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Light signaling and plant responses to blue and UV radiations—Perspectives for applications in horticulture

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ABSTRACT

Ultra-violet (UV) and blue radiations are perceived by plants through several photoreceptors. They regulate a large range of processes throughout plant life. Along with red radiations, they are involved in diverse photomorphogenic responses, *e.g.*, seedling development, branching or flowering. In this paper, we present an overview of UV- and blue-radiations signaling pathways in some key physiological processes and describe effects of plant exposure to these wavelengths on phenotype as well as on contents in useful metabolites and resistance to bio aggressors. Taking these knowledge into account, we finally discuss possible applications of the use of such radiations to improve plant production in horticulture.

Introduction

Light is one of the most important environmental factors that regulates plant growth and development (Smith, 1982). Plants need light not only for photosynthesis but also for fine-tuned regulation of their development. UV, blue and red radiations are involved in diverse photomorphogenic responses such as seedling development, vegetative growth, flowering and branching. A large amount of available literature is on the perception and the plant response to red (R), far-red (FR) and R/FR ratio, mediated by phytochromes (Demotes-Mainard et al., 2016). UV and blue radiations are also highly involved in the photomorphogenetic effects. Understanding the mechanisms involved in these responses can contribute to improving crop production (yield, resistance to pests and diseases, product quality), through (1) better management of plant density or architecture for light to better penetrate into the crop or into the tree canopy, and (2) modification of the light environment under greenhouse conditions. The need for artificial and efficient growing systems is indeed essential to feed a constantly expanding human population (Darko et al., 2014). Furthermore, as far as environmental and health issues are concerned, growers are incited to find cultural alternatives to the use of pesticides and growth retardants on crops. The use of sustainable techniques such as modulation of incoming light is one possibility.

Even if morphological responses to blue radiations are known to be species-dependent, increasing the part of blue rays in the light often reduces plant height and could be used as an alternative to the growth retardants. Moreover, high amount of blue light triggers specific biochemical and physiological processes resulting in a higher accumulation of epidermal flavonols that allows a better acclimation of pepper to UV stress (Hoffmann et al., 2015). Indeed, exposure to UV-rich radiations leads to generation of free radicals that damage DNA, proteins, lipids, chloroplasts and photosynthetic pigments (Hideg et al., 2013), but applied at lower level and during specific and short periods in plant lighting, UV

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radiations enhance plant resistance to pathogens and herbivores (Ballaré, 2014). The numerous studies on the consequences on plants of the depletion of the ozone layer, which results in local elevations in UV-B radiations (Caldwell et al., 2007; Kakani et al., 2003), provide interesting information for further applications to horticultural crops.

Moreover, greenhouses were commonly equipped with high pressure sodium (HPS) lamps with a spectrum of lighting containing small amounts of blue and high amounts of red and green lights. Now, these structures are gradually being equipped with new lighting technologies such as photo-selective films or light emitting diodes (LEDs). LEDs can cover the fluence and wavelength requirements of plants for different growth phases (Darko et al., 2014), and will contribute to quantitative and qualitative increases in crop yields.

In this context, this review focuses on plant responses to UV and blue lights, with an overview of the photoreceptors involved in the perception and signaling pathways of these wavelengths in main key physiological processes. The consequences on the phenotype of plants exposed to these wavelengths are described and this analysis leads to a discussion on the potential use of UV and blue radiations in the improvement of plant production in horticulture.

1. The light spectrum controls plant growth and development

The sensitivity range of plants to light extends from UV through the visible spectrum to far-red radiation (700–800 nm). Regarding ultraviolet radiation, UV-C (100–280 nm) radiation is thoroughly absorbed by the stratospheric ozone layer and the atmosphere; only UV-A (315–400 nm) and UV-B (280–315 nm) radiations reach plants (Fig. 1). In the visible light spectrum (400–700 nm), the major wavelengths perceived by plant photoreceptors and pigments are those corresponding to blue (400–500 nm) and red (600–700 nm) and, to a lesser extent, green (500–600 nm) (Fig. 1). A small fraction of near-infrared radiation, *i.e.,* far-red light perceived by phytochromes with a sensitivity peak at 730 nm, is also essential to plant development.

2. UV and blue radiation photoreceptors

UV and blue radiations are perceived by plants through a range of photoreceptors:

2.1. UVR8:

UV-B radiation is perceived by UV RESISTANCE LOCUS 8 (UVR8) (Fig. 1), a symmetrical homodimer made up of seven-bladed β-propeller protein homodimers bearing tryptophans that may act as a chromophore (Wu et al., 2012; Heijde and Ulm, 2012). UV-B irradiation disrupts hydrogen bonds and thus dissociates the homodimer into two monomers. UVR8 monomers then migrate from the cytosol into the nucleus where they interact with a molecular partner involved in the UV-B signal transduction pathway. Only few of these molecular players have been identified to date (Wu et al., 2012) and acts upstream of CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1, an E3-ubiquitin ligase), and LONG HYPOCOTYL5 (HY5), two well-known central regulators of other light signaling pathways. UVR8 associates with COP1 to activate UV-B responsive genes (Wu et al., 2012; Rizzini et al., 2011).

2.2. Phototropins

Phototropins (phots) are photoreceptors that perceive UV-A and blue lights (Fig. 1). They are serine/threonine protein kinases that bear flavin mononucleotide (FMN) chromophores bound to the protein at two light-oxygen-voltage (LOV) domains (Christie, 2007; Demarsy and Fankhauser, 2009). Two phototropins are present in *Arabidopsis*: phot1 and phot2. Phot1 responds to low-fluence blue light ($<1\,\mu mol\,m^{-2}\,s^{-1}$), while phot2 mediates the high-fluence response together with phot1. Blue light perception triggers conformational changes of these photoreceptors, leading to activation of the kinase domain and then autophosphorylation of the serine residues (Briggs and Christie, 2002; Inoue et al., 2008a). This triggers phot signaling, involving NONPHOTOTROPIC HYPOCOTYL 3 (NPH3) and ROOT PHOTOTROPISM2 (RPT2), two partner proteins that bind to PHOT1 (Inada et al., 2004; Motchoulski and Liscum, 1999). Phots localize at the plasma membrane and dissociate from it once activated by blue and UV-A photons. *PHOT* expression is regulated by blue light, with blue light stimulating *PHOT2* expression and downregulating *PHOT1* expression. Mutant studies in *Arabidopsis* reveal that CRYPTOCHROME 1 (CRY1) and PHYTOCHROME B (PHYB) regulate *PHOT1* expression, while CRY1, CRYPTOCHROME 2 (CRY2) and PHYTOCHROME A (PHYA) control *PHOT2* expression (Łabuz et al., 2012). Phots contribute to several developmental responses to light, and phot1 and phot2 have most often overlapping functions. In *Arabidopsis*, both are responsible for phototropism, including hypocotyl and stem bending as well as leaf positioning (Esmon

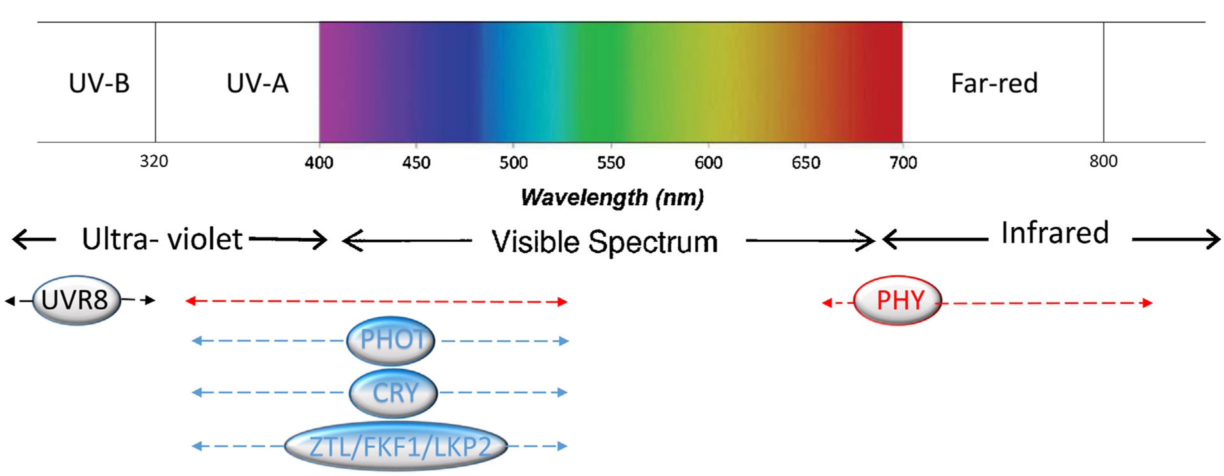

Fig. 1. The active light spectrum in plants ranges from ultra-violet (UV) to infrared, and plant photoreceptors absorb specific wavelength regions (bordered by dotted lines): UVR8, UV RESISTANCE LOCUS 8; PHOT, phototropins; CRY, cryptochromes; ZTL/FKF1/LKP2, Zeitlupe/Flavin-binding Kelch/LOV Kelch Protein; PHY, phytochromes.