

The role of far-red light (FR) in photomorphogenesis and its use in greenhouse plant production

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Received May 08, 2020; accepted May 30, 2020.
Delo je prispelo 08. maja 2020, sprejeto 30. maja 2020.

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Abstract: Light energy is one of the most important factors regulating the growth and development of plants. In greenhouses and other controlled- environments in which the natural radiation intensities are often low, plant production relies on supplementary lighting to optimize the photosynthesis, increase production levels, and enable year-round production. For a long time, the research related to artificial lighting sources focused on the optimization of the efficiency of use for photosynthesis. The quality of light in plant production has been widely addressed only recently with the development of advanced LED technology that is energy efficient and enables the control of the spectral composition of light. Red and far-red light are sensed by the phytochromes that trigger several morphological and developmental processes that impact productivity and yield quality. Thus, to efficiently exploit all the advantages of LEDs and to develop LED arrays for specific plant applications, it is essential to understand thoroughly how light quality influences plant growth and development. This paper presents an overview of the recent developments in light quality manipulation, focusing on far-red light and the R: FR ratio, to improve yield and quality of products and to manage plant architecture and flowering in vegetable and ornamental horticulture.

Key words: far-red light; greenhouse; LEDs, light quality; photomorphogenesis; R: FR ratio

Vloga dolgovalovne rdeče svetlobe v fotomorfogenezi in njena uporaba pri vzgoji rastlin v rastlinjakih

Izvleček: Svetlobna energija je eden najpomembnejših dejavnikov, ki uravnava rast in razvoj rastlin. V rastlinjakih in ostalih zavarovanih prostorih, kjer je jakost naravnega sevanja velikokrat majhna, je vzgoja rastlin odvisna od dosvetljevanja, ki omogoča optimizacijo fotosinteze, povečanje pridelka in celoletno vzgojo rastlin. Dolgo časa so se raziskave povezane z umetnimi viri osvetljevanja osredotočale predvsem na izboljšanje učinkovitosti za fotosintezo. Vloga kvalitete svetlobe pri rastlinski pridelavi je postala zanimiva šele pred kratkim, z razvojem energetske učinkovite, napredne LED tehnologije, katere glavna prednost je, da omogoča nadzor nad spektralno sestavo svetlobe. Rdeča in dolgovalovna rdeča svetloba, ki jo rastline zaznavajo s fotoreceptorji fitokromi, sprožita številne morfološke in razvojne procese, ki vplivajo na količino in kvaliteto pridelka. Za dober izkoristek vseh prednosti LED tehnologije in razvoj "LED matrik" za specifično rastlinsko uporabo, je potrebno dobro razumevanje vpliva spektralne sestave svetlobe na rast in razvoj rastlin. V prispevku je predstavljen pregled napredka na področju upravljanja s svetlobo, s poudarkom na dolgovalovni rdeči svetlobi in razmerju med rdečo in dolgovalovno rdečo svetlobo, za povečanje in izboljšanje kakovosti pridelka, ter uravnavanje zgradbe rastlin in cvetenja v pridelavi vrtnin in okrasnih rastlin.

Ključne besede: dolgovalovna rdeča svetloba; rastlinjak; LED luči; kvaliteta svetlobe; fotomorfogeneza; R : FR razmerje

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1 INTRODUCTION

Many food and ornamental horticultural crops are produced year-round in greenhouses. Recently, plant factories and vertical farms that can ensure a supply of locally produced, fresh food are also being introduced (Bantis et al., 2018). The availability of natural sunlight in these controlled-environments is often limited and could prevent or suppress plant production during large parts of the year. In such circumstances, the production of many crops rely on artificial lighting

In greenhouses, traditional artificial lighting sources, such as fluorescent, high-pressure sodium, metal halide and incandescent lamps, have long been used as a solo source or supplemental lighting to enhance photosynthesis and/or to regulate plant development (Bilodeau et al., 2019; Bantis et al., 2018). The spectral qualities of artificial light sources differ with each other and from natural light. Metal halide and especially high-pressure sodium lamps (HPS) have been usually used to provide high-intensity lighting for plant growth applications.

Recently developed lighting source in the form of light-emitting diodes (LEDs) offers many advantages over conventional artificial lighting sources (Chang et al., 2012; Olle & Viršile, 2013; Morrow, 2008; Yeh & Chung, 2009; Singh et al., 2015; Cho et al., 2017; Viršilè et al., 2017). Advantages include high-energy efficiency, long operating lifetime, narrow spectral emissions, adjustable size, etc. (Singh et al., 2015; Nelson & Bugbee, 2014). LEDs also produce significantly lower leaf temperatures and are thus suitable for low-intensity lighting within the plant canopies (Massa et al., 2005). One of the most valuable properties of LEDs is the ability to control the spectral composition of supplemental lighting, which enables investigating the effects of individual wavelengths or different spectral combinations of wavelengths on plant growth and development. The first commercially available LED fixtures were mainly designed to support photosynthesis and contained mostly red and blue diodes (10 %-25 % blue diodes). To date, many experiments have focused on designing an optimal lighting system, mostly modifying the proportion of different wavelengths within photosynthetically active radiation (PAR) region to support plant growth (Massa et al., 2008) and, more recently, also to precisely regulate plant development. The spectral quality of light affects a great number of plant developmental processes, including germination, seedling establishment, development of rosette, branching and apical dominance, the definition of adult plant architecture, the regulation of flowering, etc. (Franklin & Quail, 2010; Sánchez-Lamas et al., 2016).

The objective of this review is to present a short overview of the principles of red (R) ($\approx 625\text{-}700\text{ nm}$)

and far-red (FR) ($> 700\text{ nm}$) light perception by phytochromes and their impact on plant growth and development, which play an essential role in greenhouse plant production. We summarise the research work referring to the use of far-red light or manipulating the R : FR ratio, to improve yield and quality of products and to manage plant architecture and flowering in vegetable and ornamental horticulture.

2 RADIATION AND PLANTS

About 40-50 % of the solar energy received by ecosystem falls in the spectral region of 380-780 nm, which we perceive as visible light. The visible light range includes violet ($\approx 400\text{-}450\text{ nm}$), blue ($\approx 450\text{-}520\text{ nm}$), green ($\approx 520\text{-}560\text{ nm}$), yellow ($\approx 560\text{-}600\text{ nm}$), orange ($\approx 600\text{-}625$), red ($\approx 625\text{-}700\text{ nm}$) and far-red ($> 700\text{ nm}$). On the short-wavelength end of this region is ultraviolet radiation (UV-A, 315-380 nm; UV-B, 280-315 nm; UV-C from artificial sources of radiation, 100-280 nm) and, at the other end, there is infrared radiation (780-3000 nm). The radiation that hits the plant can be reflected at the surface, absorbed or transmitted; the degree of these three events depends on the wavelength of the radiation (Larcher, 1991) and plant organs structure. For a plant, radiation is the energy source and a stimulus regulating development, but it can also cause photo-inhibitory and photo-destructive effects.

In photo-energetic processes, the absorbed energy is used for the photosynthesis or other metabolic reactions or chemical transformations. The action spectrum of plant leaves was described as the span of wavelengths from approximately 400-700 nm, over which plants absorb and effectively use radiant light energy for photosynthesis (McCree, 1972). This photosynthetically active radiation, now commonly known as PAR, is the most important part of the light spectrum for plants; it falls within the visible light range. It relates the intensity and rate of radiant light energy per surface area emitted by a light source from within the action spectrum of plants (Bilodeau et al., 2019). The amount of light that reaches the plant within the PAR region, or the number of photosynthetically active photons that fall on a given surface each second, is measured as a photosynthetic photon flux density (PPFD) and is expressed in $\mu\text{mol m}^{-2}\text{ s}^{-1}$. The photoreceptors that play an important role in photosynthesis are chlorophylls with absorption maxima in the red and blue, along with antenna pigments that include different carotenoids, such as β -carotene, zeaxanthin, lycopene, and lutein (Singh et al., 2015).

Plants are also sensitive to other wavelengths, for example, far-red radiation of a wavelength of approxi-

mately 700-800 nm. It is known that the far-red part of spectrum strongly affects plant development. The regulation of plant growth and development by light signals is termed 'photomorphogenesis'. Recently, it was shown that far-red light could also increase photosynthetic efficiency (Zhen & van Iersel, 2017).

Plants respond to changes in light, including its intensity, spectral quality, direction and duration through different types of photoreceptors. Not considering chloroplast pigments, to date, five photosensory systems have been identified, (i) the phytochromes (phys) that absorb maximally in the red (600-700 nm) and far-red (700-750 nm) regions of the spectrum, (ii) the cryptochromes (crys), phototropins (phot) and members of the Zeitzlupe family (ztl, fkl1 and lkp2) that absorb the blue light (390-500 nm) and (iii) UV resistance locus 8 (UVR8) that monitors the ultraviolet B wavelengths (280-315 nm) (Bantis et al., 2018).

3 PHYTOCHROMES

Phytochromes are light-sensing molecules present in bacteria, cyanobacteria, fungi, algae, and land plants. The first indications of their role in plant development came from studies in the 1930s, although its chemical isolation and identification happened much later (Taiz & Zeiger, 2014).

Native phytochrome is a soluble protein with a molecular mass of about 250 kDa. It occurs as a dimer made up of two equivalent subunits. Each subunit consists of a light-absorbing pigment molecule called the 'chromophore' that is synthesized in chloroplasts and a polypeptide chain called 'apoprotein', synthesized in the cytosol. Together they form the holoprotein, which can absorb light (Taiz & Zeiger, 2014; Lagarias & Rapoport, 1980).

Phytochrome exists in two interconvertible forms that differ in their absorption spectra. The inactive Pr form is synthesized in the dark and after the absorption of red light (660 nm) changes chemically into the active Pfr form. Pfr is inactivated by the conversion back to Pr after the absorption of far-red light (730 nm) or through thermal relaxation, which depends on temperature. (Taiz & Zeiger, 2014; Legris et al., 2019). Phytochromes act as dimers and subunits are connected in three possible combinations Pr-Pr, Pfr-Pr, and Pfr-Pfr.

The photo-reversibility is the most distinctive property of phytochrome and results in a dynamic photo-equilibrium of Pr and Pfr that depends on light quantity, spectral composition and temperature (Franklin and Quail, 2010; Jung, 2016). The absorption of light by Pr induce an extensive variety of different responses that can be grouped into two types: (i) rapid biochemical events

and (ii) slower morphological changes, including movements and growth (Taiz & Zeiger, 2014).

Phytochrome is encoded by a small multigene family named *PHY*, the apoprotein without chromophore is designated 'PHY', and the holoprotein is designated 'phy' (Taiz & Zeiger, 2014). Phytochromes in seed plants diverged into three major forms, phyA, phyB, and phyC, very early in the history of seed plants. In some dicotyledonous species, two additional forms, phyE and phyD, were found and are presumably derived by gene duplication. Each phytochrome has different roles, and their relative contributions vary depending on the environmental conditions and developmental stage of the plant (Legris et al., 2019). PhyA and phyB are present in all sampled angiosperms and are the principal mediators of red/far-red-induced responses.

Research of the expression patterns of the *PHY* gene family of products has shown that there are two different classes of phytochromes with distinct properties: light labile Type I and light stable Type II (Tokuhisa et al., 1985; Furuya, 1993). Type I class, represented by phyA, induces very low fluence responses (VLFRs) and far-red high-irradiance responses (FR-HIR). The examples of conditions where phyA is activated are deep shade or few centimetres under the soil surface. Type II phytochromes (phyB-phyE) evoke signals called 'low fluence responses' (LFRs), and these are activated in more open environments (Legris et al., 2019).

Following light perception and conversion to the Pfr form, phytochromes translocate to the nucleus where they selectively interact with several classes of transcription factors and trigger downstream signalling, participating in the regulation of transcription posttranscriptional regulation, and translation (Legris et al., 2019).

In addition to light, phytochromes also contribute to temperature responses with phyB having a major role (Jung et al., 2016; Legris et al., 2019). The molecular mechanisms of photo- and thermo-morphogenesis have mostly been analysed separately, but it is now well recognised that light and temperature signalling are connected (Lorenzo et al., 2016; Patel et al., 2013).

Phytochromes can act synergistically with other photoreceptors. The interaction of phytochrome and cryptochrome signalling and interaction between phytochrome and phototropin photoreceptors have been reported in *Arabidopsis* (Ahmad et al., 1998; Mas et al., 2000; Parks et al., 1996).

3.1 PHYTOCHROMES AND R : FR RATIO IN PHOTOMORPHOGENESIS

Pr and Pfr forms of phytochromes have overlapping

absorption spectra and can monitor the R : FR ratio of light. The R : FR ratio is usually used to quantify spectral photon flux distribution in the R and FR wavelengths. The equilibrium between the Pr and Pfr forms dynamically changes with the composition of the light spectrum within the 300-800 nm range and is strongly correlated with R to FR proportions of red and far-red light in incident radiation (Holmes & Smith, 1977). Sunlight at midday has approximately equal amounts of R and FR resulting in an R : FR ratio slightly above 1, but at the beginning and end of the photoperiod it is much lower (about 0.6). The R : FR ratio slightly varies with cloud covering and is little sensitive to seasonal variation (Turnbull & Yates, 1993). However, in environments with high plant density, the R : FR ratio is considerably reduced (0.13 under ivy canopy) (Taiz & Zeiger, 2014). 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 photo-equilibrium (Demotes-Mainard et al., 2016).

Phytochromes are potent regulators of plant development and, through the perception of the R : FR ratio of light, affect a broad range of responses throughout the plant life cycle (Franklin & Quail, 2010; Sánchez-Lamas et al., 2016). The change in the R : FR ratio triggers a series of responses in plant vegetative architecture including higher stem length, bud outgrowth, leaf expansion, petiole extension, root development, leaf hyponasty and phototropism, accelerated flowering, etc., known collectively as 'shade avoidance syndrome' (SAS). Green tissues of plants with high chlorophyll content absorb mostly red (R) and blue (B) wavelengths, but let through the FR light, so with shading the R : FR ratio decreases. The greater proportion of far-red light converts more Pfr to Pr, and the ratio of active Pfr to total phytochrome (P_{total}) decreases.

The shade-avoiding response is characteristic of 'sun plants' and represents a competitive advantage as it enables the plants to acquire more PAR. The sensitivity of plants to low R : FR ratio can vary during the day (Casal et al., 1997) and it also depends on the variety and species (Casal & Smith, 1989). The SAS response is weak or not present in 'shade plants', which normally grow in the shade (Taiz & Zeiger, 2014).

One of the SAS responses triggered by a low R : FR ratio is a faster transition to flowering. It is common in many plant species, including many agronomical significant ones (Taiz & Zeiger, 2014). The first step in flowering, the flower induction, is a result of the integration of various environmental and endogenous cues that work through different genetic pathways. The photoperiod pathway is one of them and refers to the regulation of flowering in response to day length and quality of light

perceived (Srikanth & Schmid, 2011). On the basis of the photoperiod, plants can be classed as short-day (SDP) or long-day plants (LDP), although the critical factor in determining their activity is night length. Species that flower under any photoperiodic condition are referred to as 'day-neutral plants' (DNP).

4 APPLICATIONS OF FAR-RED LIGHT IN GREENHOUSE PLANT PRODUCTION

There are many areas in crop production, of both food crops and ornamental crops, for which the use of FR light has been shown to have especially promising value. In vegetable horticulture, the two main factors defining yield are biomass production and product quality, inclusive of nutritional value, visual appearance, resistance to 'environmental factors' and others. In growing ornamental plants, the main focuses are their visual appearance and flowering characteristics.

4.1 PHOTOSYNTHESIS AND BIOMASS PRODUCTION

Biomass production is usually directly correlated to photosynthesis, and it depends on the quantity of photosynthetically active radiation received by the leaves. The primary environmental factors that influence crop growth include photosynthetic light intensity and duration per day (which, when integrated formulates the photosynthetic daily light integral), light quality, temperature, and carbon dioxide concentration (Runkle, 2013).

Due to the poor absorption of far-red light ($\lambda > 700$ nm) by leaves and the low quantum yield of photosynthesis, it has long been thought that it makes no or minimal contribution to photosynthesis (McCree, 1972). It is now known that the low quantum yield of photosynthesis under far-red light is caused by unbalanced excitation of the photosystems PSI and PSII, which operate in series to carry out photochemical reactions (Myers, 1971). If shorter wavelength light is supplemented with far-red light that preferentially excites PSI, the excitation balance between the two photosystems can be restored. This can synergistically increase photochemistry and photosynthesis (Zhen & Van Iersel, 2017).

Zhen and Van Iersel (2017) report that the addition of far-red light to red/blue and warm-white light immediately increased quantum yield of photosystem II (Φ_{PSII}) of lettuce by an average of 6,5 and 3 %, respectively. Besides the short-term effect, after 20 min of exposure to far-red light, an increase of Φ_{PSII} and a decrease of non-photochemical quenching (NPQ) were noted. The in-

crease of Φ_{PSII} was associated with an increase in net photosynthesis. A 7.5 % increase in Φ_{PSII} upon adding far-red light ($90 \mu\text{mol m}^{-2} \text{s}^{-1}$ within 700–770 nm) to a red/blue measuring light ($200 \mu\text{mol m}^{-2} \text{s}^{-1}$) resulted in an 18 % increase in net photosynthetic rate. In a later study, Zhen et al. (2019) quantified the efficiency of different wavelengths of far-red light exciting PSI by measuring the change in quantum yield of PSII of lettuce grown under red/blue light or under sunlight. The Φ_{PSII} of lettuce increased with increasing wavelengths of added light from 678 to 703 nm, indicating longer wavelengths within this region are increasingly used more efficiently by PSI than by PSII. Adding 721 nm light resulted in similar Φ_{PSII} as adding 703 nm light, but Φ_{PSII} tended to decrease as wavelength increased from 721 to 731 nm, likely due to decreasing absorbance and low photon energy. Adding 752 nm light did not affect Φ_{PSII} . The beneficial effects of FR light on photosynthesis at fluctuating light was also proved in *Arabidopsis* by Kono et al. (2020).

Photosynthesis is dependent on the intensity and quality of light that reaches chloroplasts. Yang et al. (2018) studied the interactions between light intensity and the R : FR ratio on the photosynthesis of soybean leaves under shade condition. From the results of quantitative proteomic analysis, they conclude that light intensity directly affects photosynthesis by regulating the expression of photosynthetic proteins and that a low R : FR ratio could improve the photosynthetic capacity by increasing light-harvesting capacity and stimulating the electron transport of PSI (Yang et al., 2018).

Whole-plant gas exchange measurements of 16 C_3 and two C_4 species under red/blue light and red/blue plus FR light indicated that adding far-red photons (10 – 30 % of PPFD) caused similar increases in the whole canopy photosynthetic rate as adding the same amount of red/blue photons (Zhen & Bugbee, 2019). To demonstrate that far-red photons are equally efficient at driving photosynthesis, the authors grew lettuce under spectra with or without 15 % of far-red photons at the same total photon flux, and the results at harvest showed 35 % higher dry biomass in treatments with far-red photons, which was almost entirely caused by enhanced radiation capture through leaf expansion.

There is, however, a variability among studies and, in some species, the specific net assimilation rate decreases in response to a low R : FR ratio or PHYB reduced expression. The different and sometimes contrasted responses between studies may reflect variability between species and genotypes, and/or variability in the growing conditions used (Demotes-Mainard et al., 2016 citations therein).

In addition to its direct effect on photosynthesis, the R : FR ratio can influence the process also indirectly,

through its effect on morphological characters, for example, branching, leaf area and leaf orientation (Demotes-Mainard et al., 2016). A higher proportion of FR light, applied to some ornamental plant species has been shown to cause leaf expansion mediated by phytochromes, thus promoting canopy light interception and indirectly increasing plant growth during long-term cultivation (Park & Runkle, 2017).

Phytochrome B also regulates other traits involved in photosynthesis. It was shown to promote stomatal maturation in *Arabidopsis thaliana* (Kang et al., 2009), regulate the activity of some enzymes of the Calvin cycle (Bradbeer, 1971) and control the development of chloroplasts (Thiele et al., 1999).

4.2 FR AND YIELD QUALITY

The quality of the crop yield is an essential parameter for any grower. Its various aspects rely upon the light intensity and, to a larger extent, on light quality, which is the wavelengths perceived by the plant. With modifications of the light spectrum, the simultaneous increase in biomass and better quality of the product can be obtained. Most recent investigations are thus focused on both characteristics. A large number of studies in vegetable horticulture have been done using lettuce and tomato as a model species.

In a study in which lettuce was grown under cool white fluorescent lamp supplemented with R or FR LED, the plants exposed to FR light demonstrated enhanced fresh and dry mass, stem length, and leaf length and width, but the content of anthocyanin, carotenoid, and chlorophyll was reduced (Li & Kubota, 2009). Similarly, red leaf lettuce grown under R supplemented with FR light also exhibited lower anthocyanin concentration and antioxidant potential, whereas R light supplemented with blue (B) light caused the exact opposite results (Stutte et al., 2009).

Zhang et al. (2019a) performed three greenhouse experiments to determine the effects of supplemental lighting with different spectral quality on lettuce growth, colouration, and sensory attributes. Four hours of end-of-day (EOD) lighting of low intensity ($2\text{--}5 \mu\text{mol m}^{-2} \text{s}^{-1}$) had only minor effects on lettuce growth and quality attributes, but R + B LED supplemental lighting resulted in darker, redder, and less yellowish plants.

An essential role of FR light for improving the production of indoor cultivated lettuce has been demonstrated in an experiment done by Zou et al. (2019). Adding $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ of FR light to $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ of R + B, applied during the day (16 h) or as EOD (1 h), resulted in 39 % and 25 % increase in total biomass. Adding FR light

resulted in 27-49 % larger plant leaf area with an open plant canopy, which facilitated a better light interception led to higher plant radiation use efficiency (RUE).

Studies of FR effects during the fruiting stage of crops are much less frequent than research in young plants, although the reports, especially in tomato, are now increasing. Apart from plant morphological alterations, changes in the R : FR ratio also lead to the redistribution of growth and dry matter within the plants, as indicated by an increased shoot/root ratio and soluble sugar levels under radiation with a low R : FR ratio. Kalaitzoglou et al. (2019) reported that additional FR light applied as continuous and EOD treatment increased total dry mass of tomato plants in the vegetative growth stage, as well as the fruit number per plant, fresh fruit weight per plant and average fruit fresh mass. Similarly, higher total plant dry mass and higher fruit yield in tomato grown under additional FR radiation were reported by Zhang et al. (2019b). In another study on tomatoes, the R and B + FR light treatment increased the production of soluble sugar, increased the dilution by soluble and storage compounds, and water reduction dilution, leading to a strong increase in glucose, fructose and sucrose concentration in the pericarp (Fanwoua et al., 2019). However, neither study provided sufficient insights on how additional FR increases fruit growth in the fruiting stage of the crop, which is a key step in understanding the FR induced yield improvement in fruit crops like tomatoes. Kim et al. (2019) also observed a significant decrease in water content of tomato fruits produced under FR light, together with a pronounced effect of FR light on biomass allocation between vegetative and reproductive structures. Long-term exposure of tomato plants to low R : FR was associated with reductions in leaf area, chlorophyll content, and vegetative shoot biomass fraction, increases in leaf thickness and fruit biomass, and acceleration of flowering and fruiting.

Recently, intra-canopy lighting, a technique that enables more even light distribution within the crop canopy, has been widely applied for high-wire fruit vegetable production in greenhouses. In a study of Zhang et al. (2019b), tomatoes were grown under intra-canopy R and B LEDs supplemented with overhead FR lights in three different duration regimens, (i) 12 hours during the day, (ii) 1.5 hours in the afternoon and (iii) 0.5 hour in the afternoon. The additional FR lighting led to increased stem elongation, higher leaf length: width ratio, increased leaf area, 9 %-16 % increase in total biomass and slightly lower soluble sugar content. The stimulation of growth and production were similar in all three treatments (Zhang et al., 2019b).

The effects of specific spectral compositions of light on various quality parameters are often species, or even

cultivar specific, and should thus be determined for each species and application separately. The recent wide accessibility of LEDs and promising results on the effects of the FR light in some model species, widely opened the research of this topic in many other agronomical important species, like cucumber (Nishimura et al., 2012; Hao et al., 2012; Shibuya et al., 2016) spinach (Akutsu et al., 2017), kale (Meng et al., 2019), squash (Yang et al., 2012), basil (Meng & Runkle, 2019), etc.

Morphological changes induced by FR light, especially stem elongation, are often undesirable, but in some cases, the promotion of extension growth is essential. Producing seedlings with long hypocotyls is, for example, desired in vegetable grafting. Chia and Kubota (2010) used FR-rich incandescent lamps, without or with filters that reduced transmission of R light, to promote elongation of tomato seedlings. They obtained a 20 % increase in hypocotyl length under the R : FR ratio of 0.47 and 44 % at R : FR of 0.05. They concluded that only 2 to 4 mmol m⁻²d⁻¹ of FR light was needed to nearly saturate the promotion of elongation growth. There were no negative effects on dry mass, stem diameter, and plastochron index. The effectiveness of EOD FR lighting from a movable LED fixture on interspecific squash (*Cucurbita maxima* Duch. x *Cucurbita moschata* Duch. ex Poir) rootstock hypocotyl elongation was investigated by Yang et al. (2012). The extent of hypocotyl elongation under movable or stationary FR LED fixtures was statistically the same and was 55-69 % greater than non-treated control (Yang et al., 2012).

It is known that, in addition to a low R : FR ratio, shade avoidance responses are also regulated by the photosynthetic photon flux density (PPFD). In general, increasing PPFD decreases the magnitude of plant responses to the R : FR ratio. Growing sunflower (*Helianthus annuus* L.) seedlings at low R : FR ratio (0.85) at low and moderate PPFD (157 and 421 μmol m⁻²s⁻¹) resulted in increased growth, but the growth response was attenuated under the higher PPFD (Kurepin et al., 2007). Yang et al. (2018) studied the effects of interactions between light intensity and R : FR ratio on the photosynthesis of soybean leaves under shade condition. The iTRAQ technique was utilized to analyse differentially expressed proteins involved in photosynthesis, and the results showed that low R : FR could improve the photosynthetic capacity of plants under shade conditions.

Light is also a critical environmental factor for the production of secondary metabolites in plants (Kopsell & Sams, 2013). It is known that phytochemicals play a significant role in delaying or inhibiting oxidative damage caused by free radicals. Spectral quality has a pronounced effect on accumulating secondary plant metabolites in controlled environment agriculture (Alrifai et

al., 2019). The studies about the impact of FR light on the phytochemicals content are limited. As mentioned above, lettuce plants exposed to FR light demonstrated enhanced fresh and dry mass, stem length, and leaf length and width, but the content of anthocyanin, carotenoid, and chlorophyll was reduced (Li & Kubota, 2009); similarly, red leaf lettuce grown under R light supplemented with FR light also exhibited lower anthocyanin concentration and antioxidant potential (Stutte et al., 2009). In such cases, the benefits of adding FR light for increased biomass are tentative. In many studies, FR light was applied together with B and R light, and the overall effect of this light combination on secondary metabolites concentration was mostly stimulatory, while the contribution of FR alone was not evaluated (Alrifai et al., 2019). This effect could be explained by enhanced photosynthesis and, consequently, higher metabolism.

Light spectral quality can greatly affect the efficiency of the uptake of resources (water and nutrients) from the soil and affect the way of the plants to adjust the competition for soil resources (Sadras et al., 1989; Gundel et al., 2014). It was shown that the R: FR ratio affects different steps of plant nutrition that are critical for enhanced and sustainable crop production. It can affect root structure (De Simone et al., 2000; Gundel et al., 2014) or root growth (Klem et al., 2019). The establishment of a nitrogen-fixing symbiosis between legumes and rhizobia requires not only sufficient primary metabolites but also the sensing of the R: FR ratio (Suzuki et al., 2011). R: FR sensing also influences the arbuscular mycorrhizal (AM) symbiosis of a legume and non-legume through jasmonic acid and strigolactone signalling (Nagata et al., 2015). In hydroponically grown lettuce, far-red light stimulated uptake of N and K, Ca and Mg with the latter increasing by 27 %, 25 %, and 28 %, respectively, compared to plants grown under R and B light (Pinho et al., 2017).

Postharvest technology is another field in which the use of LED technology emerged as an efficient lighting source and its use, including FR light, can affect the nutritional and organoleptic parameters of vegetable plants and can be used to delay the senescence of green vegetables (Favre et al., 2018). The use of R light or light with high R: FR ratio has been shown to be the most effective in delaying senescence in broccoli (Favre et al., 2018). Similarly, tomato fruits exposed to LED light with a high R: FR ratio had increased firmness and higher titratable acidity compared to other darkness exposure or other LED lighting conditions (Nájera et al., 2018).

4.3 FR IN ORNAMENTAL HORTICULTURE (FLORICULTURE)

In growing ornamental plants, one of the essential

points to consider is the shape of plants, of which stem elongation and branching are regarded as very important. Another vital component is flowering, including flowering time and duration, and the number of floral buds. All of these contribute to the plant's visual appearance and therefore to its economic value.

The control of height and branching of many ornamental plants represents a major challenge in commercial greenhouse production. Extremely tall and branched out pot plants are prone to breakage and increase production costs. Usually, in the production of ornamentals, stem growth promotion is not desired, with some exceptions, such as the cultivation of cut flowers (Zhang & Runkle, 2019). Chemical agents, such as plant growth retardants or gibberellic acid, are commonly used to regulate stem length; however, due to the potential negative effects of plant growth retardants on human health and the environment, limitation of their use is desirable (Rajapakse et al., 1999).

The development of plant vegetative architecture, including stem elongation and branching, is regulated mostly by phytochromes, although the participation of cryptochromes in inhibition of stem elongation has been documented (Liscum et al., 1992). Most plants show some degree of shade-avoidance response in an attempt to reach more photosynthetic light. Generally, under a reduced R: FR ratio, plants elongate. For example, in *Digitalis purpurea* 'Dalmatian Peach' seedlings, the addition of 7.9 to 68.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ FR light to white light ended in a 38 % increase in shoot length in a dose-dependent manner (Elkins et al., 2019).

EOD lighting has been widely used recently to regulate extension growth by manipulating the R: FR ratio (Downs & Thomas, 1982; Islam et al., 2015; Ilias & Rajapakse, 2005). For example, Islam et al. (2014) exposed two poinsettia cultivars to R or FR EOD lighting for 30 min at 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ after a 10-hour short day (SD). After 11 weeks, the internode length was 55 % to 107 % greater under EOD-FR compared with EOD-R.

Many studies illustrate the variability in species responses to light quality and underscore the complexity of how light regulates stem extension and (flowering) in plants (Craig & Runkle, 2013). Variation in plant height was found in two poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) cultivars under the 2-h EOD lighting treatments, regardless of light quality. The effect was attributed to different cultivar specificity (Zhang & Runkle, 2019) and the results were in accordance with the findings of Rajapakse et al. (1993) (cited by Zhang & Runkle, 2019) who reports that same EOD-FR treatment increased height in one chrysanthemum cultivar by ≈ 50 % while the plant height of the other cultivar was similar to control. Different sensitivity to the R: FR ratio in stem elongation was observed between three SDP species (*Chrysanthemum x morifo-*

lium (Ramat.) Hemsl.) , *Dahlia x hortensis* A. Guillamin, and *Tagetes erecta* L.) (Craig & Runkle, 2013), as well as between five LDP species (*Campanula carpatica* Jacq., *Coreopsis x grandiflora* Hogg ex Sweet, *Lobelia x speciosa* Sweet, *Pisum sativum* L., and *Viola x wittrockiana* Gams) (Runkle & Heins, 2001). In the latter study, reaction to lower R : FR ratio was greater in the sun-adapted species *C. carpatica* and *Platycodon grandiflorus* (Jacq.) A.DC.. The extension growth was promoted in all five species under B-deficient environment. Based on the results, the authors suggested that blue light plays an important role in mediating stem extension in LDP. Similar conclusions were drawn from the study of petunia (*Petunia x hybrida* hort. ex E.Vilm.), geranium (*Pelargonium x hortorum* L.H.Bailey) and coleus (*Solenostemon scutellaroides* (L.) Codd) seedlings grown under different combinations of R, FR, and B light at various intensities in a 16-hour photoperiod. The height of the plants increased linearly with lowering R : FR ratio and moderately high B light attenuated the effects of the R : FR ratio on extension growth (Park & Runkle, 2019).

For plants marketed for their flowers, the most crucial point is coordinated control of time and duration of flowering. One of the strategies to manage flowering without using chemicals is light quality manipulation, particularly the R : FR ratio. Low-intensity photoperiodic lighting is usually used by horticulturists to alter the natural photoperiod to manipulate flowering. The EOD lighting of different duration has been used to extend the natural photoperiod and create long days; recently, the feasibility of adjusting spectral quality of EOD supplemental lighting has broadened the range of possible applications. Another favourable approach of lighting, used for flowering control, is the use of night interruption (NI) lighting, using the light of differing spectral quality. The advantage of short-term lighting is its economic feasibility as a result of its lower intensity requirements and shorter application duration (Chia & Kubota, 2010).

Photoperiodic flowering in plants is achieved by the interactions of genes involved in the developmental control of floral initiation, the regulation of the circadian clock, and the signal transduction of phytochromes and cryptochromes receptors. For successful planning of flowering, coordination of all environmental factors, including light quality and intensity, timing, temperature, etc., has to be considered.

In SDP, it is acknowledged that R light is most effective at inhibiting flowering (Craig & Runkle, 2013), but the sensitivity to the R : FR ratio and the duration of NI or EOD lighting differs between species or even cultivars.

In three SDP ornamental species chrysanthemum , dahlia , and African marigold flowering was delayed at R : FR 0.66 or greater. NI treatment that primarily emits

R light was determined to be the most effective in terms of flower inhibition for the SDP studied. The comparison between incandescent lights that emit low levels of B light and LED lighting without B light were shown to have similar effects on flowering, and it was found that B light, not FR light alone, was not needed to regulate flowering (Craig & Runkle, 2013).

In LDP, flowering is promoted most when artificial lighting contains R and FR light, creating a moderately low Pfr/Pt, compared to light deficient in FR (high Pfr/Pt) (Runkle & Heins, 2001). To determine the effect of FR, R, and B light on flowering in five LDP species (*Campanula carpatica* Jacq., *Coreopsis x grandiflora* Hogg ex Sweet, *Lobelia x speciosa* Sweet, *Pisum sativum* L., and *Viola x wittrockiana* Gams), plants were exposed to 16-hour photoperiod under R-, FR- and B-deficient photoselective filters in addition to a control (no filter). FR light promoted flowering, although the analysed species showed different sensitivity to changed R : FR ratios. Reaction to lower R : FR ratio was, similarly as in stem elongation, greater in sun-adapted species *C. carpatica* and *C. x grandiflora*. The authors observed that the time of day when the plants are exposed to FR could also have an impact on flowering. In this study, B light had little or no effect on flowering, but since the absorption of B light has been shown to accelerate flowering in *Arabidopsis* and *Hyoscyamus*, the authors speculated that the intensity of B light was too low to induce the effect. The promotion of flowering by 7-11 days at low R : FR ratio was also observed in LDP petunia (Park & Runkle, 2019). As in previously cited studies, authors found that B light had no effect on the FR light promotion of flowering.

Zahedi and Sarikhani (2016) studied the simultaneous effects of EOD FR treatment duration, temperature, and plant age on strawberry (*Fragaria x ananassa* Duchesne) development. They demonstrated their synergistic effect on the morphological traits and flower induction.

4.4 FR IN PLANT DEFENCE AND INTERACTIONS WITH ABIOTIC FACTORS

A vast number of studies has revealed the importance of phytochromes in plant development, although more recently, the evidence of their role in modulating different biotic and abiotic stresses is expanding. The understanding of the molecular mechanisms underlying the reactions controlled by phytochrome is constantly increasing. This and the availability of phytochrome mutants in different plant species facilitates further investigation of their role in the complex coordination of responses to various environmental factors. The propor-

tion of R and FR light detected by phytochromes, especially phy B, has been shown to play a role in regulating signalling induced by herbivory (Ballaré, 2017), salt stress (Cao et al., 2018), drought stress (González et al., 2012) and temperature change (Lorenzo et al., 2016). Because those environmental conditions can greatly affect plant productivity, the studies on phytochrome regulation of stress responses have become a hot spot of research.

To survive and prosper in different natural conditions, plants must precisely allocate their limited resources between growth and defence. In an environment with low R : FR ratios (shade) the numerous shade avoidance responses are triggered; however, the plant's immunity is reduced (McGuire & Agrawal, 2005; Roberts et al., 2006). The main mechanism underlying defence suppression is the simultaneous downregulation of jasmonate and salicylic acid signalling by low ratios of R : FR radiation (De Wit et al., 2013; Ballaré, 2014). Exposure to a low R : FR light reduced plant resistance against *Botrytis cinerea* Pers. in *Arabidopsis thaliana* (L.) Heynh., (Cerrudo et al., 2012; Cargnel et al., 2014) and in tomatoes (Ji et al., 2019). It was shown that fluorescent illumination with a high R : FR ratio (7.0) in comparison with low R : FR ratio (1.1) improved the resistance of cucumber seedlings to powdery mildew (Shibuya et al., 2011).

Several studies demonstrated that phytochromes, especially phyB, play a role in modulating signalling induced by drought stress. Drought tolerance can be promoted or depressed, according to species (Demotes-Mainard, 2016). Gonzalez et al. (2012) evaluated how phyB modulates drought-tolerance response by comparing wild-type *Arabidopsis thaliana* adult plants to the null phy B mutant in response to water shortage. They proposed that phyB, according to changes in the R : FR ratio, increases drought tolerance by enhancing ABA sensitivity. Drought tolerance could also be affected by morphological responses to the R : FR ratio, such as changes in leaf area and hyponasty (Demotes-Mainard et al., 2016).

Recently, it has been shown that exposure to lower R : FR ratios improve tomato tolerance to salt stress most likely through regulation of antioxidant enzymes and non-enzymatic systems and that phytochrome B1 plays a very important role in this process. The improved salt stress tolerance was accompanied by a higher actual quantum yield of photosynthesis (Φ PSII), electron transport rate (ETR), and photochemical quenching (qP), indicating overall healthier growth (Cao et al., 2018).

5 CONCLUSION

The growing knowledge about photoreceptors and the mechanisms by which light controls plant growth

and development have been successfully applied in horticulture. In recent years, light-emitting diodes (LEDs) have facilitated the control of the spectral composition of supplemental lighting and expanded the application of different solo or combined wavelengths in greenhouse plant production. Adding FR light or lowering R : FR ratio has been shown to positively affect the photosynthesis and resulting biomass of some vegetable species. FR light can simultaneously elicit different morphological and physiological responses, among which only some are desirable. To efficiently use lighting for the manipulation of desired characteristics and to provide the horticultural products of high quality, more research is needed to understand better the mutual influence of different spectral combinations of light and other environmental conditions present at cultivation (e.g., photoperiod, temperature, water availability, nutrition, etc.). In many cases, it has been shown that the photomorphogenic responses are species-specific and, since the majority of research is done on a few model species, the analyses of other species would be necessary.

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