Plant responses to red and far-red lights, applications in horticulture

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A B S T R A C T

Light drives plant growth and development, so its control is increasingly used as an environment-friendly tool to manage horticultural crops. However, this implies a comprehensive view of the main physiological processes under light control, and bridging knowledge gaps. This review presents the state of the art in (i) perception of red (R) and far-red (FR) wavelengths and of the R:FR ratio by plants, (ii) phenotypic plant responses, and (iii) the molecular mechanisms related to these responses. Changes in red or far red radiation and R:FR ratios are perceived by phytochromes. Phytochrome-mediated regulation is complex and specific to each physiological process. Our review presents the effects of red and far-red lights on germination, aerial architectural development, flowering, photosynthesis and plant nutrition. It also addresses how red and far-red radiations interact with tolerance to drought, pathogens and herbivores. Current knowledge about the mechanisms whereby red, far-red and R:FR regulate these different processes is presented. The specific actors of light signal transduction are better known for germination or flowering than for other processes such as internode elongation or bud outgrowth. The phenotypic response to red, far-red and R:FR can vary among species, but also with growing conditions. The mechanisms underlying these differences in plant responses still need to be unveiled. Current knowledge about plants' response to light is being applied in horticulture to improve crop yield and quality. To that purpose, it is now possible to manipulate light quality thanks to recent technological evolutions such as the development of photo-selective films and light-emitting diodes.

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1. Introduction

Plants perceive signals from their environment that enable them to adapt and modify their biological cycle. Specific light wavelengths are among such signals. Plants perceive changes in light quality through different types of photoreceptors, including phytochromes (see Galvão and Fankhauser, 2015; Huché-Thélier et al., 2016 this issue, for reviews). Phytochromes can be either in an inactive or active form. The equilibrium between the two forms dynamically changes with the composition of the light spectrum within the 300–800 nm range, and is strongly correlated with R/FR proportions in incident radiation (Holmes and Smith, 1977a; Sager et al., 1988). The R:FR ratio is often used to quantify spectral photon flux distribution in the R and FR wavelengths. In sunlight, the R:FR ratio is low (about 0.6) at the beginning and end of the

photoperiod, compared to its value at solar noon (about 1.0 to 1.3) (Holmes and Smith, 1977a). The R:FR ratio slightly varies with cloud covering and is little sensitive to seasonal variation (Holmes and Smith, 1975; Turnbull and Yates, 1993; Hertel et al., 2011). But the R:FR ratio is markedly reduced in canopies, (0.033 under a sugar-beet canopy for example) (Holmes and Smith, 1975). In canopies the R:FR ratio perceived by plant organs varies spatiotemporally in a range within which slight R:FR variation causes large variation in phytochrome photoequilibrium (Smith and Holmes, 1977; Chelle et al., 2007).

Phytochromes regulate different processes through the plant life cycle, including induction of seed germination, seedling de-etiolation, flowering time (Franklin and Quail, 2010; Strasser et al., 2010), fruit quality (González et al., 2015), root elongation (Salisbury et al., 2007; Costigan et al., 2011) and tolerance to biotic and abiotic stressors (Ballaré et al., 2012). Shade avoidance syndrome (SAS) is regulated by phytochromes, but also crypto-chromes, and possibly by phototropins and UVR8 as it involves perceiving not only R and FR, but also blue and UV and the equilibrium between blue and green (for reviews on SAS, see Franklin, 2008; Casal, 2012; Ruberti et al., 2012).

Farmers and horticulturists have long been lacking means to avoid undesired plant responses to R:FR decrease following canopy closure. Their most efficient levers were genotype and plant density. The recent launch of light emitting diodes (LEDs) and films now enables horticulturists to manipulate light quality efficiently. The use of such tools is particularly adapted to horticultural productions under greenhouse. Thus, evaluating how new data about plant physiological responses to R and FR light can be applied to improve ornamental and vegetable horticulture to supplement or replace more conventional factors as temperature or growth regulators is a true challenge.

In this review, we describe the phenotypic effects of R and FR lights, as well as the mechanisms underlying them, on different developmental processes crucial for plant development and survival: germination, aerial architecture development (stem elongation, leaf growth, bud outgrowth), and flowering. We also describe how R and FR radiations affect photosynthesis, mineral nutrition and plant responses to abiotic and biotic factors. The last section shows how knowledge about plants' response to R and FR radiations can be used in ornamental and vegetable horticulture.

2. Phytochromes

Phytochromes were the first light-sensing molecules discovered in plants and then identified in a broad spectrum of eukaryotic and prokaryotic phyla (Duanmu et al., 2014; Quail, 2010). The phyto-chrome molecule is a 240-kDa apoprotein synthesized in the cytosol, where it is covalently linked to a plastid-derived tetrapyrrole (billin) chromophore (Montgomery and Lagarias, 2002). Prediction of its three-dimensional structure indicates that each monomer is composed of two functionally and structurally distinctive domains (Sharrock, 2008; Nagatani, 2010). Phytochromes are encoded by a small multigene family in many species. There are five members in *Arabidopsis* and tomato (Sharrock and Quail, 1989; Clack et al., 1994, 2009; Hauser et al., 1997; Azari et al., 2010), 3 members in sorghum, black cottonwood and rice (Basu et al., 2000; Childs et al., 1997; Dehesh et al., 1991; Howe et al., 1998; Takano et al., 2009; Weller et al., 1997), and two in pea (Weller et al., 1997). PhyA and PhyB are conserved across all angiosperms investigated to date (Franklin and Quail, 2010; Kami et al., 2010), and form two subfamilies originating from a single ancestral phytochrome (Duanmu et al., 2014). Sensor functions of phytochromes resides in billin photoisomerization that quickly triggers photoconversion of the two phytochrome forms: the R light-absorbing form (Pr) is the inactive form that switches to the active FR light absorbing form (Pfr) in response to red (Nagatani,

2010; Quail, 2010). This latter translocates into the nucleus to trigger downstream signaling events (Galvão and Fankhauser, 2015; Sheerin et al., 2015) and is converted back to Pr when exposed to FR. Molecular mechanisms behind PhyA and PhyB translocation into nucleus have been well documented (For review see, Casal et al., 2014; Fankhauser and Chen, 2008; Possart et al., 2014).

Photomorphogenesis responses are categorized into three types: VLFR (Very Low Fluence Response) and FR-HIR (Far-Red High-Irradiance Response) (Schäfer and Bowler, 2002), that are mainly mediated by PHYA and LFR (Low Fluence Response) that is mainly ensured by PHYB (Casal et al., 2014; Rausenberger et al., 2011; Possart et al., 2014).

Phytochromes also contribute to blue light-dependent regula-tion redundantly or synergistically with others photoreceptors cryptochromes. For example, PhyB and cryptochromes (cry1a and cry1b) act cooperatively but independently to inhibit leaf sheath elongation in rice seedlings (Hirose et al., 2012). Photoreceptors UVR8 (UV RESISTANCE LOCUS 8) and phytochrome B cooperate to optimize plant growth and defense in patchy canopies (Mazza and Ballaré, 2015). Furthermore, physical interactions between CRY1 and PHYA proteins (Ahmad et al., 1998) and between CRY2 and PHYB (Más et al., 2000) have been reported in *Arabidopsis*. More recently, a potential role of PhyB in low PAR perception has been proposed (Trupkin et al., 2014), further supporting its major role in the monitoring of various light cues.

3. Germination

Seed germination is a crucial event in plant life. It is highly regulated by environmental factors. Among them, temperature and light are of particular importance to ensure a successful process. Seed germination is prevented by a light-sensitive mechanism based on the relative abundance of red and far-red perceived by phytochromes. PHYB and PHYA are present in the endosperm and the embryo, and are strongly involved in the photocontrol of seed germination (Lee and Lopez-Molina, 2012; Lee et al., 2012). In open areas, light is rich in R, so PHYB is the main phytochrome involved in the control of germination through the LFR that takes place right after seed imbibition. By contrast, under dense canopies, FR light is abundant, and PHYB-dependent germination is blocked: FR activates *PHYA* and allows for germination in negatively photoblastic seeds (Takaki, 2001; Lee and Lopez-Molina, 2012). PHYA is primarily implied in the VLFR, which allows seeds to respond to very low amounts of light (Casal et al., 2014). Alternatively, PHYA-dependent seed germination under canopy light conditions (low intensity and FR-rich spec-trum) might inhibit PHYB signaling, and lead to so-called explosive germination due to the disruption of intact testa by embryonic growth (Lee et al., 2012). Takaki (2001) proposed to leave aside the notion of photoblastism and rather mention control of germination by phytochromes: PHYB for germination of positively photoblastic seeds (through the LFR response), and PHYA for germination of insensitive seeds (through VLFR) and negatively photoblastic seed germination through HIR.

When a seedling emerges from the seed coat, it is located underground. When it protrudes from the ground, it gains access to light. Then a de-etiolation process rapidly takes place, mainly under the dependence of PHYB through the LFR pathway when R light is abundant (Franklin and Quail, 2010). However, the first steps of this process are quite often dependent on the VLFR pathway. This pathway is sensitive to low amounts of light and PHYA-related, particularly when litter alters light penetration, a situation commonly encountered in woods and natural conditions, but rare in crop cultures (Casal et al., 2014). PHYB-related LFR operates the de-etiolation process in open areas. PHYB is also implied in its termination when the seedling emerges from the