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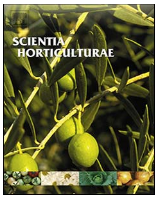

Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs)

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ABSTRACT

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

1. Introduction

1.1. Review objectives

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

1.2. Artificial lamp types

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

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

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

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

1.3. Photoreceptors

Plant responses are triggered by changes in the light intensity, quality, direction and duration and are governed and conducted by specialized photoreceptors (Kami et al., 2010). Photoreceptor proteins have a small cofactor or chromophore molecule allowing them to sense and respond to specific wavelengths of light over a continuous spectral range (Burgie et al., 2014). Five photosensory systems have been identified up to date; the phytochromes (phys) that absorb maximally in the red (600–700 nm) and far-red (700–750 nm) regions of the spectrum (Chen and Chory, 2011), while blue light (390–500 nm) is mediated by three different classes of photoreceptors: the cryptochromes (crys) (Ahmad and Cashmore, 1993), phototropins (phots) (Christie, 2007) and members of the Zeitlupe family (ztl, fkf1and lkp2) (Suetsugu and Wada, 2013). In addition, ultraviolet B (UV-B) wavelengths (280–315 nm) are monitored by the UV Resistance locus 8 (UVR8) (Jenkins, 2014).

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

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

Blue and UV-A light are also perceived by phot photoreceptors. Two phots (phot1 and phot2) have been identified In Arabidopsis. Low-fluence ($< 1\ \mathrm{mmol\ m^{-2}\ s^{-1}}$) blue light leads to phot1 response. Phot2 along with phot1 mediates the high-fluence response. Phot1 and phot2 usually have overlapping functions and contribute to a number of light mediated developmental responses. Phots are involved in transient inhibition of hypocotyl elongation and later crucial regulation of plant growth toward a directional light orientation (Folta and Spalding, 2001). They are also associated with chloroplast accumulation, as well as stomatal opening (Ma et al., 2001). The members of the Zeitlupe family (ztl, fkf1and lkp2) are also triggered by blue wavelengths and affect the regulation of the circadian clock and photoperiodic flowering (Zoltowski and Imaizumi, 2014).

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

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

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

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