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Light-Quality Manipulation to Control Plant Growth and Photomorphogenesis in Greenhouse Horticulture: The State of the Art and the Opportunities of Modern LED Systems

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Abstract

Light quantity (intensity and photoperiod) and quality (spectral composition) affect plant growth and physiology and interact with other environmental parameters and cultivation factors in determining the plant behaviour. More than providing the energy for photosynthesis, light also dictates specific signals which regulate plant development, shaping and metabolism, in the complex phenomenon of photomorphogenesis, driven by light colours. These are perceived even at very low intensity by five classes of specific photoreceptors, which have been characterized in their biochemical features and physiological roles. Knowledge about plant photomorphogenesis increased dramatically during the last years, also thanks the diffusion of light-emitting diodes (LEDs), which offer several advantages compared to the conventional light sources, such as the possibility to tailor the light spectrum and to regulate the light intensity, depending on the specific requirements of the different crops and development stages. This knowledge could be profitably applied in greenhouse horticulture to improve production schedules and crop yield and quality. This article presents a brief overview on the effects of light spectrum of artificial lighting on plant growth and photomorphogenesis in vegetable and ornamental crops, and on the state of the art of the research on LEDs in greenhouse horticulture. Particularly, we analysed these effects by approaching, when possible, each single-light waveband, as most of the review works available in the literature considers the influence of combined spectra.

Keywords Light spectrum · Photoreceptors · Lamps · Vegetables · Ornamentals · Flowers

Abbreviations

B	Blue
BF	Blue fluorescent
Chl	Chlorophyll
CL	Cool light
CRYs	Criptochromes
CWF	Cool-white fluorescent
DLI	Daily light integral
DW	Dry weight
EOD	End of day
ETR	Electron transport rate
FL	Fluorescent lamp
FR	Far red
FW	Fresh weight
G	Green
GA	Gibberellic acid
GF	Green florescent
gs	Stomatal conductance
HID	High-intensity discharge
HIR	High-irradiance response
HPS	High-pressure sodium
INC	Incandescent
LA	Leaf area
LAI	Leaf area index
LD	Long day
LEDs	Light-emitting diodes
LFR	Low-fluence response
LOV	Light oxygen or voltage
MH	Metal halide
NI	Night interruption
NB	Night break
NL	Neutral light

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NP	Net photosynthesis
NPQ	Non-photochemical quenching
PAR	Photosynthetically active radiation
PHOTs	Phototropins
PHYs	Phytochromes
PPFD	Photosynthetic photon flux density
PPE	Phytochrome photoequilibrium
Pfr	Phytochrome far red
Pr	Phytochrome red
PSI	Photosystem I
PSII	Photosystem II
Ptot	Total amount of phytochrome
R	Red
SD	Short day
S/R	Shoot/root ratio
SLA	Specific leaf area
UVR8	UV resistance Locus 8
VLFR	Very-low-fluence response
WL	White light
WF	White fluorescent
ZTL/FKF1/LKP2	Zeitlupe/Flavinbinding Kelch Repeat, F-BOX1/LOV Kelch Protein2

Introduction

Light is one of the main environmental parameters regulating plant physiology throughout the entire plant life cycle, as plants use light as both energy source for carbon fixation in photosynthesis (assimilative function), and signal to activate and regulate many other key processes related to plant growth and development (control function) (Devlin et al. 2007).

As their life depends on the assimilative function of light, plants evolved fine light-sensing mechanisms to maintain and maximize photosynthetic performance and fitness during their life span. Through these mechanisms, plants acclimate to a given light environment by means of adjustments of photosynthetic biochemistry (e.g. Rubisco content and change in PSII and PSI ratio), leaf anatomy (e.g. chloroplast size and distribution) and morphology (e.g. leaf surface and thickness), to maximize light harvesting and CO_2 capture (Terashima et al. 2006; Athanasiou et al. 2010; Kono and Terashima 2014; Vialet-Chabrand et al. 2017). On the other hand, the control function of light acts as an environmental signalling, perceived by a very sensitive detection system, regulating the plant photomorphogenetic responses, including the transition from a development stage to the next (Devlin et al. 2007). For instance, light induces the breaking of seed dormancy and drives the seedling development from a dark- to a light-grown status, inducing the cotyledon expansion and the development of chloroplasts (de-etiolation), enabling the photosynthesis and the achievement of the autotrophy (Folta and Childers 2008). During plant growth, light affects stem elongation, branch emission and leaf expansion, determining the plant architecture, and finally it drives the transition to flowering, fruit setting and seeds production (Paik and Huq 2019).

Modern agriculture has evolved towards the application of advanced technologies for plant cultivation in controlled environment, in order to guarantee high crop production even in the presence of unfavourable outdoor conditions, or in high density cultivation systems. In particular, in greenhouse horticulture and in growth chambers (e.g. for nursery or vertical farming), light is a key parameter, and a fine control of light quantity (intensity and duration) and quality (wavelength composition) is a challenge to increase the yield and value of products. In many countries (e.g. in Northern Europe), artificial lighting is applied to integrate the natural light when the solar radiation is insufficient, in terms of both intensity or duration, or variable during the day (e.g. winter season). For this purpose, it is mainly used in the view of the assimilative function to increase the photosynthetic performances, hence the annual productivity and the constancy of products yield and quality. On the other hand, in other agricultural areas (e.g. Mediterranean environment), lighting conditions remain largely uncontrolled and the seasonal trend of solar radiation affects the production scheduling, limiting the crops yield and quality.

Plant productivity is not only influenced by light quantity, as intensity (fluence rate) and duration (photoperiod), but it is also affected by light quality (wavelength composition) that influences plant growth and photomorphogenesis, and tissue composition (reviewed in Ouzounis et al. 2015a). For instance, red light affects the photosynthetic apparatus development, and red and blue light are most efficiently utilized for photosynthesis (Paradiso et al. 2011a). Blue light influences stomatal opening, plant height and chlorophyll biosynthesis, while far red light stimulates flowering in long-day plants and red/far red ratio regulates stem elongation and branching, leaf expansion, and reproduction (Zheng et al. 2019). Finally, green light can drive long-term development and short-term acclimation to light conditions, acting from a chloroplast scale to a whole-plant level. Indeed, green light penetrates deeply in the leaf mesophyll layers and reaches the lower and inner canopy levels, promoting photosynthesis in the deepest chloroplasts and in the less irradiated leaves and providing signals to respond to the environmental irradiance, hence, improving crop productivity and yield (Smith et al. 2017).

These evidences show the importance of the different wavelengths of the light spectrum, alone or in combination, in eliciting morphological and physiological responses of plants (Devlin et al. 2007; Folta and Childers 2008). However, despite the current knowledge on the spectral dependence of many plant processes, artificial

lighting in horticulture is still applied mainly with assimilative or photoperiodic function, and only recent experiences pointed out the possibility to exploit the control function of light. Particularly, in the last years innovative lighting sources, based on light-emitting diodes (LEDs), have been tested in plant cultivation, using different wavelength combinations not only to enhance plant photosynthesis and productivity but also to control photomorphogenetic responses, including bioactive compounds synthesis (Bantis et al. 2018).

Recently, the creation of blue LEDs allowed the extension of the spectrum range and also the realization of white light LEDs. This revolutionary progress in the lighting sector was endorsed by the Royal Academy of Sciences of Sweden, which in 2014 conferred the Nobel Prize in Physics for the "invention of blue light-emitting diodes". Consistently with this acknowledgement, the General Assembly of the United Nations declared the 2015 as the "International Year of Light and Light-Based Technologies", with the aim to promote knowledge on the potential of light science to contribute to a sustainable development and to improve the life quality in the World.

Referring to the control function of light in plants, recent review papers summarized the most relevant knowledge on the modulatory effects of light spectrum in horticultural crops, with reference to only recent advances (Zheng et al. 2019), selected leafy vegetables (Thoma et al. 2020) or microgreens (Alrifai et al. 2019), LED systems (Bantis et al. 2018), and utilization in plant factories in urban horticulture (Kozai 2016). Besides, comprehensive overview deepened the influence of LED lighting on the biosynthesis of bioactive compounds and crop quality, in both the visible spectrum (Hasan et al. 2017) and the UV region (Rai and Agrawal 2017).

Our review summarizes data on plant responses to light spectrum of artificial lighting in vegetable and ornamental crops, in terms of growth and photomorphogenesis, and the state of the art of the research on LEDs in greenhouse horticulture. It is worthy to emphasize that, because of the magnitude of data available and the intense research activity in recent times on this topic, many papers even including relevant findings probably eluded our literature inspection. This particularly happened for articles published in the last months, when our efforts were mainly addressed to writing. Just as an example, we point out the latest collection "Crop Physiology under LED Lighting", published by the journal Frontiers in Plant Science (https://www.frontiersin.org/research-topics/12923/crop-physiology-under-led-lighting; Editors Marcelis L., Goto E., Grodzinski B., Torre S., Wargent J., Bugbee B.).

The Solar Radiation and the Plant Functions

The quantity and quality of the incident light affect both the crop yield and the qualitative characteristics of the produces, by sustaining plant growth and influencing the plant reproduction, and by driving the primary and secondary metabolism. The radiation within the 400–700 nm waveband of photosynthetically active radiation (PAR) controls the photochemical reactions, converting light energy in chemical energy, through the synthesis of ATP and NADPH used to assemble carbon atoms in organic molecules in the Calvin cycle, in the reduction of NO_3^- and in the synthesis of amino acids and lipids (Malkin and Niyogi 2000). The useful spectrum for photosynthesis in the range of PAR is perceived through photosynthetic pigments, chlorophylls, carotenoids as β-carotene, zeaxanthin, lutein and lycopene, which respond to precise wavelengths included in this range. Indeed, the light harvesting complex in the thylakoids of chloroplasts includes chlorophyll *a* and chlorophyll *b*, showing the peaks of maximum absorption at 430, 662 nm, and at 453, 642 nm, respectively (Ouzounis et al. 2015a). Carotenoids are accessory photosynthetic pigments, harvesting and transferring light energy to chlorophylls, with absorption peaks in the range of 400–500 nm, showing a key role in plant protection to oxidative stress, by the dissipation of excess light energy absorption by photosystems (Bantis et al. 2018).

The light quantity, as intensity and photoperiod, is perceived by plants through a complex mechanism including the light signals perception at the leaf level and their transduction to target systems that activates molecular reactions ensuring the fine control of metabolic processes associated to the induced functions (Paik and Huq 2019). For instance, minimal variations of photoperiod can trigger a significant advance or delay in specific physiological responses linked to plant development, such as flowering, tuberization and bud development (Mawphlang and Kharshiing 2017). Due to the relevance of these essential functions, plants have developed an endogenous system for a precise measurement of photoperiod, represented by circadian rhythms, synchronized with the prevailing environmental conditions (Battle and Jones 2020). Plant response to photoperiod is a wide and complex phenomenon; comprehensive assays can be found for example in Johansson and Köster (2019) and in Creux and Harmer (2019).

Referring to the light quality, the influence of the light spectrum on plant growth and development has been highlighted since the last century. Just as a few examples, already in 1948, Borthwich et al. used coloured glass filters to provide plants with light of different colours, highlighting differential responses in plant behaviour in

relation with the spectral characteristics of light (Kasperbauer and Kaul 1996). In 1972, McCree demonstrated that, at the same light intensity, the photosynthetic efficiency changes with the wavelength composition and, in the majority of the species, the most useful wavelengths for photosynthesis are in the blue and red regions, according to a trend strictly correlated to the spectrum of absorption of photosynthetic pigments. Oyaert et al. (1999) tested coloured polyethylene filters with different B:R and R:FR ratios on *Chrysanthemum morifolium* plants, highlighting the effects of this tool for growth regulation and quality improvement in ornamental crops.

Nowadays, it is known that the different wavebands of light spectrum transmit to plant photoreceptors specific signals inducing the expression of genes related with physiological and metabolic functions (Fukuda 2013; Weller and Kendrik 2015). The mechanisms underlying the perception and response of plants to spectral composition of the incident light are the subject of topical studies, focused on the role and functions of specific photoreceptors sensitive to different regions of light spectrum (Mawphlang and Kharshiing 2017; Paik and Huq 2019).

Different classes of photoreceptors perceive the wavelengths corresponding to blue (B, 445–500 nm), green (G, 500–580 nm), red (R, 620–700 nm), and far red (FR, 700–775 nm), while specific photoreceptors perceive ultraviolet (UV) radiation, in particular the UV-A (315–380 nm) and UV-B (280–315 nm) types (Zheng et al. 2019). A very important feature of these molecules is represented by the magnitude of light intensity required to trigger a related response, since they are usually activated by a lower intensity than that required for photosynthetic processes (Costa Galvão and Fankhauser 2015). From an operational point of view, this implies the possibility to regulate photomorphogenetic processes through artificial lighting, with relatively small investments in terms of operating costs.

Photomorphogenesis and Photoreceptors

Plants have evolved sophisticated mechanisms to detect and respond to light quantity and quality, activating a network of photosensory pathways which are the basis of photomorphogenesis processes. Photomorphogenesis defines plant morphology and development, phototropic orientation to light, photoperiodic responses, and it induces the synthesis of numerous metabolites essential for plant life (Alrifai et al. 2019; Thoma et al. 2020).

The different spectra received from a natural or artificial source of light strongly influence the plant behaviour, eliciting different metabolic effects. Besides the photosynthetic pigments, the light perception related to photomorphogenesis counts on other specific photoreceptors, independent to photosynthetic metabolism (Weller and Kendrik 2015). These are present in different parts of the plant, and the site of light perception can correspond to the part of the plant responding to the light stimulus (e.g. chloroplasts for their own movement), or it can be distant, as light induces a response by long-distance molecular signals (as in floral transition) (Costa Galvão and Fankhauser 2015).

Five classes of photoreceptors proteins were characterized to initiate plant responses to light (Fig. 1). The first class is represented by the phytochrome family, absorbing R and FR wavelengths; three different photoreceptor proteins, cryptochromes, phototropins and the ZTL/FKF1/LKP2 complex, absorb B and UV-A wavelengths; the UVR8 is sensitive to UV-B wavelengths (Wu et al. 2012). These photoreceptors, except for UVR8, are represented by a family of molecules, with each member encoded by a different gene and showing a high degree of similarity with the others.

Higher plants contain multiple phytochromes (phy A to phy E) (Hughes 2013), three cryptochromes (cry1, cry2 and cry3), two phototropins (phot1 and phot2), and one UVR8 photoreceptor. Moreover, a more complex family of B light absorbing proteins, referred as ZTL/FKF1/LKP2, is defined by a combination of the activity of photoreceptors and F-box proteins within the same molecule (Mawphlang and Kharshiing 2017).

Phytochromes

Phytochromes (PHYs) have been found and analysed in plants since 1950 (Borthwick et al. 1952). PHYs are soluble proteins, binding phytochromobilin as chromophores, absorbing R and FR light, responsible for different plant light responses (Hughes 2013). Light converts PHYs in two photoreversible forms in vivo: Pr absorbing R light, with an absorption peak at 650–670 nm, and Pfr absorbing FR, with an absorption peak at 705–740 nm. Pr absorbs R light and is converted to its active form Pfr; on the contrary, Pfr absorbs FR light and is converted to its inactive form Pr.

The active forms of PHYs translocate from the cytoplasm to the nucleus to regulate the expression of different genes linked to the photomorphogenic responses. PHYs can mediate a Very-Low-Fluence Response (VLFR), a Low Fluence Response (LFR), and a High-Irradiance Response (HIR), in relation to the intensity of incident light. The VLFR is activated by extremely low light intensities and very low levels of Pfr, while higher Pfr levels are needed to induce a LFR response. Instead, the extended or continuous irradiation, with a long exposure to a high light intensity (over 1000 µmol m^{-2}), can stimulate HIR. In these processes, phyA and phyB play major roles. PhyA is responsible for the VLFR, given its high sensitivity to R light, and can activate a response also at very low radiative flux (0.1–100 nmol m^{-2}), and only a small portion of phyA is converted into its active

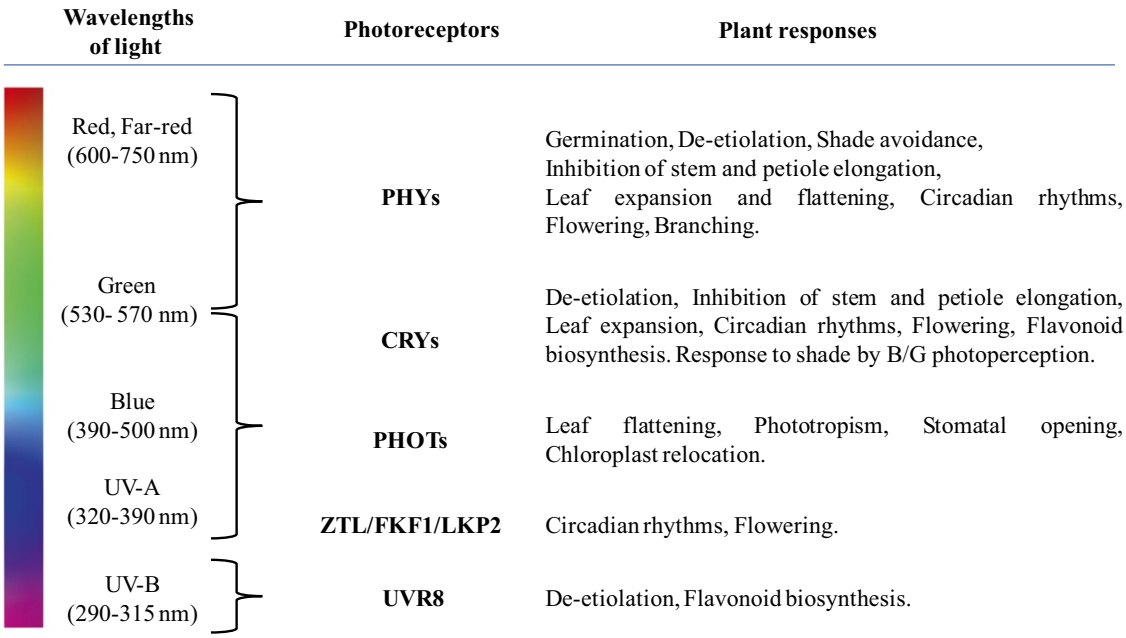

Fig. 1 Spectral wavelength specificity of the main plant photoreceptors and related plant photomorphogenesis responses. Phytochromes (PHYs), cryptochromes (CRYs), phototropins (PHOTs), Zeitlupe family proteins (ZTL/FKF1/LKP2), and UV resistance Locus 8 (UVR8)

form (Shinomura et al. 1996). PhyB principally triggers LFR, responding to low-irradiation conditions (not exceeding 1000 µmol m^{-2}), induced by short exposures to R light. HIR-type responses can involve both phyA and phyB in relation to the R or FR portions. In contrast to LFR, HIR and VLFR do not show R:FR photo-reversibility (Casal et al. 1996). VLFR is implemented during light-induced seed germination, as well as LFR-type response is characteristic of seed germination and of responses to short light pulses. HIRs include de-etiolation and anthocyanin accumulation in plants. Some authors showed that the response to red wavelengths can be induced also by cryptochromes, indicating a synergy of photoreceptors to control photomorphogenetic processes (Ahmad et al. 1998; Màs et al. 2000).

The phytochromes photoequilibrium at plant level, calculated as PPE = Pfr/(Pr + Pfr), is strongly related to the R:FR ratio of the incident light (Demotes-Mainard et al. 2016). Spectral composition of the incident light changes during the day and coherently the R:FR ratio varies from 1.15 to 0.70 (Craig and Runkle 2016; Wang et al. 2020). This value, and consequently the Pfr:Pr ratio, decrease also along the plant canopy from the top to the bottom, as a consequence of the different light exposure and wavelengths penetration. Similarly, a decrease of R:FR and Pfr:Pr ratio occurs in plants surrounded by nearby vegetation. These shading conditions induce a complex response defined shade avoidance, including stem and petiole elongation, lower leaf mass, stomata density and chlorophyll content per unit of leaf area, and early flowering (Casal 2013). The shade avoidance response increases the plant survival under unfavourable light conditions; however, it can compromise crop yield when modern intensive cropping methods, based on high planting density, are applied (Wang et al. 2020).

Finally, the R:FR ratio also affects the plant mineral nutrition. Nitrogen assimilation is inhibited by a low R:FR ratio, which affects the activity of key enzymes of nitrogen metabolism, such as nitrate and nitrite reductase, and glutamine synthetase. In contrast, a reduced R:FR ratio increases the allocation of nutrients to the plant shoot, resulting in a faster development of the aerial part compared to the roots (Demotes-Mainard et al. 2016).

Cryptochrome, Phototropins and ZTL/FKF1/LKP2

Cryptochrome family photoreceptors (CRYs) are flavoproteins activated by B and UV-A light absorption, identified in bacteria, fungi, animals and higher plants (Meng et al. 2013). In *Arabidopsis*, CRYs have a key role in seed germination, leaf senescence, stress responses and regulation of transcription; moreover, they can regulate seedlings de-etiolation and growth in shaded environments, and control plant height, flowering time and circadian rhythms (Devlin et al. 2007; Pedmale et al. 2016).

CRYs, in synergic action with PHYs, have been identified also as receptors of G light, lacking a specific photosensory system for this region of light spectrum. Battle and

Jones (2020) suggested that CRYs and PHYs can absorb portions of the G waveband, even though with a lower sensitivity compared to that for B and R wavelengths. Smith et al. (2017) proposed the G light perception, particularly the B/G ratio, as an alternative and a fine tuner signalling for plant reaction to shade, resulting as an additional response of shade avoidance than the R/FR perception. The current knowledge suggests that G until 530 nm is included in the CRYs and phototropins B light response, whereas longer wavelengths of G-Y (570 nm) promote the inactivation of B-light-induced CRYs (Battle and Jones 2020), justifying the antagonist mechanism of G and B on photoperception by CRYs (Thoma et al. 2020).

Green light can be absorbed also by photosynthetic pigments, underlying the importance of this wavelength for CO_2 assimilation and biomass production, and for both long- and short-term plant responses to environmental conditions (Smith et al. 2017). The role of CRYs on regulating processes linked to circadian rhythms, phototropic responses, and metabolites accumulation, confers to plants adaptive advantages and affects important traits associated to productivity and quality of crop (Giliberto et al. 2005; Mawphlang and Kharshiing 2017).

Phototropins (PHOTs) are plasma membrane-associated Serine-Threonine kinases, showing a photoactivation through phosphorylation induced by B light (Briggs and Christie 2002; Christie et al. 2015). The function and structure of PHOTs were identified in *Arabidopsis thaliana*, in which two phototropins, phot1 and phot2, were characterized under a molecular point of view. PHOTs can respond to light environment through the control of plant photosynthetic process. Indeed, PHOTs control the movement, density and rearrangement of chloroplasts in plant leaves, to enhance the photosynthetic light harvesting and to minimize the photo-damage under low or high light conditions, respectively. In *Arabidopsis* mutants, where phototropins are lacking, a significant reduction of photosynthesis was observed (Boccalandro et al. 2012), principally induced to the deficient adjustment of chloroplasts that decreases the use of photosynthetically active radiation (PAR) by plants. PHOTs define also the stomatal opening, for the optimization of CO_2 and water exchange (Boccalandro et al. 2012). Although phot1 and phot2 show some functional differences to light responses, they have overlapping functions in plants, with the phot1 activation under a larger range of B light intensity and phot2 activation under higher B intensity.

The family of LOV (Light Oxygen or Voltage) photoreceptors was described and defined in *Arabidopsis* as Zeitlupe/Flavinbinding Kelch Repeat, F-BOX1/LOV Kelch Protein2 (ZTL/FKF1/LKP2), sensitive to B and UV-A wavelengths, (Nelson et al. 2000; Somers et al. 2000). Analysis of genes encoding for these photoreceptors shows differences between two genetic groups in dicots and monocots (Taylor et al. 2010), underlining different functions for these genes. The high level of structural conservation of gene homologs among monocots and dicots observed indicated their functional conservation to regulate similar developmental pathways across different species (Yon et al. 2016). In *Arabidopsis*, KF1 and LKP2 control circadian rhythm (Baudry et al. 2010), photoperiodic flowering (Song et al. 2016) and, as soybean GmZTL3 (homolog of *Arabidopsis* ZTL) has been suggested to control the timing of flowering (Xue et al. 2012).

UVR8 Photoreceptors

In addition to the above-mentioned specific photoreceptors for UV-A radiation, plants can also intercept UV-B radiation by means of the UV RESISTENCE LOCUS8 (UVR8) receptors (Wu et al. 2012). UVR8 proteins are homodimers in the cytoplasm, binding monomer of tryptophan with a chromophore function. In response to UV-B radiation, these photoreceptors are activated by molecular dissociation. UVR8 monomers are accumulated in the nucleus where they perform its regulatory functions (Jenkins 2014). The UV-B photoreceptors allow plants to counteract the harmful effects of UV-B inducing changes in gene expression, leading to morphological adaptations and production of different metabolites, mostly with antioxidant functions. In addition, UVR8 photoreceptors mediate essential processes such as stomatal movements, opening and closure (Huché-Thélier et al. 2015). Furthermore, UVR8 defines the chlorophyll *a* content in response to UV-B wavelengths, determining variation of chlorophyll *a*/*b* ratio (Jenkins 2009).

Despite the knowledge achieved during the last years on molecular mechanisms of photomorphogenesis, different topics remain unclear as the molecular nature and activity of UVR8 photoreceptors, the uncertainty about the presence in plants of a specific G receptor and the mechanism of synergic action of different photoreceptors in eliciting light responses. Since photoreceptors control plant–environment interactions, more information about their biochemical characteristics might suggest the lighting scheduling more efficient to increase plant fitness, yield and quality in agriculture.

Artificial Lighting in Horticulture: Historical and Modern Light Sources

Electric lamps have been used for artificial lighting in plant cultivation for nearly 150 years (Wheeler 2008; Morrow 2008). As might be imagined, plant lighting closely followed the paths of lighting for civil use, based on three main technologies: (1) incandescent lighting, which was refined by Edison's invention of the incandescent filament lamp in

1879; (2) open arc lighting, which typically used carbon rods and became popular for street lighting in some cities in the late 1800s and (3) enclosed gaseous discharge lamps, which were initially developed with mercury vapour in the late 1800s (Wheeler 2008 and references therein).

Among the different lamp types, each fits with specific applications, depending on the purpose of lighting. Referring to assimilation lighting, fluorescent lamps, particularly those having enhanced blue and red spectra (i.e. cool fluorescent white lamps), are widely used in growth chambers, together with additional light sources to achieve a sustained photosynthetic photon fluence. High-intensity discharge (HID) lamps, such as metal halide (MH) and high-pressure sodium lamps (HPS), are typically used in greenhouses and plant growth chambers (Nelson and Bugbee 2014). MH lamps can be used to totally replace sunlight or partially supplementing it during periods of low solar radiation. The inclusion of metal halides during manufacture optimizes the spectrum of the emitted radiation. Besides, fluorescent lamps, particularly the white ones, are widely used in phytotrons and for in vitro propagation (Darko et al. 2014).

HID lamps have high fluence and a good efficiency in energy conversion (light emitted per unit of energy consumed) to PAR (until 50%); however, they show some disadvantages, including the relevant energy requirement, the bulky volume and the high operational temperature, which prevent the placement close to the canopy (even though the heat emission is used in temperature control in Northern countries), and the risk inherent the presence of pressurized gas in glass bulbs. In addition, the spectral distribution shows a high proportion of green-yellow region, significant ultraviolet radiation, scarce blue and FR, altered and instable R:FR ratio, and does not allow modulation of light spectrum. Hence, HIDs are neither spectrally nor energetically optimal. Besides, they are considered not environmental friendly, because of CO_2 emissions and light pollution, particularly in Northern countries, where greenhouse lighting is widely spread (Pinho et al. 2012; Battistelli 2013).

Fundamental advances in plant artificial lighting started in the mid 1980s when tests with light-emitting diodes (LEDs) begun. LEDs are solid-state semi-conductors and generate light through electroluminescence and, thus, are fundamentally different from other lamps used to date in plants and are the first light source suitable to control light spectral composition and to regulate intensity. Indeed, depending on the semi-conductor used, they produce light at specific wavelengths (colours) of the visible spectrum and beyond, from 250 nm (ultraviolet C) to 1000 nm (infrared), in relatively narrow wavebands, offering the possibility of a targeted compilation of the spectrum. They show higher energy efficiency compared to the traditional light sources (Cocetta et al. 2017) and, thanks to the solid state, they are safer and more robust than lamps with filament, pressurized gas, or mercury in glass and are suitable to be used at low temperature (till − 40 °C) and high humidity (Nelson and Bugbee 2014). The lower heat radiation does not interfere with controlled climate and, also thanks to the smaller volume, allows to place the lamps close to the canopy, in modern multi-layer and interlighting systems. In addition, they are suitable to be powered by low voltage, with consequent advantages in engineering, and the insensitivity to the switching frequency determines lower cost for maintenance and longer duration. Finally, LEDs equipped with driver chips provide the additional benefits of operational flexibility, suitability for digital control and light protocols (i.e. daily light integral), while the dimmability makes possible the simulation of sunrise and sunset.

LEDs duration is determined differently compared to traditional lamps. Indeed, since this type of light source does not burn out but only tends to attenuation of intensity over time, duration is better expressed as time of operation until 70% of the original intensity. Individual high-brightness LEDs have a predicted lifetime up to 50,000 h (corresponding to about 16.7 years when used an average of 8 h per day), when operated at favourable temperatures, which is 2–3 times higher than fluorescent and HID lamps (for details about technical parameters see Nelson and Bugbee 2014).

Despite the numerous advantages, LEDs still present several constraints, such as the higher cost compared the traditional light sources, the difficulty to obtain diffused light and the risks of eye damage for operators in case of prolonged exposure (e.g. for UV emission of blue and white LEDs).

Monochromatic Light and Photomorphogenesis in Vegetable and Flower Crops

Much of the early work on plant production under LEDs was conducted by researchers affiliated with NASA (National Aeronautics and Space Administration of United States) and aimed to design lighting systems for plant cultivation in Space, to develop plant-based regenerative life-support systems for future Moon and Mars colonies (Bula et al. 1991). Later on, LED lighting systems have been studied to totally replace traditional light sources in space greenhouses, as reviewed by Zabel et al. (2016) and Berkovich et al. (2017), to optimize crop production and quality in Space through specific light recipes to be used in plant chambers aboard of space outposts such as the International Space Station (ISS) (Mickens et al. 2018).

LEDs of different colours can be combined to obtain a tailored light spectrum at the desired intensity to modulate the different plant functions, providing a useful tool to control plant growth and photomorphogenesis (Darko et al. 2014). Accordingly, they can be used for several purposes, such as

the control of size in potted ornamentals, the scheduling of flowering in cut flower crops, the strengthening of mechanisms of stress tolerance and the improvement of chemical composition of plant food (Huché-Thélier et al. 2015; Singh et al. 2015). In this respect, it is worth noting that, even though a distinction is often done between assimilation light and control light, the latter also influences the biomass accumulation. For instance, blue light, which has an important role in controlling plant height, can improve photosynthetic capacity per leaf area unit by increasing both the stomatal opening and the quantum yield. On the other hand, leaf area itself influences photosynthesis and plant growth, by determining light interception through the leaf surface, morphology and orientation. This is particularly important in noncontinuous canopies (e.g. young plants), where the incident light is only partially intercepted and photomorphogenetic responses have a relevant impact on plant growth and productivity (Hogewoning et al. 2010). Accordingly, He et al. (2019) highlighted that the impact of LED light quality on productivity can be linked to the induced modification of leaf traits more than the change in photosynthetic performance on a leaf area basis. However, it has to be taken into account that also the arrangement of light sources affects the light use efficiency (Paradiso and Marcelis 2012; Paradiso et al. 2020).

In the early studies, plant response to monochromatic light was investigated mainly in instantaneous measurements and after short exposure, while data collection on long-term acclimation of the whole crops started later and were focused at the beginning on plant adaptability and growth and yield. Yet, the last generation experiments have been concentrating on plant metabolism. Particularly, more than primary metabolism, consisting in essential synthesis mechanisms directly involved in plants growth, development and reproduction, current research frequently deals with the secondary metabolism, responsible for production of minor compounds, such as carotenoids, phenolics (particularly anthocyanins and flavonols), ascorbate and glutathione that, despite the occurrence in low concentrations, contribute to plant adaptability and acclimation to changeable environment and tolerance to biotic and abiotic stresses (Thoma et al. 2020). Typical functions of secondary metabolites are cell pigmentation, to attract pollinators and seed dispersers, and antioxidant activity, useful in protection against UV radiation or other stresses. In addition, they are crucial for nutritional quality of plant food for humans as they display various beneficial healthy effects, most related to the antioxidant activity.

Many recent researches focused on the identification of the best combination of light intensity and light quality for vegetable crops, to promote the most suitable composition of plant tissue for human nutrition; however, the *plethora* of additional environmental (temperature and relative humidity) or cultivation variables (e.g. fertilization) complicate defining specific light recipes.

The following paragraphs summarises the most relevant evidences observed in plant growth and photomorphogenesis as response to changes in light environment by means of LEDs, in both vegetable and flower crops, and information useful to design LED-based lighting systems, depending on the crop and the desired response. Some details of the most relevant cited works are given in Tables 1, 2, and 3, for leaf vegetables, fruit vegetables and flower crops, respectively. Data on the effects of light spectrum treatments on photosynthesis are reported when given; however, they do not fall within the main topics of this review. Unless it is not differently specified, all data refer to plants during cultivation and, for vegetables, chemical composition concerns the edible part of the plant (e.g. leaves and fruits). In a few cases, data on in vitro plantlets or on seedlings are reported for those crops in which LED application focuses on plant propagation.

Red and Blue Light

Vegetable Crops

Early tests of Space research mainly concerned LED R light and demonstrated the need for B radiation to obtain a balanced plant growth. Bula et al. (1991) reported that plant growth of lettuce under R LEDs (660 nm) combined with B fluorescent lamps (BF, used as source of B before the invention of blue LEDs) was equivalent to those obtained under cool-white fluorescent light (CWF) combined with incandescent lamps (INC, Table 1). Red light determined better growth compared to B light in lettuce (Yanagi et al. 1996; Table 1). However, in this crop, R alone determined hypocotyl etiolation, but this effect was prevented by B addition (10% of total PPFD) (Hoenecke et al. 1992; Table 1). Accordingly, experiments on wheat confirmed the need for B radiation to prevent etiolation and demonstrated that seedlings grown under R light only did not synthesized chlorophyll, while the addition of B (6% of 500 µmol m^{-2} s^{-1} PPFD) reactivated Chl synthesis (Tripathy and Brown 1995). Besides, it was demonstrated that B added to R improved plant photosynthetic performance and growth: in pepper lighted with only R, R + BF and R + FR LEDs compared to MH lamps, plants showed a better growth under the wider spectrum of MH, and decreasing growth under R + BF, only R and R + FR, in the absence of B wavelengths (Brown et al. 1995; Table 2).

Comparing the effects of R LEDs, R + 1% BF, and R + 10% BF to CWF on wheat (24 h photoperiod, 350 µmol m^{-2} s^{-1} PPFD), Goins et al. (1997) demonstrated that plants could complete a seed-to-seed cycle under

Table 1 Effects of light quality on plant growth, photosynthesis (when available) and secondary metabolites content in leafy vegetables

Leafy vegetables		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		References
Species	Cultivar			Increase	Decrease	
Lactuca sativa L.	Grand Rapids	PPFD = 325 16 h Growth chamber	CWF + INC vs LED R100 + BFL	No difference	No difference	Bula et al. (1991)
	Grand Rapids	PPFD = 150 and 300 24 h Growth chamber	CWF vs LED R100 LED R + BFL at complementary ratio from 0 to 60		B 0–60: hypocotyl height B 0–15: cotyledon length	Hoenecke et al. (1992)
	Okayama-saradana	PPFD = 85 and 170 16 h Growth chamber	LED R, B, RB	RB: leaves number B and RB: leaf inclination angle 170 PPFD: plant DW	B: curvature of the leaf margin	Yanagi et al. (1996)
	Grand Rapids	PPFD = 200 and 500 16 h Growth chamber	HPS + B filters 0.1, 2, 6% MH + B filters 6, 12, 26%	Increasing B: leaf, stem and root DW, chls (under both lamp types) HPS + B 0–6% at 200 and B 0–2% at 500: LA	Increasing B: stem length, SLA (under both lamp types)	Dougher and Bugbee (2001)
	Waldman's green	PPFD = 300 18 h Growth chamber	CWF vs LED R100 LED R + BFL R90:B10		LED R100: shoot and root DW, gs	Yorio et al. (2001)
	Red fire	PPFD = 300 12 h Growth chamber	WFL vs BFL = B:G:R 75:24:1 RFL = B:G:R 2:19:79 BFL + RFL = B:G:R 26:22:52	BFL: leaf length/width ratio BFL and BFL + RFL: ascorbic acid RFL: leaf number, SLA, LA RFL and BFL + RFL: total chl	BFL: total carotenoids, soluble sugars, nitrate RFL and BFL + RFL: chl a/b ratio, SLA, shoot DW	Ohashi-Kaneko et al. (2007)
	Red Cross	PPFD = 300 16 h Growth chamber	CWF vs LED FR 160 R 130 CWF vs LEDs G 130 B 130 UV-A 18	FR: stem and leaf length, leaf thickness, LA, plant FW and DW R: phenolics B and UV-A: anthocyanins, ascorbic acid B: carotenoids	FR: anthocyanins, carotenoids and chls B and UV-A: stem and leaf length	Li and Kubota (2009)
	Outredgeous	PPFD = 300 18 h Growth chamber	FL vs LED R 300 LED R:FR 300 + 20 FL vs LED B:G:R 25 + 5 + 270 LED B:R 30 + 270	R:FR: total biomass, LA, leaf elongation, plant DW B addition: leaf expansion and unrolling BR: anthocyanins	R: plant DW	Stutte et al. (2009)

Table 1 (continued)

Leafy vegetables		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		References
Species	Cultivar			Increase	Decrease	
	Red Fire	PPFD = 100, 200 or 300 24 h Growth chamber	FL vs LED G510 (510 nm), G520 (524 nm), G530 (532 nm)	FL 200: LA and leaf FW, S/R, LED G increasing PPFD: root DW G510 300: leaf number, petiole length, G520 and G530 100 and G530 300: petiole length, G510 and G520 increasing PPFD: petiole width, G 200 and G510 100: Pn	FL 300: leaf length and width, S/R G: LA, leaf FW, shoot DW G 200 and 300: S/R FL and G510 increasing PPFD: SLA	Johkan et al. (2012)
	Capitata	PPFD = 210 16 h Growth chamber	FL vs commercially light sources RBW, RB	FL and RBW: shoot and roots FW and DW, crispness, sweetness, leaf shape index RBW: soluble sugars, S/R ratio	RB: LA, SLA RBW: nitrate	Lin et al. (2013)
	Red Sunmang and Green Grand Rapid TBR	PPFD = 171 12 h Growth chamber	LED B:R 0:100, 13:87, 26:74, 35:65, 47:53, 59:41	B0: leaf shape index, leaf elongation, shoot and root FW and DW, LA B35, B47, B59: chls, phenolics, flavonoids, antioxidant capacity (in both red and green leaves)	B:R 0:100: chls Increasing B: plant growth	Son and Oh (2013)
	Red Sunmang and Green Grand Rapid TBR	PPFD = 173 12 h Growth chamber	FL vs LED R9B1 = B:G:R 1:0:9 R9G1 = B:G:R 0:1:9 R8B2 = B:G:R 2:0:8 R8G1B1 = B:G:R = 1:1:8 R7B3 = B:G:R 3:0:7 R7G1B2 = B:G:R 2:1:7	R: FW and DW of shoot and root, R and B: LA Increasing B: SLDW (both cvs) R8G1B1 and R7G1B2: shoot FW, chls (in Sunmang) R8G1B1: chls (in Gran Rapid TBR)	FL and R7B3: plant FW (in Gran Rapid TBR), R9G1: SLDW (both cvs), chls (in Gran Rapid TBR)	Son and Oh (2013)

Table 1 (continued)

Leafy vegetables		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		References
Species	Cultivar			Increase	Decrease	
	Green Batavia and Lollo Rossa	DLI (January and February) 6.1 mol m^{-2} day^{-1} Greenhouse	NL vs NL + HPS (90) NL + B LED (45 or 80)	Batavia-B: plant compactness, gs, chls, Fv/Fm, phenolic acids, flavonoids Lollo-B: plant compactness, NPQ, chls, carotenoids, phenolic acids, flavonoids	Lollo-B: PSII quantum yield, ETR	Ouzounis et al. (2015b)
	Waldmann's Green	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool-white R, G, B, RB, RGB LEDs	B: DM, SLA, SLA 500 PPFD: DM, LAI, NP 500 PPFD and B: DM, NP	G: LAI, chls 500 PPFD: SLA	Snowden et al. (2016)
	–	PPFD = 200 16 h Growth chamber	LED R, B, R:B (1, 4, 8, 12)	R:B 1–12: shoot DW R:B 8 and 12: leaf number, LA	R:B 1–12: leaf photosynthetic capacity, NP, gs, stomatal density R:B from 1 to 12: stomatal density High B: PSII quantum yield, Fv'/Fm'	Wang et al. (2016)
	Green Oak Leaf	PPFD = 135 and 105 W LEDs 16 h Growth chamber	W LED vs W LED + FR, R, Y, G, B LEDs (30 PPFD each)	WR and WB: shoot FW WFR: S/R ratio, ascorbic acid	WFR: shoot FW, biomass, pigments	Chen et al. (2016)
	Buttercrunch	PPFD = 200 16 h Growth chamber	LED R100 vs R:B 83:17, 91:9, 95:5	R100: plant height R:B 95:5: plant FW and DW R:B 91:9: plant FW and DW chl *a*, chl *b*, total chls, total carotenoids R:B (83:17): antioxidant capacity		Naznin et al. (2019)

Table 1 (continued)

Leafy vegetables		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		References
Species	Cultivar			Increase	Decrease	
Spinacia oleracea L.	Nordic IV	PPFD = 300 18 h Growth chamber	CWF vs LED R100 LED R + BFL (R90: B10)		R100 and LED R + BFL: shoot and root DW R100: total chls	Yorio et al. (2001)
	Okame	PPFD = 300 12 h Growth chamber	WFL vs BFL = B:G:R 75:24:1 RFL = B:G:R 2:19:79 BFL + RFL = B:G:R 26:22:52	BFL: total chl, chl *a*/*b* ratio, total carotenoids RFL + BFL: ascorbic acid	BFL: shoot DW, LA, leaf length/width ratio, petiole length RFL: soluble sugars, nitrate	Ohashi-Kaneko et al. (2007)
	Unipack 151	PPFD = 200 16 h Growth chamber	LED R100 vs R:B 83:17, 91:9, 95:5	R:B 83:17: antioxidant capacity R:B 95:5: total leaf number, plant FW and DW R:B 91:9: plant FW and DW, chl *a*, chl *b*, and total chls, total carotenoids		Naznin et al. (2019)
Brassica campestris L.	Komatsuna	PPFD = 300 12 h Growth chamber	WFL vs BFL = B:G:R 75:24:1 RFL = B:G:R 2:19:79 BFL + RFL = B:G:R 26:22:52	RFL: shoot DW, LA, BFL: SLA, ascorbic acid	RFL + BFL: SLA, leaf length/width ratio, RFL: chl *a*/*b* ratio, carotenoids BFL: total chls, soluble sugars RFL and RFL + BFL: ascorbic acid	Ohashi-Kaneko et al. (2007)
	Te'aiqing	PPFD = 150 12 h Growth chamber	LED B, G, Y, R, R:B (6:1)	R: plant height B: soluble sugar, chl *a*/*b* RB: soluble protein, chls	R: chls Y: plant DW, soluble sugar, proteins G: chl *a*/*b* B, RB: plant height	Fan et al. (2013)

Table 1 (continued)

Leafy vegetables		Lighting conditions: (PPFD = µmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		References
Species	Cultivar			Increase	Decrease	
Ocinum basilicum L.	Napolitanisches Basilikum	PPFD = 300 16 h Greenhouse	HPS treatment vs HPS + supplemental B LED treatment (SB)	SB: phenolic acids, flavonoids		Taulavuori et al. (2013)
	Genovese	PPFD = 200 16 h Growth chamber	FL vs LED R, B R:B ratio: 0.7, 1.1, 1.5, 5.5	R:B 0.7: plant FW, energy use efficiency All LED treatments: antioxidant capacity, phenolics, flavonoids	R:B 5.5: assimilation rate R:B 1.1, 1.5, 5.5: leaf FW, plant FW R:B 0.7, 1.1, 1.5: nitrate	Piovene et al. (2015)
	Lettuce Leaf, Red Rubin, Mountain Athos (hybrid)	PPFD = 200 24 h Growth chamber	FL vs LED B:G:R:FR 12:19:61:8 B:G:R:FR 8:2:65:25 B:G:R:FR 14:16:53:17 UV:B:G:R:FR 1:20:39:35:5	FL, G2, G19 in Lettuce Leaf, G2 in Red Rubin: growth rate FL: LA (both cvs) G16 in Lettuce Leaf: roots length G2, G16, UV1: total biomass (both cvs) UV1: root/shoot ratio (both cvs) FL, G16 in Lettuce Leaf, G19 in Red Rubin: new roots development UV1: phenolics (both cvs)	FL = root/shoot ratio (both cvs)	Bantis et al. (2016)
	Improved Genovese Compact (green) Red Rubin (purple)	PPFD = 160 and 224 UV = 16 16 h Greenhouse	Control no UV vs five UV-B doses: 1 h day^{-1} 2 days: 1H2D 2 h day^{-1} 2 days: 2H2D 1 h day^{-1} 5 days: 1H5D 2 h day^{-1} 5 days: 2H5D	224 PPFD: plant yield Supplemental UV-B: anthocyanins, phenolics, flavonoids in green basil 1H2D: phenolics, flavonoids in purple basil	Supplemental UV-B: NP, chls SPAD, Fv'/Fm', plant growth, yield, shoot FW (both cvs) 2H5D: Pn, E and gs (both cvs)	Dou et al. (2019)
	G Lemon Basil	PPFD = 200 16 h Growth chamber	LED R100 vs R:B (83:17, 91:9, 95:5)	R:B 91:9: plant FW and DW, chl *a*, chl *b*, and total chls, antioxidant capacity R:B (83:17): carotenoids		Naznin et al. (2019)

Table 1 (continued)

Leafy vegetables		Lighting conditions: (PPFD = µmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		References
Species	Cultivar			Increase	Decrease	
Microgreens *Brassica oleacea*	Italica	PPFD = 350 24 h Growth chamber	LED R:B (88:12) vs B100: 5 days before harvest	B100: plant elongation, chl *a*/*b* ratio, β-carotene, violaxanthin, xanthophyll cycle pigments, aliphatic and aromatic glucosinolates, essential macro and micronutrients	B100: green colour, chl *b*	Kopsell and Sams (2013)
Microgreens *Brassica juncea*, *Beta vulgaris*, *Petroselinum crispum*	Mustard cv. Red Lion Beet cv. Bulls Blood Parsley cvs Plain Leaved, French	PPFD = 300 16 h Growth chamber	LED R:FR 170:2.5 + B: 0, 16, 25, 33%	B8%: carotenoids in beet, B 16–33%:—and β-carotene in mustard, beet and parsley B16%: xanthophylls in mustard, beet and parsley B25%: xanthophylls in mustard, parsley, carotenoids, chls in mustard B33%: lutein in beet and parsley, violaxanthin in beet, zeaxanthin in beet and parsley, chls in beet and mustard, carotenoids in beet B 16%: tocopherol in mustard, beet and parsley	B 0%: chl *a*, chl *b* and carotenoids in beet B 0–16%: chl index in mustard B 16%: chl index in parsley, chl *a* in mustard	Samuolienė et al. (2017)
Brassica rapa, Amaranthus tricolor, Lepidium sativum, Portulaca oleracea L.	Mizuna japonica cv. Greens, Amaranth cv. Red garnet, Cress cv. Curled, Common purslane	PPFD = 300 12 h Growth chamber	LED R = B:G:R 0:10:90 B = B:G:R 90:10:0 RB = B:G:R 45:10:45	R: FW in mizuna, lipophilic antioxidant activity, carotenoids in purslane, R and B: K, Na in all species, B: nitrate in all species, RB: FW in cress and purslane, DW in amaranth, lutein, β-carotene, lipophilic antioxidant activity in amaranth, cress, mizuna	R and B: Ca, Mg in all species, RB: FW in mizuna, DW in cress, individual phenolic compounds, total phenolics in all species	Kyriacou et al. (2019)

Table 1 (continued)

Leafy vegetables		Lighting conditions: (PPFD = µmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		References
Species	Cultivar			Increase	Decrease	
Microgreens *Brassica oleacea, rapa, juncea, napus, narinosa*	21 varieties	PPFD = 150 24 h Growth chamber	R:B 80:20, 20:80 vs R:G:B 70:10:20, 20:10:70	R:G:B 70:10:20: hypocotyl length, FW, DW, LA R:B (80:20): mineral, phylloquinone, α-tocopherol, ascorbic acid and β-carotene		Kamal et al. (2020)

continuous R light; however, growth and seeds production improved when B light was added. Specifically, 1% BF determined a plant leaf area similar to that under white light, and 10% B gave the same number of sprouts, while improving photosynthetic rate and dry matter accumulation.

Yorio et al. (2001) reviewed several previous works and summarized that in lettuce, spinach and radish under R LEDs only, dry matter accumulation was lower than under radiation including 10%BF, at the same total light intensity (Table 1); however, in NASA studies, the B requirement for some traits (e.g. stem length) was found to be genotype specific in some crops (e.g. potato). Accordingly, studying the effects of 6 levels of B (from 0.1 to 26%) from HPS and MH filtered light at two intensities (200 and 500 µmol m^{-2} s^{-1}) on lettuce, soybean and wheat, Dougher and Bugbee (2001) highlighted species-dependent responses and a different sensitivity to the absolute intensity and the proportion of B in the total PPFD in several traits (Table 1). For instance, stem length was more influenced by B intensity in lettuce and by B proportion in soybean. Later, Hogewoning et al. (2010) found a dose-dependent response to B radiation in plant leaf area and dry matter accumulation in cucumber (Table 2).

Thanks to the invention of blue LEDs, further researches confirmed promoting effects of B light on stomatal conductance (g_s), as previously shown for photosynthesis, highlighting the role of B radiation in stomatal control in spinach (Ohashi-Kaneko et al. 2007) and lettuce (Li and Kubota 2009) (Table 1), as well as in other vegetable and flower crops (same Authors; Tables 2 and 3). Later, van Ieperen et al. (2012) demonstrated that prolonged plants exposure to different LED spectra (R or B and their combinations) influenced gas exchange not only through the stomatal opening but also the stomatal density, underlying the importance of light composition (and particularly of the B amount) also in transpiration control and plant water relation.

In fruit production, Samuolienė et al. (2010) reported that in strawberry, additional R–B light at 7:1 ratio resulted in bigger fruits with higher sugar content compared to R alone, which also induced stem elongation and inhibited flowering (Yoshida et al. 2012; Table 2). In radish, soybean and wheat, the comparison of 3 types of white LEDs, warm (WaL), neutral (NL) and cold (CL) light, with 11, 19 and 28% of B, respectively (PPFD 200 and 500 µmol m^{-2} s^{-1}, same R:FR), revealed that the lowest B level of WaL LEDs promoted stem elongation and leaf expansion, while the highest in CL LEDs resulted in more compact plants, and stronger differences among the light sources were found under the lower light intensity (Cope and Bugbee 2013; Table 2). When grown in a greenhouse, tomato fresh and dry weights were positively affected by supplementation of natural light with W or R LEDs. W light also enhanced the fruit growth rate compared to monochromatic R or B addition or no supplemented light (Lu et al. 2012; Table 2). A study with two tomato cultivars

Table 2 Effects of light quality on plant growth, photosynthesis (when available) and secondary metabolites content in fruit vegetables and some root crops

Fruit vegetables		Lighting conditions: (PPFD = µmol m^{-2} s^{-1}; DLI; daylength) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Capsicum annuum L.	Hungarian Wax	PPFD = 300 12 h Growth chamber	MH vs LED R100, R + BF, R + FR	R + FR: stem length, stem mass	R100: plant biomass, leaf DW, stem and root DW, R + FR: root DW, R and R + FR: leaf number	Brown et al. (1995)
	California Wonder	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: NP, chls 500 PPFD: DM, LAI 500 PPFD and B: NP	B: plant DW, LAI, stem and petiole length G: SLA 500 PPFD and B: DM	Snowden et al. (2016)
	Redstart-dwarf Sweet Pepper	PPFD = 200 16 h Growth chamber	LED R100 vs R:B 83:17, 91:9, 95:5	R100: plant weight R:B (95:5): leaf, flower and fruit number, plant FW and DW R:B (91:9): plant FW and DW, chl *a*, chl *b*, antioxidant capacity R:B (83:17): carotenoids		Naznin et al. (2019)
Cucumis sativus L.	Hoffman's Giganta	PPFD = 100 16 h Growth chamber	WF vs R 100% R + B 7, 15, 22, 30, 50, 100%	B until 50%: photosynthetic capacity, leaf mass per unit leaf area, nitrogen and chls, gs	R 100% photosynthetic dysfunction, Fv/Fm, PSII quantum, ETR, quantum yield for CO_2 fixation	Hogewoning et al. (2010)
	Samona	PPFD = 312 NL + 221 HPS or + 139 HPS or + 82 LED 20 h Greenhouse	NL vs NL + HPS top lighting NL + LED R:B 80:20 intracanopy lighting	RB: leaf mass per unit leaf area, leaf DW, leaf curling	RB: leaf appearance rate, plant height	Trouwborst et al. (2010)
	Venice	PPFD = NL + 75 16 h Greenhouse	NL + artificial sunlight (ASL) or HPS or LED R:B 85:15 R-FR:B 85:15	R-FR:B LED: stem length, plant DW, stem DW	HPS: stem length and DW R:B: stem length, NP	Hogewoning et al. (2012)
	Cumlaude	PPFD = High DLI 16.2 mol m^{-2} day^{-1} Low DLI 5.2 mol m^{-2} day^{-1} 18 h Greenhouse	NL vs NL + B:R 0:100 B:R 4:96, 16:84 (High and low DLI)	Low DLI and more B: plant FW and DW, leaf number, stem diameter, NP, chls	Low DLI and more B: hypocotyl and epicotyls length, gs	Hernández and Kubota (2014)
	Mini cucumber Picowell	PPFD = NL + 165 top-lighting with HPS or Plasma light (PL) NL + top and bottom 10 B, 10 R, 8 FR LED 17 h Greenhouse	NL NL + HPS or PL NL + HPS or PL + 4 LED vertical treatments Top FR + bottom B Top B + bottom FR Top FR + bottom R Top R + bottom FR	Interaction of top-lighting and LED: fruit yield Top FR LED: fruit yield PL: average fruit size	PL, top B LED: leaf size, plant height and fruit yield (first month)	Guo et al. (2016)

Table 2 (continued)

Fruit vegetables		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; daylength) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
	Cumlaude	PPFD = 100 18 h Growth chamber	CWF vs six treatments with LED R from 100 to 0% in combination with LED B from 0 to 100%	RB with high B percentage: leaf mass per unit leaf area, NP, gs, chls	RB with high B percentage: plant height, hypocotyl and epicotyl length, LA, shoot FW and DW	Hernández and Kubota (2014)
	Sweet Slice	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: NP, chls G: LAI 500 PPFD: DM, LAI, NP	B: stem and petiole length, plant DW, LAI, SLA G: NP, chls 500 PPFD and B: DM 200 PPFD and B: NP	Snowden et al. (2016)
	Mini-cucumber Toploader	PPFD = NL + HPS-HPS = 290 + 90 LED-LED = 60 + 125 HPS-LED = 90 + 125 Greenhouse	Three top-light and intra-canopy light combinations with HPS and LED FR:R:G:B: 17:53:16:14%	LED-LED: light use efficiency, leaf expansion, stem growth, fruit abortion rate HPS-LED: yield, leaf and flower appearance rate	LED-LED: number of fruits, yield, flower initiation rate HPS-LED: fruit abortion rate	Särkkä et al. (2017)
Lycopersicon esculentum Mill.	Mecano	PPFD = NL plus 75 16 h Growth chamber	NL + artificial sunlight (ASL) or HPS or LED R:B: 85:15, R-FR:B LED: 85:15	R-FR:B: stem length, stem DW, total DW, R:B: stem diameter, total LA, leaf DW, NP	R:B LED: stem length and DW	Hogewoning et al. (2012)
	Momotaro Natsumi	PPFDD = 360 16 h Growth chamber	FL + W, R, B LED	W: fruit FW	B: fresh yield and DW per plant	Lu et al. (2012)
	–	PPFD = variable values Growth chamber	LED B:R = 0.1 and 1 LED R = 25, 50, 75	Decreasing B:R ratio: NP LED 75 PPFD and B:R < 1.0: promote flowering	B:R 1.0: stem length B:R 0.1: node position LED 75 PPFD and B:R < 1.0: suppress thin growth	Nanya et al. (2012)
	Tomato rootstock Maxifort (*Solanum lycopersicum* × *S. habrochaites*) + scions Komeett and Success	DLI = 9 mol m^{-2} day^{-1} 18 h Greenhouse	NL + HPS overhead lighting lamps (HPS-OHL) vs NL + LED intracanopy lighting (LED-ICL) towers	HPS-OHL and LED-ICL: early fruit production, node number, fruit number, total fruit FW LED-ICL: energy conversion efficiency into fruit biomass (+ 75% than HPS-OHL) HPS-OHL: lighting cost per fruit (+ 403% than LED-ICL)		Gómez et al. (2013)
	Chocolate Cherry	PPFD = 300 16 h Greenhouse	HPS treatment and supplemental B LED treatment (SB)	SB: yield, phenolic acids, flavonoids in leaves		Taulavuori et al. (2013)

Table 2 (continued)

Fruit vegetables		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; daylength) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
	Tomato rootstock (*Solanum lycopersicum* × *Solanum habrochaites*, cv. Beaufort)	Exp. 1 PPFD = 69 (CWF) Exp. 2 PPFD = 102 (LED) Both 18 h Greenhouse	Exp. 1: CWF vs LED R:B 90:10 R:B + EoD FR (65.9 PPFD) Exp. 2: LED R:B 90:10, 25:75 R:B + FR (0 to 74.5 PPFD)	Low R:FR ratio increased shoot height	EoD FR: intumescence R:B (25:75) + EoD FR: reduced leaf intumescences and stem elongation	Eguchi et al. (2016)
	Solanum lycopersicum cv. Foronti grafted on rootstock cv. Stallone	PPFD = 165 16 h Greenhouse	NL + HPS + LED FR 0, 8, 16, 24 PPFD	Increasing FR: stem length, fruit yield (first month), carotenoids		Hao et al. (2016)
	Nine tomato genotypes (*Solanum lycopersicum*, *S. pimpinellifolium*, *S. habrochaites*)	PPFD = 150 16 h Greenhouse	LED R:B 88:12 compared to R LED	R:B: total DW in 7 genotypes; chls and flavonols in 3 genotypes	R:B: upward or downward leaf curling	Ouzounis et al. (2016)
	Nine genotypes	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: chl G: stem length 500 PPFD: DM, LAI 500 PPFD and B: DM, NP	B: plant DW, LAI, stem and petiole length 500 PPFD and B: DM	Snowden et al. (2016)
	NS3389	PPFD = 200 16 h Greenhouse	NL + RB 3:1 NL + LED WRB 3:2:1 WRFR 3:2:1 WB 2:1 intracanopy or underneath the canopy	Underneath canopy, WRB, WB: health index, development rate, CO_2 assimilation efficiency, energy dissipation Intracanopy: gs, leaf CO_2 supply, ETR In all treatments, WRB and WB: stomatal opening, ETR, NP		Song et al. (2016)
	Solanum lycopersicum L. Foundation; Nunhems, Haelen, Netherlands	PPFD = LED overhead 99 LED intracanopy 48 16 h Greenhouse	NL + LED R:B (B 0, 6, 12, 24%)	Increasing B: total biomass, number and yield of fruits; photosynthetic capacity B 6–12%: growth and yield	Increasing B: stem, internode length, LA B 24%: growth	Kaiser et al. (2019)

Table 2 (continued)

Fruit vegetables		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; daylength) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Raphanus sativus L.	Cherriette	PPFD = 300 18 h Growth chamber	CWF vs LED R100 LED R + BFL R90:B10		R100: top tissue and storage root DW, leaf NP, chls	Yorio et al. (2001)
	Cherry Belle	PPFD = 200 and 500 16 h Growth chamber	200/500 PPFD LED Neutral light: 19% B LED Warm W: 11% B LED Cold W: 28% B	Low B from Warm W LED: stem elongation, leaf expansion High B from CW LED: plant compactness	Increasing B: stem length, LA	Cope and Bugbee (2013)
	Cherry Belle	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: NP and chls G: petiole length 500 PPFD: LAI 500 PPFD and B: DM, NP	B: plant DW, stem and petiole length, LAI G: DM	Snowden et al. (2016)
Solanum tuberosum L.	Avanti, Colomba	PPFD = 200 12 h Growth chamber	WF vs LED RB 8:1	WF: NP from the vegetative phase until flowering (both cultivars) RB: NP, PSII maximum quantum use efficiency, photochemical parameters, tuber yield in both cultivars; total chl and carotenoids in cv. Avanti	WF: NP during tuber bulking in both cvs RB: stem elongation in both cvs; leaf number, LA, aerial biomass per plant, chls, carotenoids in Colomba	Paradiso et al. (2019)
Fragaria × *ananassa* Duch.	Elkat	PPFD = 200 16 h Growth chamber	LED R: (200) LED R + B: (174.5 + 25.5)	R + B: plant growth, carbohydrate accumulation, pigments, runners, inflorescence and crown R: flower stem elongation, S/R	R: fruit size	Samuolienė et al. (2010)
	HS138	PPFD = 225 16 h vs 24 h Growth chamber	WF, LED B or R	B and 24 h light: early flowering, fruit yield		Yoshida et al. (2012)
	Fukuoka S6	PPFD ≥ 400 (at plant height of 10 and 30 cm) 12 h Greenhouse	NL + FL NL + LED W	W: NP, leaf DW, LA, SLDW, average fruit weight, fruit number, marketable yield, fruit soluble solids		Hidaka et al. (2013)
	Elsinore	PPFD = 200 16 h Growth chamber	FL and LED R, B, W R:B ratio ranging 0.7–5.5	All LED treatments: plant FW R:B = 0.7 and 1.1: fruit yield R:B = 0.7, 1.1, 1.5, R, B, W LED: energy use efficiency	R:B 5.5: assimilation rate (vs R:B 0.7) R:B 0.7: antioxidant R:B 0.7, 1.1, 5.5: nitrate	Piovene et al. (2015)

Table 3 Effects of light quality on the plant growth, photosynthetic parameters and metabolites content in flower and ornamental species

Flower and ornamental species		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Antirrhinum majus L.	Rocket Pink	Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R:B 85:15, 70:30 More compact, stem caliper, chls	R:B 85:15: plant height	Randall and Lopez (2014)
	Liberty Classic Cherry	Supplemental HPS PPFD = 60–90 9-h (SD)+, 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDs with 7 R:FR ratios (from only R to only FR) and different PPE from 0.16 (FR light) to 0.89 (R light)	NI with an intermediate PPE: early flowering	SDs or NI with highest or lowest PPE: delay of flowering	Craig and Runkle (2016)
	Montego Yellow	Supplemental HPS or LEDs PPFD = 10 and 90 16 h Greenhouse	HPS_{10}, HPS_{90} or LEDs B:R 10:90, 45:55 B:G:R 10:5:85 B:G:R 12:20:68 + FR	HPS_{90}: early flowering, more inflorescences B:G:R 12:20:68 + FR: LA, early flowering, more inflorescences	HPS_{10}: shoot and root DW B:G:R 12:20:68 + FR: plant height	Poel and Runkle (2017)
Campanula portenschlagiana	BluOne	PPFD = 200 16 h Greenhouse	WL vs R:B 100:0, 80:20, 60:40	R:B 60:40: gs	R:B 60:40: leaf area	Ouzounis et al. (2014)
Catharanthus roseus L. G. Don	Titan Punch	Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R:B 85:15, 70:30 More compact, stem caliper, chls	R:B 85:15: plant height	Randall and Lopez (2014)
Celosia argentea L. var. plumosa L.	Fresh Look Gold			R:B 85:15, 70:30 More compact, stem caliper, chls	R:B 85:15: plant height	
Chrisantemum (*Dendranthema grandiflorum*)	Reagen	PPFD = 150 12 h Intensity of irradiation during the night: Low = 1.34 Medium = 3.34 High = 4.17 Growth chamber	INC, FL, B LED Irradiation during the night: low = 6 h INC, 4 h FL, 2 h LED Medium = 4 h INC, 2 h FL, 6 h LED Hight = 2 h INC, 6 h FL, 4 h LED FL (B:R = 1.15, B:FR = 11.97, R:FR 10.41) INC (B:R = 0.17, B:FR = 0.12, R:FR = 0.70) B LED	INC: stem and internode elongation Dark period: internode relative elongation rate (%/h)	B: stem growth, internode elongation rate Light period: internode relative elongation rate (%/h)	Zhiyu et al. (2007)

Table 3 (continued)

Flower and ornamental species		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Chrysanthemum × *morifolium* Ramat	Coral Charm	PPFD = 200 16 h Greenhouse	WL vs R:B 100:0, 80:20, 60:40	R:B 60:40: stomatal conductance R:B 80:20: leaf area, net assimilation	R:B 100:0: total biomass R:B 60:40: plant height	Ouzounis et al. (2014)
	Zembla	PPFD = 100 15 h Climate tents	LED light treatments: RB: 11 h R + B RB + B: 11 h RB + 4 h B LRB + B: 15 h RB + 4 h B RB + LB: 11 h RB + 13 h B	RB: NP, RB + LB: stem and internode length, RB and RB + B: fully developed flower buds, LRB + B, RB + B: number of internodes	RB: stem DW, RB and RB + B: leaf DW, LA	Jeong et al. (2014)
	Golden Cheryl	DLI = 11.5–13.3 mol m^{-2} day^{-1} Supplemental HPS = 60–90 9-h natural short-day photoperiod (SD) + 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDS W, B, B + R, B + FR, B + R + FR, R + FR	W, B + R + FR, R + FR NI: flower bud or inflorescence number, B + R + FR NI: stem length	W LEDs: inhibition of flowering, NI with B + R + FR, R + FR: delay flowering SD and B: stem length	Meng and Runkle (2015)
Cordyline australis	Red Star	PPFD = 100 16 h Growth chamber	8 weeks light treatment LEDs W, R100, B100, R:B 75:25	B100 and RB: Fv/Fm and ΦPSII, B100: gs	R100: biomass (both FW and DW), stomatal index	Zheng and Labeke (2017)
Cosmos sulfureus	Cosmic Yellow	DLI = 11.5–13.3 mol m^{-2} day^{-1} Supplemental HPS = 60–90 9-h natural short day photoperiod (SD) + 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDS W, B, B + R, B + FR, B + R + FR, R + FR	*C. sulfureus* W: bud and inflorescence, W, B + R, B + FR and R + FR NI: stem length	B: stem length	Meng and Runkle (2015)
Dahlia pinnata	Leanne, Gallery Pablo			*D. pinnata* B + R, B + R + FR, R + FR NI, for Leanne and B + R + FR, R + FR and INC NI for Gallery Pablo: stem length	SD and B for Leanne: stem length	
Dianthus chinensis	Super Parfait Raspberry			*D. chinensis* SD: day to flower, SD, INC, B: bud and inflorescence, B + R + FR, R + FR: stem length		

Table 3 (continued)

Flower and ornamental species		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Euphorbia pulcherrima Willd. ex Klotzsch	Christmas Spirit, Christmas Eve, Advent Red	PPFD = 100 10 h LEDs and EoD R LEDs Greenhouse and growth chamber	HPS vs LEDs R:B 80:20	HPS: shoot length	LED: plant height, LA, bract area, plants DW, chls HPS: stem extension	Islam et al. (2012)
Ficus Benjamina	Exotica	PPFD = 100 16 h Growth chamber	8 weeks light treatment LED: W, R100, B100, R:B 75:25	B100 and RB: Fv/Fm and ΦPSII, B100: leaf thickness, palisade parenchyma, gs	R100: biomass (both FW and DW), stomatal index and stomatal density	Zheng and Labeke (2017)
Fuchsia × *hybrida*	Trailing Swingtime	9-h (SD) + 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDs with 7 R:FR ratios (from only R to only FR) and different PPE from 0.16 (FR light) to 0.89 (R light)	NI: promoted flowering except for the highest PPE NI		Craig and Runkle (2012)
		Supplemental HPS PPFD = 60–90 9-h (SD) +, 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDs with 7 R:FR ratios (from only R to only FR) and different PPE from 0.16 (FR light) to 0.89 (R light)	NI with increasing PPE: flower bud or inflorescence	NI with increasing PPE: extension growth, flowering time	Craig and Runkle (2016)
Impatiens walleriana Hook f.	Dazzler Blue Pearl	Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R:B (85:15, 70:30): compactness, stem caliper, chls	R:B 85:15: plant height	Randall and Lopez (2014)
Kalanchoe pinnata (Lamarck) Persoon	RB292.697	PPFD = 100–400 + B = 4–12 + UV = 6–25 16 h Greenhouse	W, W + B, W + UV	B: antioxidant activity, changes in phenolic profile, polyphenols, antioxidants		Nascimento et al. (2013)
Orchids						
Cymbidium	Golden Bird	PPFD = 45 16 h Propagation chamber	FL vs Superbright B and R LEDs	R: leaf growth B: chls	R: chls B: leaf growth	Tanaka et al. (1998)

Table 3 (continued)

Flower and ornamental species		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Oncidium	Gower Ramsey	PPFD = 50 16 h Growth chamber	FL vs B, R, FR LEDs	FR + R, FR + B and FR + RFr: leaf expansion, number of leaves and root, chls, plant FW and DW		Chung et al. (2010)
		PPFD = 50 16 h In vitro Growth chamber	FL vs LEDs R:B: 90:10 (1BR) R:B: 80:20 (2BR) R:B: 70:30 (3BR) R:B:FR: 80:10:10 R:B:G: 80:10:10	R: induction, proliferation, carbohydrate in protocorm-like bodies (PLBs), plantlet length B: differentiation, proteins, enzyme activities and pigments in PLBs, plantlets development R + B: energy efficiency, DW, enzyme activities in plantlets		Mengxi et al. (2011)
Paphiopedilum		PPFD In vitro	CW vs 6 LED light treatments	CW: shoot FW, R:G:B 8:1:1: shoot DW B: root growth, root FW B and R: root DW CW and R:G:B 8:1:1: yield value, Fv/Fm	B: leaf length and width	Lee et al. (2011)
Pelargonium × *hortorum* L.H. Bailey	Bullseye Scarlet	Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R85:B15 and R70:B30: compactness, stem caliper, chls	R:B 85:15: plant height	Randall and Lopez (2014)
	Black Velvet	DLI = 9–11 mol m^{-2} day^{-1} Day extension with HPS: PPFD = 70 or LED: PPFD = 100 16 h Greenhouse	End-of-production (EoP) of 3–14 days supplemental lighting PPFD = 100 LED B:R = 100:0, 13:87, 50:50, 13:87	DLI 9 mol m^{-2} day^{-1} and HPS and LEDs (PPFD = 100) 14 days of EOP: chls (both species)		Owen and Lopez (2017)
	Pinto Premium Salmon	Supplemental HPS or LEDs PPFD = 10 and 90 16 h Greenhouse	HPS_{10}, HPS_{90} or LEDs B:R 10:90, 45:55, B:G:R 10:5:85, 12:20:68 + FR	HPS_{90}, B:G:R 12:20:68 + FR: early flowering, more inflorescence	HPS_{10}: shoot DW	Poel and Runkle 2017)

Table 3 (continued)

Flower and ornamental species		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Pennisetum setaceum Forsk. Chiov.	Rubrum	DLI = 9–11 mol m^{-2} day^{-1} Day extension lighting from HPS: PPFD = 70, or LED: PPFD = 100 16 h Greenhouse	End-of-production (EoP) of 3–14 days supplemental lighting PPFD = 100 LED B:R = 100:0, 13:87, 50:50, 13:87	DLI 9 mol m^{-2} day^{-1} and HPS and LEDs (PPFD = 100) 14 days of EOP: chls (both species)		Owen and Lopez (2017)
Petunia × *hybrida* Vilm	Shock Wave Ivory, Easy Wave White, Wave Purple Improved	9-h (SD) + 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDs with 7 R:FR ratios (from only R to only FR) and different PPE from 0.16 (FR light) to 0.89 (R light)	INC NI (R:FR = 0.59) + LED R:FR of 0.28–1.07: flowering Moderate R:FR: plant height		Craig and Runkle (2012)
	Plush Blue	Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R:B (70:30): leaf dry mass, root dry mass, root mass ratio and root:shoot ratio, R:B (85:15): quality index (QI)	R:B (85:15): plant height	Randall and Lopez (2014)
	Shock Wave Ivory, Easy Wave White, Wave Purple Improved	Supplemental HPS PPFD = 60–90 9-h (SD)+, 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDs with 7 R:FR ratios (from only R to only FR) and different PPE from 0.16 (FR light) to 0.89 (R light)	PPE = 0.46–0.72: promoted flowering PPE = 0.63 or 0.64: extension growth in Easy Wave White	NI with a PPE = 0.16: delayed flowering, flowering percentage NI with a PPE = 0.64: lateral branches in Shock Wave Ivory SD: delayed flowering in Easy Wave White	Craig and Runkle (2016)
	Baccarat Blue	PPFD = 70 or 150 16 h Growth chamber	W LEDs vs R and B LEDs	B: shoot elongation, gibberellins (GA1, GA4), early flowering High R and temporal switching to B: floral development	R: shoot elongation, lower levels of gibberellins (GA1, GA4), RB: shoot elongation	Fukuda et al. (2016)
	Single Dreams White	Supplemental HPS or LEDs PPFD = 10 and 90 16 h Greenhouse	HPS_{10}, HPS_{90} or LEDs B:R 10:90, 45:55, B:G:R 10:5:85, 12:20:68 + FR	HPS_{90}, B:G:R 12:20:68 + FR: early flowering, more inflorescence	HPS_{10}: shoot and root DW	Poel and Runkle (2017)

Table 3 (continued)

Flower and ornamental species		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Rosa hybrida L.	Toril	PPFD = NL + 100 20 h Greenhouse and growth chamber	HPS B5% vs LED R:B: 80:20	HPS: LA, plant height, leaf DW LEDs: sun-type leaf anatomy, thorns, better storability and delayed senescence, higher water content of leaves, photosynthetic capacity, SLDW, gs, chls, anthocyanin, soluble carbohydrates	LEDs: stem and pedicle length	Terfa et al. (2012a, b)
	Scarlet	PPFD = 200 16 h Greenhouse	WL vs R:B 100:0, 80:20, 60:40	R:B (60:40): stomatal conductance R:B (80:20): leaf area	R100: morphological abnormality, R:B 60:40: plant height	Ouzounis et al. (2014)
Rudbeckia hirta	Indian Summer	DLI = 11.5–13.3 mol m^{-2} day^{-1} Supplemental HPS = 60–90 9-h natural short day photoperiod (SD) + 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDS W, B, B + R, B + FR, B + R + FR, R + FR	NI lighting + R light: promotion of flowering B + R + FR: stem length	SD, B, B + FR: no flowering	Meng and Runkle (2015)
	Denver Daisy	Supplemental HPS PPFD = 60–90 9-h (SD)+, 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDs with 7 R:FR ratios (from only R to only FR) and different PPE from 0.16 (FR light) to 0.89 (R light)	All NI treatments (vs FR-only NI): time to flowering, bud and inflorescence number, plant height at flowering	FR-only NI, SDs: no flowering	Craig and Runkle (2016)
Salvia splendens F. Sello ex Ruem & Schult	Vista Red	PPFD = 70 16 h Growth chamber	FL vs FL + R, FL + B, FL + FR, R, B	FL + B, FL + R, FL + FR: DW FL + FR: stem length	R: stem length	Heo et al. (2002)
		Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R:B 70:30: quality index (QI)	R:B 85:15: plant height	Randall and Lopez (2014)
Sinningia speciosa	Sonata Red	PPFD = 100 16 h Growth chamber	LED 8 weeks light treatment W, R100, B100, R:B 75:25	B100 and RB: Fv/Fm and ΦPSII, palisade parenchyma B100: gs, stomatal index, stomatal density	R100: biomass (both FW and DW)	Zheng and Labeke (2017)

Table 3 (continued)

Flower and ornamental species		Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; day length) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
Species	Cultivar			Increase	Decrease	
Stevia rebaudiana (Bertoni)	–	PPFD = 50–400 8–24 h Growth chamber	FL and R, FR LEDs NI = FL (PPFD = 20, 50) R and FR (PPFD = 20) EOD FR (5, 15 min–50) EOD R (15 min–50)	NI and 8 h photoperiod: leaf biomass, steviol glycosides (SGs), EoD FR (15 min PPFD = 50): leaf biomass		Yoneda et al. (2017)
Tagetes erecta L.	Orange Boy	PPFD = 70 16 h Growth chamber	FL vs FL + R, FL + B, FL + FR, R, B	R, FL + R and FL: DW FL + R: number flower buds B: stem length	B: DW	Heo et al. (2002)
	American Antigua Yellow	9-h (SD) + 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDs with 7 R:FR ratios (from only R to only FR) and different PPE from 0.16 (FR light) to 0.89 (R light)	Moderate R:FR: plant height	R:FR ≥ 0.66 inhibited flowering	Craig and Runkle (2012)
	American Antigua Yellow	DLI = 11.5–13.3 mol m^{-2} day^{-1} Supplemental HPS = 60–90 9-h natural short day photoperiod (SD) + 4-h night interruption (NI) Greenhouse	SD vs SD + NI with INC or LEDS W, B, B + R, B + FR, B + R + FR, R + FR	INC, W, B + R + FR, R + FR: flower bud or inflorescence, leaf number, R + FR: stem length	W, B + FR NI: inhibition of flowering B + R + FR, R + FR NI: delay flowering SD and B: stem length	Meng and Runkle (2015)
Tagetes patula L.	Bonanza Flame	Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R:B (85:15, 70:30): compactness, larger stem caliper, chls	R:B 85:15: plant height	Randall and Lopez (2014)
Viola × *wittrockiana* Gams	Mammoth Big Red	Supplemental HPS or LEDs PPFD = 100 16 h Greenhouse	NL + HPS vs NL + R:B LED 100:0, 85:15, 70:30	R:B 100:0: quality index (QI)	R:B 85:15: plant height	

revealed longer harvest period, and higher number of nodes and fruits and total fresh weight when 95% R + 5% B LEDs were used for intracanopy lighting, compared to natural light (Gómez et al. 2013; Table 2). Similarly, natural light supplemented with LED white light enhanced a number of leaf characteristics in strawberry, including leaf photosynthetic rates, leaf dry mass, area and specific weight; moreover, average fruit weight and number and soluble solids content were also favoured by supplemental light (Hidaka et al. 2013; Table 2).

Many results demonstrated that light quantity and quality interact in determining plant photomorphogenesis. In cucumber grown in greenhouse with or without light integration with LEDs, at variable R:B ratios and two daily light integrals, growth parameters always improved under LED additional light (Hernández and Kubota 2014; Table 2). In particular, no differences were found in plant response to the R:B ratios at high light intensity, while increasing values of leaf Chl content and reduction of leaf dry matter accumulation occurred at increasing doses of B at low intensity (Table 2), suggesting that light recipe in terms of spectral composition has to be determined considering the intensity applied. In mini-cucumber, combinations of FR, R and B by top and bottom vertical LEDs resulted in more than 10% increase in fruit yield; moreover, plasma light supplemented with vertical B light from the top of the canopy reduced plant growth and fruit yield in the first month, while FR from the top of the canopy increased fruit yield compared to that from the bottom (Guo et al. 2016; Table 2). In addition to intracanopy lighting, Song et al. (2016) tested the impact of different light qualities when applied underneath the plant canopy and found that lighting from both directions positively affected the photosynthetic process, especially under WRB and WB (compared to RB and WRFR) (Table 2). The authors also reported different mechanisms of photosynthesis improvement, with intracanopy lighting increasing stomatal conductance, CO_2 supply and electron transport activity, while underneath lighting increasing CO_2 assimilation efficiency and excess energy dissipation leading to higher photosynthetic rate.

Cucumber cultivated under LEDs (14% B, 16% G, 53% R, 17% FR) top lighting or intracanopy lighting showed greater light use efficiency, leaf expansion and stem growth, but decreased number of fruits, with higher fruit abortion rate, and lower flower initiation rate and yield compared to HPS-HPS and HPS-LEDs top lighting—intracanopy lighting combinations (Särkkä et al. 2017; Table 2).

Several studies report inter- and intra-specific differences with respect to the response to the R:B ratio. The absolute B light intensity rather than the percentage of B was reported to control hypocotyl length and stem extension in tomato (Nanya et al. 2012). Son and Oh (2013) found a decrease in growth rate in lettuce cultivars with the increase in B and UV-A light, while Wang et al. (2016) reported that leaf photosynthetic capacity and photosynthetic rate increased with decreasing R:B ratio, along with promoted shoot dry weight (Table 1). In sweet basil and strawberry, the R:B ratio of 0.7 was found to be optimal based on a range of analyses (morphological, physiological and biochemical elements), among 5 LEDs ratios (0.7, 1.2, 1.5, 5.5) and compared to white fluorescent light as a control (Piovene et al. 2015; Tables 1 and 2), whereas previously Folta and Childers (2008) had observed the greatest growth rate of strawberry plants under 34% B–66% R, among 4 different B:R ratios (100–0, 66–34, 34–66, 0–100%). In greenhouse production, Kaiser et al. (2019) supplied tomato with different R:B ratios (0, 6, 12 and 24%) in integration to sunlight, which resulted in an increase in total biomass and fruit number until the optimum of 12% (Table 2). Naznin et al. (2019) investigated the effect of R:B ratio in lettuce, spinach, kale, basil and pepper, and concluded that additional B is essential to promote growth, pigmentation and antioxidant content of these vegetables, although the optimal ratio is species dependent (Tables 1 and 2).

It has been hypothesized that B requirement can vary with plant age, in accordance with the hypothesis that it responds to the plant need to balance leaf expansion, to maximise light interception (which is higher in young plants), while preventing excessive stem elongation (Cope and Bugbee 2013). This hypothesis agrees with the evidence that leaf optical properties (absorbance, transmittance and reflectance) depend on leaf ontogenesis (age and position in the canopy), that influences anatomical and functional parameters involved in light absorption, such as pigment composition (Paradiso et al. 2011a, b; Izzo et al. 2019).

In terms of nutritional quality, application of B light promoted antocyanin and carotenoid accumulation in lettuce (Stutte et al. 2009; Li and Kubota 2009) and of ascorbic acid in lettuce and Japanese green mustard (komatsuna), while these effects did not occur in spinach (Ohashi-Kaneko et al. 2007; Table 1). Irradiation with B increased the concentration of glucosinolates (beneficial active compounds in Brassicaceae) in cauliflower and of chlorogenic acid (antioxidant polyphenol) in basil and tomato, while reducing dangerous metabolites, such as oxalates and nitrates (Ohashi-Kaneko et al. 2007; Taulavuori et al. 2013) (Tables 1 and 2). Also, light intensity influenced the biosynthesis of secondary metabolites, with increasing light intensity resulting in decrease of amounts of nitrate and oxalate, and increase of ascorbate (Proietti et al. 2004), as well as an increase in polyphenols production in herbs (Manukyan 2013).

Fan et al. (2013) reported various responses of non-heading Chinese cabbage under the influence of monochromatic and dichromatic LEDs (Table 1). Particularly, R light increased plant height but induced negative effects on chlorophyll and carotenoid concentration, Y light reduced

dry mass production, as well as soluble sugar and protein concentration, G light decreased chl *a*/*b* ratio, while B and RB light decreased plant height but promoted the concentration of soluble proteins, chlorophylls and carotenoids.

Blue and UV wavelengths are known to be effective in promoting bioactive compounds accumulation in plant tissues by upregulating the expression of synthesis pathways genes (Hasan et al. 2017). Bian et al. (2015) highlighted the promoting effects of B, UV-A and UV-B on the synthesis of phenolic compounds in general and anthocyanins in particular, and of B, R and UV-B on carotenoids, in several vegetables. This is in accordance with focused experience demonstrating that improved accumulation of phenolics can be achieved through discontinuous application of UV-B radiation, without affecting the efficiency of photosynthetic apparatus (Mosadegh et al. 2018). Blue light, via the cryptochromes and phototropins, was proved to drive the synthesis of chlorophylls and anthocyanins in strawberry (Kadomura-Ishikawa et al. 2013) and of total phenolics and flavonoids in lettuce (Zhang et al. 2018).

In two basil cultivars grown under LED continuous spectra, Bantis et al. (2016) reported that the most B and UV (1%) containing light decreased the shoot/root ratio and increased total phenolic content, while low R:FR ratio (highest in R and FR, and high in B, R) had a positive effect on plant height and enhanced the total biomass production compared to FL (Table 1).

In nine tomato genotypes, B supplemented to R light had positive effect on plant biomass, attenuated upward or downward leaf curling due to R only and led to increased soluble protein, chlorophyll and carotenoid concentration (Ouzounis et al. 2016; Table 2).

No significant effect in carotenoid concentration of lettuce was found under B and R LEDs or under HPS lamps supplementing compared to sunlight (Martineau et al. 2012). However, Ouzounis et al. (2015a, b) reported higher pigment (chlorophylls and carotenoids) and phenolic (phenolic acids and flavonoids) content in green and red leaf lettuce under natural light supplemented with B LEDs compared to natural light with HPS; further, they recorded increased stomatal conductance and non-photochemical quenching (NPQ) in green lettuce, while quantum yield of PSII decreased in red lettuce under supplemented B light (Table 1).

In potato grown in phytotron under controlled environment, Paradiso et al. (2019) compared two cultivars and two light sources, white fluorescent tubes (WF) and R and B LEDs at 8:1 ratio (RB) (Table 2). Tuber yield was higher under RB in both the cultivars. Light quality did not influence the tuber content of starch and total glycoalkaloids, while it affected differently in the cultivars the protein content and the profile of glycoalkaloids (anti-nutritional factors in potato).

Blue component has been recognized at the basis of morphological alteration in several species. In bean, intumescence and oedema in elder leaves were observed at B doses lower than 10% of total radiation, while in pepper oedema on leaves and flower buds in plants grown under R + B LEDs were not reduced by increasing B intensity (Massa et al. 2008). On the contrary, tomato plants under similar R–B combinations showed a normal leaf development, indicating that, within the same botanical family, plant sensitivity to spectral-dependent disorders vary among the species (Massa et al. 2008). High B proportion combined with small dose of end-of-day (EOD) FR can suppress intumescence injury in tomato (Eguchi et al. 2016). In tomato grown in a climatic chamber at PPFD of 200 µmol m^{-2} s^{-1}, R:B (2:1 ratio) induced a significant increase of leaf net photosynthesis and a significant decrease of leaf lamina thickness compared to WF light (Arena 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 height under LED (20% B:80% R) intracanopy lighting compared with HPS, both applied to supplement the natural light.

The influence of R or B LED light was investigated also as a short-term treatment before harvest, in different vegetables (as example: Wanlai et al. 2013; Kwack et al. 2015; Samuolienė et al. 2017; Kitazaki et al. 2018), as well as in aromatic herbs (as example: Amaki et al. 2011) and microgreens (reviewed by Alrifai et al. 2019). In these latter, recent researches on variation in productivity, nutritive and functional quality (mineral–carotenoid–polyphenolic profiles and antioxidant capacity) in novel microgreens (amaranth, cress, mizuna, purslane) in response to select spectral bandwidths (red, blue, blue-red) highlighted that optimized genetic background combined with effective light management might facilitate the production of superior functional microgreens (Kyriacou et al. 2019).

Flower and Ornamental Crops

In ornamental species, plant shape represents a relevant aspect of ornamental quality hence of commercial value, and plant size is one of the most important features. Blue light is known to inhibit stem elongation in many species, however this response is species dependent, as plant morphological responses to B light, as well as to R:FR ratio, are associated with differences in the relative contributions of blue-sensitive photoreceptors (cryptochromes and phototropins) and phytochromes.

Several experiments were carried out in the first years of testing in the in vitro propagation of orchid species (Table 3). In *Cymbidium* lighted with B and R LEDs in growth chamber, B light reduced the leaf growth while increased the chlorophyll content, compared with WF lamps, while the reverse

effect was observed under R light (Tanaka et al. 1998). In *Oncidium*, B, R and FR LEDs in growth chamber increased leaf number and expansion, chlorophyll content and fresh and dry weight compared with WF lamps (Chung et al. 2010). In the same species, increasing B (10–30%) over R LED light in growth chambers increased the dry weight and protein accumulation compared with WF lamps (Mengxi et al. 2011). In *Paphiopedilum*, B LED light in growth chamber determined more compact plants, and lower leaf length and width compared with CWF light (Lee et al. 2011).

In marigold and salvia seedlings, Heo et al. (2002) investigated the effects of monochromatic B or R LEDs or mixed radiation from a WF light with B, R and FR LEDs compared with WF only (Table 3). Dry weight in marigold increased under R, WF + R or WF and decreased under B, whereas in salvia it was greater under WF + B, WF + R and WF + FR. Stem length was three times greater in B than in FLR or FL in marigold and increased in WF + FR while decreased in R in salvia. The number of flowers in marigold was much higher in WF + R and WF control (five times greater than in B or R), while in salvia it varied slightly in the treatments. Light quality also influenced the duration of the blooming period in both the species. No flower buds were formed under monochromic B or R in salvia and WF + FR inhibited flower formation in marigold.

In roses, B (20%) and R (80%) LED lighting in growth chamber increased the dry weight proportion allocated to the leaves, but decreased plant leaf area, plant height and shoot biomass, without affecting flowering compared to HPS lamps (Terfa et al. 2012a, b; Table 3).

In poinsettia, 80%B + 20%R LED light reduced the plant height and the area of leaves and bracts and the leaf chlorophyll content compared to HPS (5% B), even though with no influence on flowering time and postproduction duration, in both growth chamber and greenhouse (Islam et al. 2012; Table 3). Similarly, in seed annual species crops (*Antirrhinum*, *Catharanthus*, *Celosia*, *Impatiens*, *Pelargonium*, *Petunia*, *Tagetes*, *Salvia* and *Viola*) grown under solar light supplemented with HPS light, increasing doses of B from LEDs (from 0 to 30% of 100 µmol m^{-2} s^{-1} total PPF) reduced the plant height compared to R in several species, and in most of them R + B determined similar or better global quality than HPS (Randall and Lopez 2014; Table 3). Increasing proportion of B (from 20 to 100%, with R varying from 80 to 0%) reduced plant height also in rose and chrysanthemum, while it did not affect it in campanula, compared to R and W light; accordingly, different responses among the species were found in plant biomass accumulation (Ouzounis et al. 2014; Table 3). Beside the morphological effects, higher B radiation increased the stomatal conductance, without affecting the rate of photosynthesis, indicating an excessive stomatal opening compared to the leaf photosynthetic capacity; on the other hand, high B doses promoted flavonoids and phenolic acids biosynthesis, confirming the contribution of B in improving plant response to stress conditions (Ouzounis et al. 2014).

The influence of B radiation was also studied in photoperiodic control of flowering in chrysanthemum, by comparing 4 LED treatments, with increasing duration of light period: RB (11 h R + B), RB + B (11 h RB + 4 h B), LRB + B (15 h RB + 4 h B) and RB + LB (11 h RB e 13 h B), in growth chamber (Jeong et al. 2014; Table 3). Stem length increased through RB, RB + B, LRB + B and RB + LB treatments, and flowering occurred only under short light duration with RB e RB + B, in accordance with the short day (SD) requirement of the species. As a consequence, in chrysanthemum B light can be used to promote stem elongation with no inhibition of flowering even when it is applied in a 15 h photoperiod.

Fukuda et al. (2016) investigated the influence of light spectrum on growth and flowering and hormones implied in flowering in petunia (a quantitative long-day plant, LD), comparing R, B and white (W) LEDs at low (L) and high (H) intensity (Table 3). Conversely to what expected, R light drastically inhibited shoot elongation, with a parallel reduction of giberellin content, while B-promoted stem growth and giberellin synthesis. Compared to W and B (H and L), R-H light anticipated flowering, which was prevented in R-L, where it was restored by night interruption with B but not by GA application. The Authors concluded that in petunia B and R light represent signals for stem lengthening promotion or inhibition respectively, by means of modulation of GA biosynthesis, and while B is a strong signal for flower initiation, the effect of R depends on the light irradiance, suggesting the existence of a photosynthesis-dependent pathway of flowering in this species.

Several studies demonstrated that the response to monochromatic B light strictly depends on plant genotype. Indeed, whereas certain reports founded that monochromatic B induced the greatest biomass accumulation compared to wider spectra in some species (like balloon flower, *Platycodon grandiflorum*; Liu et al. 2014), some described inhibited photosynthesis and biomass accumulation under R–B or broader spectra in others (like lettuce; Wang et al. 2016; Table 1).

Also in ornamental species, some experiments studied the effects of light-quality treatments on secondary metabolism, together with the morphological response. In *Dieffenbachia* and *Ficus* grown in greenhouse, supplemental B plus R LEDs increased the plant height, but no apparent effect on sugar, chlorophyll and carotenoid content was observed (Heo et al. 2010). In *chrysanthemum*, Jeong et al. (2012) characterized 9 polyphenols and highlighted a promoting effects of R and G light on polyphenol biosynthesis (Table 3). In *Kalanchoe*, supplemental LED B light decreased leaf fresh weight and increased flavonoid content and antioxidant

activity compared with WF lamps (Nascimento et al. 2013; Table 3).

In some pot foliage plants (e.g. *Guzmania lingulata*), in which the leaf colour and variegation are the main quality parameters, additional R and B LED light can be applied for a limited period at the end of the growing cycle to promote the synthesis of anthocyanins and carotenoids, while improving the leaf pigmentation and plant attractiveness, particularly in northern areas where light intensity might be a limiting factor (De Keyser et al. 2019).

As in vegetables, in some ornamentals monochromatic light has been reported to cause leaf curling in many works (Oda et al. 2012; Hughes 2013; De Keyser et al. 2019). For instance, in rose the exposure to only R light determines leaf downwards curling, while B light addition restores the normal morphology (Ouzounis et al. 2014; Table 3). Light spectrum- induced modifications of leaf anatomy, such as those in leaf thickness, have been proved to depend on changes in leaf anatomy, and particularly in palisade parenchyma (Zheng and Van Labeke 2017; Table 3).

Far Red Light and Red:Far Red Ratio

Vegetable Crops

In greenhouse vegetables, essential components of marketable value are biomass accumulation and product quality, in terms of both aesthetical aspect and nutritional value. In early experiments, pepper lighted with R, R + BF and R + FR LEDs compared to MH lamps, FR addition (corresponding to a decrease of R:FR ratio) resulted in taller plants with greater stem mass than R alone, prefiguring the importance of FR and FR proportion in photomorphogenetic responses (Brown et al. 1995) (Table 1). Schuerger et al. (1997) examined structural changes in pepper leaves under R LEDs combined with FR LEDs (FR, 735 nm) or BF lamps (1%B), compared to MH (20%B) (PPFD 330 µmol m^{-2} s^{-1}, photoperiod 12 h). Results showed that leaf anatomy depended more by B level than by R:FR ratio, and the increase of B increased the cross section and the number of chloroplasts, with a consequent increase of photosynthetic activity and biomass accumulation.

Positive effects on plant productivity of photomorphogenetic response promoting biomass accumulation were found in lettuce grown in growth chamber under WF with or without LED light addition: the addition of R did not influence the dry matter accumulation compared to WF, conversely a significant increase was observed under FR, which increased the plant leaf area (Li and Kubota 2009; Table 1).

In tomato and cucumber grown in greenhouse, the comparison among three lighting treatments in addition to natural light, HPS, B:R LEDs and B:R:FR LED at different percentage, showed that B:R determined more compact plants, with no difference in biomass accumulation compared to HPS, while in B:R:FR the reduction in plant size was related to an increase in fruit weight (+ 15% and + 21%, respectively) (Hogewoning et al. 2012; Table 2). These results depended on the effect of FR on leaf orientation, which improved light interception even without difference in leaf area and photosynthetic rate. In accordance, it has been demonstrated in tomato that the FR amount (also given in brief treatments at the end of day) influenced the stem architecture (i.e. length of internodes and leaf insertion angle) with consequent reduction of leaves self-shading, which has a relevant impact on light penetration and light use efficiency (Sarlikioti et al. 2011). Later, other experiments on cucumber highlighted that the addition of LED R light as interlighting to assimilation HPS light and natural light, in order to raise the R:FR ratio, did not increase fruit yield while promoted Chl synthesis, with consequent increase in fruit colour and improvement of visual appearance (Hao et al. 2016; Table 2).

The above described results highlighted that it can happen that the addition of R light does not influence directly the biomass accumulation, while it is efficient in exerting photomorphogenetic responses when applied in combination with FR doses able to modify the R:FR ratio. R light alone, however, can be efficient in improving the nutritional value of several vegetable products, by promoting the antioxidant production (Olle and Viršile 2013), such as phenols in lettuce (till + 6%; Li and Kubota 2009). Conversely, the addition of FR to R can reduce the antioxidant synthesis in some species: for instance, in lettuce an increase in plant biomass was associated to a lower anthocyanin content (Li and Kubota 2009; Table 1). Conversely, in tomato increasing FR LED light, added to natural light supplemented with HPS, positively affected the stem length and fruit yield in the first month of the trial, as well as carotenoid content during the whole experiment (Hao et al. 2016).

In ornamental plants, one of the most striking effect of light composition on plant architecture is the shade avoidance syndrome, occurring in high density canopies in low R:FR conditions, implying increased internode and petiole elongation, inhibited axillary bud outgrowth and leaves hyponasty. In pot and garden chrysanthemum, R LED light increased bud outgrowth while B + FR decreased it and reduced plant height, even though the effect was genotype dependent (Dierck et al. 2017). Treatment with B + FR in 25 decapitated cuttings determined a strong elongation of the top-most axillary bud and inhibition of underlying buds in pot and cut flower genotypes. This effect also persisted in greenhouse conditions.

Flower and Ornamental Crops

Commercial quality in flowering potted plants strictly depends on flowering characteristics in terms of earliness, duration and intensity (number of flower buds) and on foliage density. These features are usually controlled through genotypes selection, irrigation strategies (e.g. moderate drought stress), temperature control (day–night differential temperature) and growth regulators.

Under natural light conditions, the reduction of R:FR ratio, determined by the increase of canopy density during plant growth, causes some undesired responses (excessive stem elongation, inhibition of buds development), which are usually prevented by the reduction of plant density, the application of chemicals and, more recently, the use of FR filtering films in greenhouse. However, in some crops these strategies could be integrated or replaced by using LEDs, while limiting or avoiding chemicals, if plant response to monochromatic light addition would be known.

In a growth chamber lighted with fluorescent tubes, the plant height was not influenced by the addition of R light (FL + R) and it was increased by the addition of B or FR light (FL + B and FL + FR) in *Tagetes erecta*, while it increased under all the lighting treatments in *Salvia splendens*, compared to FL, with a parallel reduction in the number of flowers in presence of B and FR only in *Tagetes* (Heo et al. 2002; Table 3).

The importance of the phytochrome photoequilibria (PPE) value induced at plant level by R and FR light in the regulation of the flowering process of long-day (LD) plants has been recently investigated, thanks to the diffusion of LEDs. Photoperiodic light quality affects flowering of LD plants, by influencing the PPE at plant level, however the most effective light spectrum to promote flowering is still unknown for most the flower crops. In photoperiodic species, the addition of FR to R to extend the duration of day or to interrupt the night was proved to be useful to control flowering in LD plants. In fact, it is known that incandescent lamps (Inc) determine an intermediate PPE (0.68), resulting sometimes more efficient of light source with higher R:FR ratio (e.g. fluorescent lamps) which create at plant level a higher PPE. In this respect, the use of combined LEDs (R:FR > 0.66, PPE > 0.63) was useful to replace Inc lamps (R:FR = 0.59), widely used in the past with photoperiodic purpose and now forbidden by law in many countries, with significant advance in flowering of petunia, snapdragon and fuchsia, even though with effects on stem elongation variable among the plant species (Craig and Runkle 2012; Table 3).

Also in chrysanthemum (short day, SD species), in which flowering is inhibited with night break (NB) with R or B light, the reversibility of this effect by successive exposure to FR flashes indicated the involvement of phytochrome and, more specifically, of two different phytochrome-mediated mechanisms, and that the quality of the light provided during the day influences the quality of the light required for an efficient NB (Higuchi et al. 2012). In particular, flowering occurred only under SD conditions, with white or R or B light monochromatic light (W-SD, R-SD and B-SD), however in W-SD, NB with R was more efficient in inhibiting flowering compared to B and FR, on the contrary in B-SD the stronger inhibition was by NB-B and FR. Finally, when B-SD was supplemented by monochromatic R light (B + R-SD), NB-B and NB-FR were not efficient.

In two chrysanthemum cultivars grown under short day photoperiod, treated with night break, shoot elongation was enhanced under treatments that emitted FR compared to short day treatment and R containing LED light with no FR (Liao et al. 2014).

Meng and Runkle (2014) compared INC, HPS and CFL lamps with R + FR + W LEDs for night interruption (NI) to extend day length on seven long-day ornamentals, in a commercial greenhouse, and found that in most species LED, INC and HPS lamps were equally effective in controlling flowering. The same authors investigated whether low intensity B ($\approx$ 1.5 µmol m^{-2} s^{-1}), added to R and/or FR light in NI, influences flowering in five SDPs (chrysanthemum, cosmos, two cultivars of dahlia and marigold) and two LDPs (*dianthus* and *rudbeckia*), grown in greenhouse under SD (Meng and Runkle 2015; Table 3). Blue light alone was not perceived as a LD by all the SDPs and LDPs tested. For all SDPs, W LEDs inhibited flowering most effectively and B + R was as effective as W for all species except chrysanthemum. B + FR inhibited flowering of marigold and one dahlia cultivar, but not chrysanthemum and the other dahlia, while was less effective than treatments with R light in marigold. B + R + FR and R + FR similarly delayed flowering of all SDPs, except one dahlia. NI treatments containing R promoted flowering of LD rudbeckia. The authors concluded that in these crops a low intensity B during the night does not influence flowering, and that W LEDs that emit little FR light are effective at creating LD for SDPs and in some LDPs. R light alone can inhibit flowering of SDPs, whereas combinations of R and FR promote flowering of some LDPs.

Whole-plant net assimilation was increased in geranium, snapdragon and impatiens with additional FR radiation, while FR promoted flowering of the LD snapdragon (Park and Runkle 2017).

In *Phalaenopsis*, the possibility to replace the reduction of temperature (8 weeks at 19 °C) respect to vegetative phase (22 °C) to promote flower induction by means of light stimuli was evaluated by applying lighting treatments with a high R:FR (estimated PPE 0.85) or a low R:FR (PPE 0.71) (Dueck et al. 2016). Results showed that, even though thermal control determined the highest percentage of multiple inflorescences (regardless of light spectrum), similar results were obtained by the exposure for 8 weeks to R and

by cooling for 4 weeks followed by high PPE light (regardless of temperature). These results suggested that hormones responsible for flowering in *Phalaenopsis* are stimulated by a high PPE during the induction period, and temperature and/or light spectrum in the second part of the treatment are more important to obtain multiple inflorescences, probably through the apical dominance suppression. This prefigures the possibility to integrate with LED lighting the inductive thermal treatment, which is energetically more expensive in the summer.

Photoperiodic lighting with R and FR proportion creating an intermediate PPE (0.63–0.80) has been proved to be more effective to promote flowering in some LD species (*Antirrhinum majus*, *Fuchsia*×*hybrida*, *Petunia*×*hybrida*, *Rudbeckia hirta*) compared to a R and FR lighting creating an high PPE (above 0.80) (Craig and Runkle 2016) (Table 3). However, light requirement in terms of intensity and quality vary among the species and are not known for many crops. Recent experiments on photoperiodic lighting in LD plants showed hybrid-specific responses to both day length and light quality, highlighting that genotype sensitivity to light duration and spectrum should be taken into account to optimize lighting protocols in commercial farms. For instance in *Ranunculus asiaticus* L., Modarelli et al. (2020) tested three light sources, with different PPEs induced at plant level, compared to natural light. Results showed differences between the hybrids in plant growth and flowering and also in sensitivity to photoperiodic lighting: this improved plant growth and reduced the flowering time in only one hybrid, with a stronger effect under R:FR 3:1 light (estimated PPE 0.84). In both the hybrids, the increase of FR increased the plant leaf area and elongated the flower stems.

Green Light

Vegetable Crops

Green light is a significant portion of solar radiation. It is known that plant leaves appear in green because they reflect the wavelengths producing this colour, hence G has always been considered little useful for plants, in accordance with the limited absorption capacity of leaf pigments. However, as mentioned, many of the early works with LEDs pointed out that plant growth was better under W light or when G was added to B and R, suggesting a contribution of this minor wavelength. Moreover, sometimes plants under only R and B light showed abnormal colouring, which also made difficult the diagnosis of possible disorders, and recent data indicate that it modulates light-induced plant responses. Indeed, G interacts with FR light in determining some phytochrome responses (Tanada 1997), in a complex way that has not been fully clarified to date (Folta and Maruhnich 2007; Wang and Folta 2013). The coaction of G and other wavebands provides a strategy for plants to precisely tune its morphology to adapt to changing light environment: for instance, G light affects plant biomass and reverses UV-B and B- light-mediated stomatal opening (Wang and Folta 2013). Nowadays, it is known that G light penetrates deeper into the plant canopy because of its high transmittance and reflectance, and may potentially increase light interception and whole-canopy photosynthesis, being R and FR absorbed primarily by upper leaves. Moreover, it induces shade avoidance responses and regulates secondary metabolism in plants.

Among the earliest experiments, to evaluate the influence of G light, Kim et al. (2005) cultivated lettuce under R and B LEDs (RB), with or without the addition of G (6 µmol m^{-2} s^{-1}), at equal values of PPFD (136 µmol m^{-2} s^{-1}). Results did not showed differences in plant growth, however the exposure to higher G levels (RGB, 24% G), CWF (51% G) and green fluorescent light (GF, 86% G) compared to RB determined the highest dry matter accumulation in RGB, despite the lower stomatal conductance compared to CWF and the lowest growth under GF. The authors concluded that the addition of G improved the plant growth until 24% of the total light amount (also in other species), while it reduced it over 50%.

The first studies did not provide clear information about how much the influence of G on plant growth depended on a contribution to plant assimilation or on photomorphogenetic responses. Only later, G light was recognized as able to influence plant morphology by means of effects on leaf expansion, stomatal conductance and stem elongation, through a dual mechanism cryptochrome dependent and cryptochrome independent: nowadays, it is known that the mechanism of G perception fine tunes small adjustments in plant growth and development in concert with that induced by R and B light (Folta and Maruhnich 2007).

Terashima et al. (2009) demonstrated that the addition of high-intensity G to white light improved photosynthesis in sunflower and hypothesized that the contribution of G had been underestimated until then because of the too low levels applied in the experiments. The authors reported that, while R and B are mainly absorbed at the adaxial leaf side, G penetrates in the mesophyll and is absorbed in deeper leaf layers. In this respect, considering that G is able to penetrate deeper and in greater amount in the canopy, the transmitted G light assumed a relevant role in photosynthesis in lower and inner leaves, even though less efficient in terms of quantum yield than R and B. In these parts of the canopy, exposed to an altered light microclimate compared to the upper and outer layers (lower light intensity, depleted in R and B and enriched in G and FR), green wavelengths play a key role in plant assimilation. This also occurs in

etiolated plants, with scarce chlorophyll content, during the first phases of emergence.

In lettuce, Johkan et al. (2012) confirmed that G light determined a substantial contribution at high light intensity to assimilation, to primary and secondary metabolism and to photomorphogenesis. Specifically, the authors determined in growth chamber the precise effect of 3 wavelengths peaks (510, 520 and 530 nm) applied at 3 radiation intensities (100, 200 and 300 µmol m^{-2} s^{-1}), compared to white fluorescent light (FL) (Table 1). Plants grown under PPF 300 G light, particularly at 510 nm, showed size and morphology similar to those under FL, confirming the efficiency of G on plant growth and morphogenesis when applied at sufficient doses.

Son and Oh (2013) determined the effect of R, G and B LED ratios on growth, photosynthetic and antioxidant parameters in two lettuce cultivars, with red ('Sunmang') or green ('Grand Rapid TBR') leaves in growth chamber, comparing six ratios: R:B 9:1, 8:2, 7:3; R:G:B 9:1:0, 8:1:1, 7:1:2, by LEDs (Table 1). Red light improved fresh and dry weight of shoots and roots, and leaf area in combination with B. The substitution of B with G in the presence of a fixed proportion of R enhanced the growth of lettuce. Meanwhile, growth under B led to the accumulation of antioxidants in 'Sunmang'. The supplemental irradiation of G to a combination of R and B can improve lettuce growth.

In lettuce grown hydroponically in growth chamber under white (W) LED light and supplemental B, G, Y, R or FR, plants were compact and vigorous under WR, while they looked sparse and twisted with WY and WFR, and dwarfed with large leaves under WB (Chen et al. 2016; Table 1). Compared to W control, fresh weight increased with supplemental R and B, while it decreased with supplemental FR. Chlorophyll and carotenoid contents were significantly higher with supplemental R and B. Supplemental B and G resulted in decrease of nitrate content, and G significantly promoted soluble sugar accumulation. Supplemental FR increased S/R ratio and ascorbic acid accumulation but resulted in lower pigment contents.

Green light positively affected leaf area index (LAI) in cucumber, stem length of tomato, petiole length of radish and specific leaf area of pepper compared to cool-white light (Snowden et al. 2016). In general, G light alone reduced chlorophyll concentration in cucumber, while B light alone reduced dry mass, LAI, stem and petiole length in tomato, cucumber, pepper and radish. However, plant response to light spectrum depended on light intensity and varied among the species.

Zheng et al. (2019) showed the effects of B and G during the dark period in tea plants (*Camellia sinensis* L.) to understanding the spectral effects on secondary metabolism and light signalling interactions. Results indicated the possibility of a targeted use of B and G to regulate the amount of functional metabolites, such as anthocyanins, catechins and L-ascorbate, to enhance tea quality and taste and to potentially trigger defense mechanisms in tea plants.

Dou et al. (2019) investigated the effects of substituting partial R and/or B with G light on plant growth in a green and a purple cultivar of basil (Table 1). The net photosynthesis (Pn) did not change in green plants whereas it increased in purple plants in presence of G light compared with RB only. The addition of G induced stem elongation in both the cultivars while did not influence leaf characteristics and yield in green plants and decreased leaf thickness and yield in purple plants,. Concentrations of phenolics and flavonoids, and antioxidant capacity decreased under R:B:G = 74:16:10 and R:B:G = 42:13:45 in green leaves and under R:B:G = 44:24:32 and R:B:G = 42:13:45 in purple leaves. Combining yield and nutritional values, a W light with low G proportion (10%) is recommended for basil production in controlled environment.

Flower and Ornamental Crops

In snapdragon grown as bedding plant, under natural light supplemented with HPS or 4 BGR LEDs proportions with or without FR, BGR + FR light led to faster flowering by 7 days on average and also increased the leaf area and plant height in snapdragon compared to HPS light (Poel and Runkle 2017; Table 3). The authors concluded that radiation quality of supplemental light had a relatively little effect on seedling growth and flowering although in some crops, flowering may be earlier when it includes FR radiation.

Owen and Lopez (2017; Table 3) reported that the foliage colour of geranium and purple fountain grass was enhanced under a low greenhouse daily light integral (9 mol m^{-2} day^{-1}), after 14 days of end-of-production supplemental lighting (100 µmol m^{-2} 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.

Conclusion

Artificial lighting in horticulture has been used for a long time with both assimilation and photoperiodic functions. More recently, the increasing knowledge in plant photomorphogenesis and metabolism paved the way to the application of innovative lighting systems, as well as of other strategies (e.g. photo-selective greenhouse covers), to control plant development and metabolism by means of light spectrum manipulation. In this respect, the considerable advance in LED technology pushed greatly the research on modern systems, based on monochromatic or multispectral light, as only or additional light source and for both assimilative and control functions.

Based on the current knowledge on plant response in the main horticultural crops, LED lighting could improve the product yield and quality, and the sustainability of the greenhouse industry. In particular, many experiments showed as R light alone can promote the synthesis of pigments and active metabolites in different species, improving the product nutritional quality. Responses to R:FR ratio are well defined, in term of processes such as germination, plant shaping, flowering, photosynthesis and biomass accumulation. Red light interacts with B to regulate plant responses and the optimal R:B ratio enhances photosynthetic capacity and improves growth and yield, when the proper light intensity is applied. Blue wavelengths are known to promote the photosynthetic process by inducing stomatal opening and chloroplast relocation and to increase the accumulation of antioxidant compounds and pigments in vegetables and fruits. Finally, G significantly contributes to photosynthesis and biomass accumulation, particularly in inner and lower leaf layers of the canopy, and can influence secondary metabolism. Besides, G wavelengths can tighter control plant growth and morphology by acclimation to light environment, in concert with R- and B-promoted effects, so it is increasingly considered, although much studies are still needed to better unravel their role.

In conclusion, LEDs could revolutionise the facility greenhouse through the realization of smart lighting systems. However, because of the peculiarity of the emitted light (single colour, narrow band), the precise knowledge of plant responses for the different crops, for any single process and developmental stage, is strictly required for their profitable application. In this respect, even though research on LED lighting of plants has been making fast progresses in the last years, several research gaps still need to be solved. For instance, the optimal light spectrum and intensity required by the different species in each phenological stage to optimize yield and product quality are still not known for many crops. Besides, interactions between light intensity and light spectrum and both these light features with other environmental parameters should be better characterized. These progresses are also desirable in the view of the numerous LED possible applications, including the greenhouse cultivation and the nursery production of many vegetables and ornamentals, the realization of plant food enriched in health-promoting bioactive compounds, the vertical farming in urban environment and in the farer scenario of cultivation on higher plants in bioregenerative life-support systems for human exploration of Space.

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