levels of lycopene (Liu et al., 2009).

Postharvest application of R LED light at an intensity of 50  $\mu$ mol  $m^{-2} s^{-1}$  for six days had beneficial effect on Satsuma mandarin nutritional value by enhancing the carotenoids content (Ma et al., 2012). In the same study the use of B LED light did not alter the carotenoid content. On a later study the R LED light was combined with

the use of ethylene on citrus, since the exogenous application of ethylene is common practice to accelerate chlorophyll degradation of citrus fruit (Ma et al., 2014a). The results show that the combination of the two treatments significantly achieves higher concentration of  $\beta$ -cryptoxanthin and lutein in the flavedo of citrus fruit. The above positive result correlated with the simultaneous increase of  $\alpha$ -carotene and  $\beta$ -carotene biosynthesis pathway genes (Ma et al., 2014a). The application of B LED light on chlorophyll and carotenoid metabolism of ethphon-degreened mandarin fruit were evaluated by Yuan et al. (2017). Positive results with faster chlorophyll degradation and the accumulation of carotenoids in ethphon-degreened fruit was observed with B LED lighting.

Application of LED lighting of different wavelengths (385 nm, 470 nm, 525 nm, and 630 nm) on immature strawberries resulted better soluble solids content as well as higher amounts of vitamin C, anthocyanin and total phenolics after 4 days storage (Kim et al., 2011). Similarly, LED lighting has been proposed to be a technique to improve marketability and nutritional value of Chinese bayberry fruit. The application of B LED light resulted in the significant increase of anthocyanin accumulation and this result was correlated with the increased of related genes of anthocyanin biosynthetic pathway (Shi et al., 2014). Finally, compounds affecting sensory fruit and flower qualities can be manipulated by light, as reported by Colquhoun et al. (2013) who found increased 2-phenylethanol (an essential floral volatile) under R and FR LEDs, in petunia.

Postharvest light has an effect on the shelf life and quality of horticultural products by potentially (1) increasing soluble carbohydrates which is the substrate for respiration during postharvest storage, (2) increasing or maintaining the levels of phytochemicals (vitamin C, anthocyanins, total phenolics, soluble sugars, secondary antioxidants) as well as (3) improving or maintaining the visual appearance by the accumulation of pigments (lycopene, carotenoids, anthocyanins). As LEDs are being developed vigorously for application in horticulture, they will potentially play a significant role also in postharvest applications (D'Souza et al., 2015).

### 3. Conclusions and future perspectives

Large-scale seedling and plant production with CEA (growth chambers, greenhouses, vertical farming) could be favored with the use of LEDs that significantly reduce electricity consumption while producing high-quality plant material. This is quite important when the ongoing climate change scenarios and the related environmental constraints, could potentially lead in the reduction of the cultivated lands availability. In our review we provided a comprehensive treatise on the recent achievements made in the use of LEDs for the horticulture field. It is now obvious that there is tremendous information when it comes to light recipes and combinations both for researchers as well as growers. Most light combinations, (monochromatic, bichromatic, polychromatic, ranging from UV to FR) have been extensively studied, with different proportions and in numerous species. We reaffirm that: a) R/B and R/FR ratios strongly regulate and are determinant for growing plants of high quality, b) B light has been proven essential in enhancing the production and accumulation of phytochemical compounds such as phenolics, carotenoids and volatiles, and subsequently increasing plant antioxidant activity, and c) ultraviolet radiation is not currently used in horticulture but its effects on plant development and secondary metabolism could be implemented (especially UV-A in small amounts) for the production of high quality compact plants. Even though most studies in the past years were focused on R and B light combinations due to the chlorophyll absorption peaks (and the pervasive theory that energy outside those bands would be simply wasted on the plants), this stereotype is now dispelled and researchers are now more and more conducting experiments with W, G, FR light, as they have also been shown to affect physiological and metabolic processes. Regarding the applicability, besides the common top-light applications we now see

more research being focused on intracanopy lighting (even from underneath lighting) as well as on multilayer cultivation in vertical farms and plant factories. Technological advancements will allow for these combinations to take place to a higher extend.

More research would add valuable knowledge in order to validate the appropriate and ideal wavelength combinations for important plant species and phytochemicals, as well as to deeply understand the impact of less studied wavelengths (UV, Y, G) on plants. More focus though is and should be given to the nutrition and health of the plants as plant metabolism is strongly affected by LED lighting both in a pre-harvest and postharvest manner. Additionally, we should not neglect ornamentals that can be benefited from LED lighting with respect to faster flowering and better coloring. Furthermore, a greater understanding of spectral combinations and other cultivation conditions (e.g. photoperiod, temperature, nutrition) would be of utmost importance for horticultural products of higher quality. As a note, due to high lamp and electricity costs, research and applications have been limited to relatively low intensities, while plants can take up higher intensities.

Different anatomical, morphological, physiological, photosynthetic, developmental, and metabolic parameters have been shown to be regulated by LED lighting in horticultural species. Therefore breeding companies have a lot of information to focus on the traits and attributes that are the most important for each plant species and produce LED light use efficient genotypes. It is critical for researchers to absorb this information to the highest degree but also to understand that different environmental conditions and practices might affect the results. Therefore, this will define the appropriateness when breeding companies introduce their light use efficient genotypes in commercial practice.

Another inference drawn from the literature review is that a great number of commercially and nutritionally important plant species have not been tested thoroughly, or even studied at all yet at agronomic and/or postharvest level. Even though lettuce has been extensively under research, other leafy vegetables such as spinach, rucola and Brussels sprouts appear in a few or no publications. Similarly, aromatic herbs such as rosemary, sage, mint, parsley and dill have not been meticulously studied yet. Many important commercially produced seedlings and even fruits such as melon, watermelon, zucchini and eggplant could be favored under particular wavelengths and cultivation practices. Although medicinal cannabis is also understudied in greenhouses, however, it is a promising alternative as cultivation conditions can strongly benefit from LED lighting with respect to cannabidiol and tetrahydrocannabinol (substances important for treating human diseases). Another interesting suggestion for future research could be the investigation of the phytochemical content of several edible horticultural species, which are known for their high antioxidant value and are used for pharmaceutical purposes.

In the near future, all these approaches with LED lighting will lead to a greater understanding regarding the spectral quality effects on plant growth and morphology, further pinpointing the importance of LED lighting in CEA. Therefore it should be noted that a big dataset is currently created and will enhance in the near future. Consequently, it is now a necessity to introduce an information and communication technology system, since nowadays the cost of data/information processing storage and transfer is very low (Kozai et al., 2016). The combination of information and communication technology, the big data mining and deep learning, the bioinformatics and the internet of things will be integrated in a big plant production system that will shape CEA (Kozai et al., 2016).

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