

REVIEW

Pest and disease management by red light

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Abstract

Light is essential for plant life. It provides a source of energy through photosynthesis and regulates plant growth and development and other cellular processes, such as by controlling the endogenous circadian clock. Light intensity, quality, duration and timing are all important determinants of plant responses, especially to biotic stress. Red light can positively influence plant defence mechanisms against different pathogens, but the molecular mechanism behind this phenomenon is not fully understood. Therefore, we reviewed the impact of red light on plant biotic stress responses against viruses, bacteria, fungi and nematodes, with a focus on the physiological effects of red light treatment and hormonal crosstalk under biotic stress in plants. We found evidence suggesting that exposing plants to red light increases levels of salicylic acid (SA) and induces SA signalling mediating the production of reactive oxygen species, with substantial differences between species and plant organs. Such changes in SA levels could be vital for plants to survive infections. Therefore, the application of red light provides a multidimensional aspect to developing innovative and environmentally friendly approaches to plant and crop disease management.

KEYWORDS

LED, light, pathogens, phytochrome, reactive oxygen species, resistance, salicylic acid

1 | INTRODUCTION

Rapid human population growth is increasing the pressure on agriculture for increased crop production (Foley et al., 2011; Godfray et al., 2010). The use of irrigation, synthetic fertilizers, supplemental lighting and pesticides in greenhouses are beneficial to increasing crop yields (Damalas & Eleftherohorinos, 2011; Roberts & Mattoo, 2018). However, increases in agricultural production lead to increased climate change and have negative impacts on biodiversity, soil and the availability and quality of freshwater (Palm, Blanco-Canqui, DeClerck, Gatere, & Grace, 2014; Power, 2010). These effects of the agricultural sector and the high costs of crop production have resulted in significant scientific and social debates around the development of new and

sustainable plant and crop protection strategies to elevate food production (Roberts & Mattoo, 2018, 2019; Simkin, López-Calcano, & Raines, 2019). The key to overcoming these problems is the development of environmentally friendly and high-yielding approaches with fewer adverse effects on the environment.

Light is a dynamic component of the terrestrial environment, and it plays a pivotal role in regulating plant life, such as optimal plant growth and development, as well as different defence responses against pathogens (Hua, 2013). Light has both quantitative and qualitative features, and plants, as well as microorganisms, are able to sense light using various photoreceptors (Folta & Carvalho, 2015). Light-induced signal transduction pathways, the circadian clock and photosynthetic activity mediate the molecular, biochemical and

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physiological responses of both plants and microorganisms (Ballaré, 2014; Chen, Chory, & Fankhauser, 2004; Fernández-Milmanda et al., 2020; Kazan & Manners, 2011; Roberts & Paul, 2006). The presence or absence, period, quality, intensity and timing of available light can alter and influence plant responses and metabolism to various stress effects, as well as the composition, habits and lifestyle of microorganisms in the phyllosphere (Carvalho & Castillo, 2018). Therefore, artificial manipulation of light characteristics during cultivation can influence crop production and trigger plant defence mechanisms against pathogens.

This review aims to summarize available knowledge on red light-regulated plant defence mechanisms, especially focusing on the role of phytohormones in these processes. This knowledge could contribute to the development of new strategies for plant protection and crop science.

2 | LIGHT SENSING AND PLANT RESPONSES

Light is electromagnetic radiation from the sun. White light is a mixture of the colours of the visible spectrum, which ranges from 400 to 700 nm: violet (400 nm), indigo (445 nm), blue (475 nm), green (510 nm), yellow (570 nm), orange (590 nm) and red (650 nm). Infra-red radiation has a longer wavelength than visible red light, and ultra-violet (UV) radiation has a shorter wavelength than visible violet light (Thind & Schilder, 2018).

Light is as essential as an energy source and environmental signal for plants. It regulates a wide range of developmental processes, including germination, de-etiolation, stomatal development, circadian rhythm and flowering (de Wit, Galvão, & Fankhauser, 2016). Furthermore, it can influence growth and developmental processes, including

different metabolic pathways in plant-pathogen interactions (Purschwitz, Müller, Kastner, & Fischer, 2006; Thind & Schilder, 2018; Tisch & Schmoll, 2010; van der Horst, Key, & Hellingwerf, 2007). In contrast to optimal light conditions, high and low light intensity, including darkness, induce different signalling and regulation pathways modulated by phytohormones, especially jasmonic acid (JA) and salicylic acid (SA) (Ballaré, 2014; Deepika, Sagar, & Singh, 2020; Roberts & Paul, 2006).

Light is interpreted as an informational signal by photoreceptors, which absorb photons via a specific prosthetic chromophore and induce structural changes in the protein part of the receptor (Folta & Carvalho, 2015). There are various photoreceptors in plants: red/far-red-light-sensing phytochromes (phyA-phyE), blue-light-sensing cryptochromes (cry1-3) and phototropins (phot1 and phot2), Zeitlupe family members (ZTL, FKF1 and LKP2) and UV-B receptor UVR8 (Demarsy, Goldschmidt-Clermont, & Ulm, 2018; Paik & Huq, 2019) (Figure 1).

The analysis of *Arabidopsis thaliana* photoreceptor mutants showed that phyB is the primary photoreceptor for red light perception and inhibits hypocotyl growth, whereas phyA senses far-red light and induces hypocotyl growth and shade avoidance. PhyA and phyB, which are a unique type of photoreceptors, are synthesized in the cytosol in an inactive form and they are transported within minutes into the nucleus after the activation by red light (Sheerin et al., 2015; Yamaguchi, Nakamura, Mochizuki, Kay, & Nagatani, 1999). Red light absorption results in a photoreversible conformational change from the inactive cytosol-localized red-light-absorbing form (Pr) to the active far-red-light-absorbing form (Pfr), which induces phy-mediated physiological responses through the transcriptional regulation of numerous genes (Nagatani, 2004; Su et al., 2017).

Activated phytochromes induce a network of downstream processes. They mediate the phosphorylation and degradation of

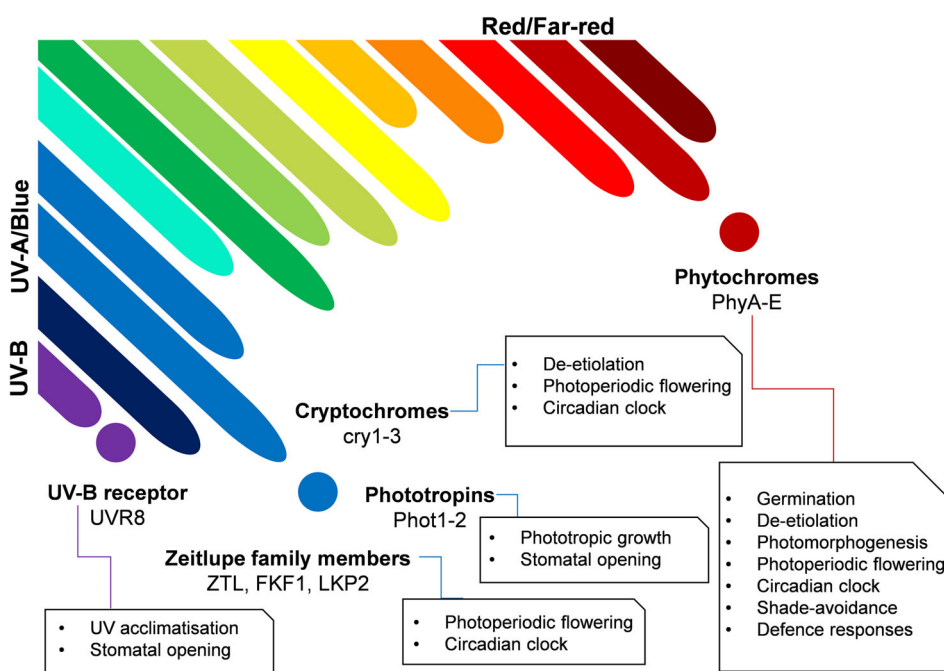


FIGURE 1 Plant photoreceptors and their role in plant life regulation. Red/far-red-light is sensed by phytochromes (phyA-phyE), blue-light is absorbed by cryptochromes (cry1-3), phototropins (phot1 and phot2) and Zeitlupe family members (ZTL, FKF1 and LKP2). UV-B is perceived by UVR8. Photoreceptors mediated plant responses are shown in boxes (based on Paik & Huq, 2019) [Colour figure can be viewed at wileyonlinelibrary.com]

phytochrome-interacting factors (PIFs), as they repress the activity of the constitutively photomorphogenic 1 (COP1)/suppressor of phyA-105 (SPA) complex, which inhibits the photomorphogenesis or shade-avoidance responses through the transcriptional inhibition of the auxin biosynthetic genes (Casal, 2013; Hoang, Han, & Kim, 2019; Li et al., 2012; Sheerin et al., 2015).

There is a close interaction between light signalling and photomorphogenesis, which is regulated by phytohormones, such as by JA (Goossens, Fernández-Calvo, Schweizer, & Goossens, 2016). If the ratio between red and far-red is high, phyB suppresses the shade-avoidance response and enhances sensitivity to JA, and promotes defence mechanisms (Robson et al., 2010; Xiang, Wu, Jing, Chen, & Yu, 2021). In a low ratio of red/far-red light, phyB is inactivated, shade responses are activated and sensitivity to JA is reduced (Moreno, Tao, Chory, & Ballaré, 2009). Besides their essential role in shade avoidance, phytochromes regulate seed germination, de-etiolation, photomorphogenesis, photoperiodic flowering and the circadian clock (Casal, 2013; Hernando, Murcia, Pereyra, Sellaro, & Casal, 2021; Pierik & de Wit, 2014; Su et al., 2017).

3 | THE ROLE OF LIGHT AND THE KEY DEFENCE-RELATED PHYTOHORMONES IN PLANTS

Various phytohormones play a role in the regulation of plant defence responses depending on the light (Ballaré, 2014; Deepika et al., 2020; Roberts & Paul, 2006). SA is required to establish both local and systemic acquired resistance after pathogen infection. The elevated concentration of SA under stress conditions induces the rapid accumulation of reactive oxygen- (ROS) and nitrogen species (e.g., nitric oxide; peroxyxynitrite), leading to oxidized proteins and hypersensitive response-like cell death in infected tissues, which is more pronounced under high light (Loake & Grant, 2007; Poór, 2020; Vlot, Dempsey, & Klessig, 2009). Moreover, SA plays a crucial role in systemic responses, which promotes a faster and stronger response to a secondary infection (Arif, Sami, Siddiqui, Bajguz, & Hayat, 2020; Klessig, Choi, & Dempsey, 2018). SA regulates various components of defence responses, such as synthesis of antioxidants, such as ascorbate; disease inhibitor polyphenols and flavonoids; antimicrobial phytoalexins, such as camalexin; and pathogenesis-related (PR) proteins, such as β -1,3-glucanases and chitinases (Klessig et al., 2018; Tripathi, Raikhy, & Kumar, 2019). At the same time, it was also reported that SA had a direct effect on microbes. Among the others, SA inhibited the spore germination and colony growth rate of *Harpophora maydis* (Degani, Drori, & Goldblat, 2015) and reduced hyphal growth of *Aspergillus flavus* (Panahirad, Zaare-Nahandi, Mohammadi, Alizadeh-Salteh, & Safaie, 2014).

Although SA plays a primary role in resistance against biotrophic and hemibiotrophic pathogens, JA and gaseous ethylene (ET) regulate the plant immune response against necrotrophic and herbivorous insect pathogens (Glazebrook, 2005; Vlot et al., 2009). Numerous studies have already indicated that JA activates the anti-nutritive

defence of plants against herbivores by inducing the synthesis of proteinase inhibitors and polyphenol oxidases. Further, JA increases the activity of other defensive enzymes, such as peroxidase (POD), chitinase and lipoxygenase, and it promotes the accumulation of some secondary metabolites responsible for plant defence responses, such as alkaloids, flavonoids and other phenolic compounds (Vasyukova & Ozeretskovskaya, 2009; Wasternack & Hause, 2013). The direct effects of JA and ET on microbes were also reported. JA reduced the spore germination and mycelium growth of *Fusarium oxysporum* f. sp. *lycopersici* in vitro (Król, Igielski, Pollmann, & Kępczyńska, 2015). In addition, ET also affected spore germination and hyphal growth of *Botrytis cinerea* (Chagué et al., 2006). At the same time, the SA-dependent defence is antagonistic with JA-/ET-dependent defence signalling, but this hormonal crosstalk could be different and highly depends on other phytohormones (e.g., gibberellins), on the plant-pathogen systems or environmental conditions, such as available light (De Vleeschauwer et al., 2016; Klessig et al., 2018; Koo, Heo, & Choi, 2020; Robert-Seilaniantz, Grant, & Jones, 2011). Therefore, it can be concluded that the presence or absence of light is a crucial factor in phytohormone-mediated responses.

At the same time, endogenous contents of SA and JA in plants show daily changes (Wasternack & Hause, 2013). The basal levels of these phytohormones, which affect plant immunity, are regulated also by the circadian clock (Karapetyan & Dong, 2018; Lu, McClung, & Zhang, 2017; Roden & Ingle, 2009; Spoel & van Ooijen, 2014). Time for coffee (TIC), a night-expressed clock gene, inhibits JA signalling in the evening and contributes to a stronger JA responsiveness in the morning. JA content shows a high peak in the middle of the day, whereas SA peaks in the middle of the night, because the expression of the key enzyme responsible for SA biosynthesis (e.g., isochorismate synthase 1) is driven by the evening-phased clock transcription factor CCA1 hiking expedition (CHE) (Zheng et al., 2015). Considering these observations, not only the availability of light but the circadian rhythm can also influence the basal phytohormone-mediated defence responses of plants.

Finally, it should be mentioned that there is a dynamic interaction between plants and other microbes, which can modulate the phytohormone levels in the host by regulating the mutualistic and/or pathogenic strategies of bacteria or fungi (Fonseca, Radhakrishnan, Prasad, & Chini, 2018). Namely, plant pathogens are able to manipulate and/or diminish phytohormone signalling for their own benefit, and as a consequence promote the infection development in the host organism (Shen, Liu, & Naqvi, 2018). There are many data confirming that abscisic acid, gibberellic acid and ET produced by fungi influence the pathogenicity (Chanclud & Morel, 2016). Among others, the necrotrophic *Moniliophthora perniciosa* can produce SA and JA, which manipulate the defence signalling in the host, cocoa plants (Chaves & Gianfagna, 2006; Kilaru, Bailey, & Hasenstein, 2007). Some publications suggested that auxin and cytokinins produced by fungi could be positive regulators of virulence (Chanclud & Morel, 2016; Shen et al., 2018). Similar phytohormone level modulating ability of auxin, cytokinins and gibberellic acid has been reported in various bacteria (Olanrewaju, Glick, & Babalola, 2017). The ET generation inhibition by

the bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase is one of the well-investigated interaction in rhizobacteria-plant relation (Singh, Shelke, Kumar, & Jha, 2015).

4 | LIGHT SENSING AND PHYTOPATHOGEN RESPONSES

In contrast to plants, little information is available about the impact of light signals on microbial virulence (Santamaría-Hernando et al., 2018). Similar to plants, plant pathogenic bacteria possess diverse photoreceptors, which can be classified into six families according to the chemical structure of chromophores: rhodopsins, red-light-sensing phytochromes, xanthopsins, cryptochromes, blue-light-sensing light, oxygen and voltage (LOV) and blue-light sensing using flavin (BLUF) proteins (van der Horst et al., 2007). Light not only provides positional information to pathogens on top of the soil/leaf surface (Carvalho & Castillo, 2018), but several studies have reported that it regulates numerous physiological features, especially motility, adhesion and virulence of plant pathogens, for example, in *Pseudomonas syringae* pv. *syringae* B728a (McGrane & Beattie, 2017; Wu, McGrane, & Beattie, 2013), *P. syringae* pv. *tomato* (Moriconi et al., 2013; Río-Alvarez et al. 2014; Ricci, Dramis, Shah, Gärtner, & Losi, 2015; Shah, Pathak, Drepper, & Gärtner, 2016; Santamaría-Hernando et al., 2018; Moyano et al., 2020), *Pseudomonas cichorii* (Nagendran & Lee, 2015; Rajalingam & Lee, 2018), *Agrobacterium fabrum* (Bai, Rottwinkel, Feng, Liu, & Lamparter, 2016), *Xanthomonas campestris* (Bonomi et al., 2016) and *Xanthomonas citri* subsp. *citri* (Kraiselburd et al., 2012).

Light also regulates the life cycle of fungi by controlling gene expressions, and it has a significant effect on sporulation, primary metabolic pathways and secondary metabolite production. However, only a few different photoreceptors have been described in fungi, such as flavin-binding blue-light receptors, retinal-containing green-light sensors and red-light sensor-containing proteins with a linear tetrapyrrole as the functional part of the chromophore. Blue- and red-light receptors have nuclear functions, and they can directly regulate the expression of different genes and metabolic and morphogenetic pathways (Thind & Schilder, 2018; Yu & Fischer, 2019). Light has an effect on fungal growth, and it can directly inhibit metabolism, hyphal development, sexual reproduction and sporulation. Furthermore, it can reduce virulence. These effects have been proven for *Alternaria alternata* (Hubballi, Nakkeeran, Raguchander, Anand, & Samiyappan, 2010), *Aspergillus carbonarius* (Cheong et al., 2016), *Botryodiplodia theobromae* (Alam, Begum, Sarkar, Islam, & Alam, 2001), *B. cinerea* (Caires, Rodrigues, & Furtado, 2015; Canessa, Schumacher, Hevia, Tudzynski, & Larrondo, 2013; Schumacher, Simon, Cohrs, Viaud, & Tudzynski, 2014; Zhu et al., 2013), *Bremia lactucae* (Nordskog, Gadoury, Seem, & Hermansen, 2007), *Colletotrichum acutatum* (Yu, Ramkumar, & Lee, 2013), *Cryptonectria parasitica* (Hillman, Shapira, & Nuss, 1990), *Fusarium graminearum* (Beyer, Rödning, Ludewig, & Verreet, 2004), *Fusarium verticillioides* (Velmurugan et al., 2010), *Magnaporthe oryzae* (Lee et al., 2006),

Peronospora belbahrii (Cohen, Vaknin, Ben-Naim, & Rubin, 2013), *Phakopsora pachyrhizi* (Li, Mo, Guo, & Yang, 2010), *Plasmopara viticola* (Rumbolz et al., 2002), and *Puccinia hemerocallidis* (Dong & Buck, 2011; Mueller & Buck, 2003).

It is evident that life in the phyllosphere depends on whether it is day or night, and on light quantity and quality. Therefore, understanding perception regulation and the effects of different light spectra, signalling and metabolism are crucial to providing deeper insight into plant-microbe interactions. Such knowledge could inform the development of alternative methods of effective plant disease control and pest management.

5 | LED AS THE NEW SUN

Light sources are generally used in modern agriculture in addition to natural sunlight to maximize the photosynthetic activity of plants and improve crop yield (Massa, Kim, Wheeler, & Mitchell, 2008). Many conventional light systems are already available on the market, such as fluorescent light, metal halide, high-pressure sodium and incandescent lamps, with a wide range of wavelengths from 350 to 750 nm. However, emitted photosynthetically active radiation from above could be limited in the phyllosphere, and then utilized light cannot reach its goal to sustain high crop productivity (Olle & Viršile, 2013). New and highly developed light-emitting diode (LED) technology provides an economically viable option to improve crop production. LED is a unique type of semiconductor diode that can emit a wide range of light from UV-C (~250 nm) to infrared (~1,000 nm) (Bourget, 2008). Moreover, LED technology has many other advantages over other light sources. It is relatively cheap, energy-saving, functional, not fragile, emits minimal heat and not hazardous. Furthermore, it can easily be integrated into a digital control system (Morrow, 2008; Olle & Viršile, 2013; Singh, Basu, Meinhardt-Wollweber, & Roth, 2015). In addition, LED is the first light source that can control the light spectra during a cultivation period. Therefore, it can be used for precise manipulation of biological plant responses to light, such as photosynthesis, photomorphogenesis, flowering, metabolite production and plant defence (Davis & Burns, 2016; Gómez & Izzo, 2018). However, precise control of spectral quality and light intensity requires fundamental knowledge about the responses of plants and their associated microorganisms. The use of LEDs provides many eco-friendly and sustainable solutions for the regulation of plant growth, development and productivity, as well as defence against microbial pathogens. LEDs can be used as a supplemental light source and for inter-light systems, vertical farming in conventional and urban agriculture and disease and pest control (Davis & Burns, 2016; Gómez & Izzo, 2018; Olle & Viršile, 2013; Wu, Hitti, MacPherson, Orsat, & Lefsrud, 2020). Moreover, LED technology provides a daily light system or photoperiodic lighting with different spectra. These applications can revolutionize greenhouse farming and horticultural technologies.

Precise manipulation of light intensity and quality has already been proposed as a novel plant disease management strategy. However, the physiological and molecular mechanism is not fully

understood (Demotes-Mainard et al., 2016). Therefore, investigating red light-induced molecular, biochemical and physiological changes in both the host and its particular pathogens is essential to accelerate the application of red light as supplemental lighting, inter-lighting and nocturnal lighting in plant disease management.

In the next subchapter, the effects of red light on plant–viruses, plant–bacteria, plant–fungi and plant–nematode interactions are collated and critically discussed based on the process of pathogenesis. The role of ROS and SA in red light-induced resistance of plants is particularly scrutinized in these interactions.

6 | RED LIGHT INHIBITS THE PATHOGENESIS

While beneficial role of red light treatment for plants was described under the infection of many different types of pathogens, the common protective effect of red light in different pathosystems is still unclear. Despite the mechanism of pathogenesis depends on the type of infectious agents (Brader et al., 2017; Grimmer, John Foulkes, & Paveley, 2012; Serrano, Coluccia, Torres, L'Haridon, & Métraux, 2014), the rapid local and long-term systemic defence responses by plants upon red light are general. In this subchapter, these responses are collected and compared. In addition, various lightening methods are also discussed.

6.1 | Pathogen perception

Limited information is available in the literature about the effects of red light on pattern recognition receptors such as LRR receptor-like serine/threonine-protein kinase FLS2, calcium signalling, activation of calmodulin and calcium-dependent protein kinases or mitogen-activated protein kinase during the pathogenesis (Feng & Zhou, 2012; Serrano et al., 2012). Yang et al. (2015) found that nightly red light illumination enhanced resistance against *P. syringae* pv. *tomato*, which was correlated with increased SA accumulation and the transcription of defence-related genes in tomato plant leaves (*Solanum lycopersicum* L.). Using RNA-seq analysis, they observed that 12 h of red light exposure at night up-regulated calcium homeostasis-related genes (calmodulin and calmodulin-binding protein) (Yang et al. 2015). Calcium, as a second messenger regulates downstream signalling resulting in the activation of defence-and/or cell death-related genes (Ranf, Eschen-Lippold, Pecher, Lee, & Scheel, 2011; Wang et al., 2019). In addition, there is a strong interaction between intercellular elevation of calcium and ROS, which in waves transmit long-distance signals via cell-to-cell communication pathway under stress (Fichman & Mittler, 2020; Gilroy et al., 2014). Moreover, there is a strong interaction between ROS and defence-related phytohormone signalling such as in the case of SA locally and systemically (Klessig et al., 2018; Vlot et al., 2009). In the next paragraphs, the role of ROS and SA signalling in the pathogenesis under red light exposure is discussed.

6.2 | ROS metabolism regulation

Changes in ROS metabolism upon red light under the infection can be an integrated part of the plant defence. This was supported by the observation that the plasma membrane-localized NADPH oxidase is a crucial component of PR defence signalling under red light, contributing to the first, priming oxidative burst after pathogen infection (Jiménez-Quesada, Traverso, & Alché, 2016) and mediating programmed cell death (Van Aken & Van Breusegem, 2015). NADPH oxidase is able to translocate electrons from cytosolic NADPH to oxygen, leading to the generation of superoxide in the apoplast (Sagi & Fluhr, 2006). This was confirmed in broad beans (*Vicia faba* L.) against *B. cinerea* infection where the activation of NADPH oxidase was inhibited by diphenyleneiodonium, therefore, necrotic lesions were formed by the pathogen (Khanam, Kihara, Honda, Tsukamoto, & Arase, 2005; Khanam, Ueno, Kihara, Honda, & Arase, 2005). Moreover, 12 hours-long red light exposure at night up-regulated the expression of NADPH oxidase (*Respiratory burst oxidase homologue; RBOH*) in tomato plant leaves under *P. syringae* infection (Yang et al. 2015).

Besides the NADPH oxidase-generated superoxide, hydrogen peroxide (H_2O_2) plays also a crucial role in cellular responses of the living organism under the infection. These reactive molecules are generated by plants rapidly and as strong oxidizing compounds can disturb the cell integrity by targeting lipids, proteins and nucleic acids. As a consequence, programmed cell death at the site of the infection is induced (Czarnocka & Karpiński, 2018; Noctor, Reichheld, & Foyer, 2018). H_2O_2 is known as the most stable and diffusible ROS. H_2O_2 works as a signalling molecule at low concentration mediating defence responses of plants by influencing anti-oxidant enzymes even in distal parts from the site of the infection. At high concentration, it induces oxidative stress (Kocsy et al., 2013; Van Aken & Van Breusegem, 2015). H_2O_2 is generated by superoxide dismutase (SOD) from the conversion of superoxide to molecular oxygen and water (Alscher et al., 2002) and degraded enzymatically in several ways. Peroxisome-localized catalase (CAT) and the cytosolic or chloroplastic ascorbate peroxidase (APX), as well as several other enzymes (e.g., other peroxidases, POD) degrade H_2O_2 to water. Other non-enzymatic systems such the ascorbate/dehydroascorbate and the glutathione/glutathione disulphide are also able to diminish the H_2O_2 level (Foyer & Noctor, 2009; Mhamdi et al., 2010).

Significant changes in ROS metabolism mediated by red light in various plant species and organs were observed under plant–virus, –bacterium, –fungi and nematode interactions, respectively. Mosaic viruses, such as cucumber mosaic viruses, have a wide host range and cause severe damage to various crops (Palukaitis, Roossinck, Dietzgen, & Francki, 1992). Symptoms of cucumber mosaic virus are significantly decreased under red light exposure at 7 days post-infection in tobacco (*Nicotiana tabacum* L.) leaves (Chen, Zhao, Zhang, Lin, & Xi, 2015). In addition, red light reduces ROS formation and the production of superoxide and H_2O_2 . In parallel, it induces SOD, CAT and POD activities, as well as increases ascorbate and glutathione

level in tobacco leaves under cucumber mosaic virus infection (Chen et al., 2015).

Beneficial effects of red light illumination in the defence against fungal pathogens regulated by ROS metabolism were found in various plant species (Figure 2). The grey mould, *B. cinerea*, is one of the most significant necrotrophs and causes severe economic losses in at least 200 plant species worldwide. *B. cinerea* produces a range of cell-wall-degrading enzymes and toxins triggering programmed cell death in the host (Williamson, Tudzynski, Tudzynski, & van Kan, 2007); however, red light exposure for 3 and 4 days significantly reduce *B. cinerea*-induced lesion development in tomato detached leaves in contrast to those ones kept in the dark (Hui, Fu, Li, & Rui, 2017). In addition, red light treatment significantly induced the activity of SOD, CAT and POD after 2 days during a *B. cinerea* infection event, and in parallel, they significantly decreased the superoxide and H₂O₂ content in detached tomato leaves (Hui et al., 2017). A photoperiod of 16 h red light increased total phenol, flavonoid, chlorophyll and anthocyanin contents but significantly decreased H₂O₂ level after 4 weeks in strawberry (*Fragaria × ananassa* “Elsanta”) leaves compared to those ones kept under white light where the level of these compounds was

found to be significantly lower except for H₂O₂, which showed elevated levels (Meng, Höfte, & Van Labeke, 2019). Rice blast caused by *M. oryzae*, is one of the most severe diseases of rice plants (Ebbola, 2007). Interestingly, red light exposed a significant effect on H₂O₂ reduction via increasing CAT activity under *M. grisea* infection in detached rice (*Oryza sativa* L.) leaves (Ueno, Imaoka, Kihara, & Arase, 2007). *Podosphaera* species are one of the most important fungal pathogens of greenhouse-grown plants (Debener & Byrne, 2014). Under *Podosphaera xanthii* infection, decreased H₂O₂ content and increased content of lignin-binding hydroxyproline-rich glycoprotein, POD activity and gene expression were found upon red light application compared with white light, which mainly play a role in cell wall modification (Jing et al., 2018). Activation of defence mechanisms in *Sphaerotheca fuliginea*-infected cucumber (*Cucumis sativus* L.) leaves after red light treatment was described by Wang et al. (2010). Red light illumination decreased the powdery mildew colony number after 10 days of infection and H₂O₂ accumulation was observed in these leaves in the consequence of the decreased APX and CAT enzyme activities (Wang et al., 2010). The red light-modified ROS metabolism is also a significant part of defence mechanisms against nematodes.

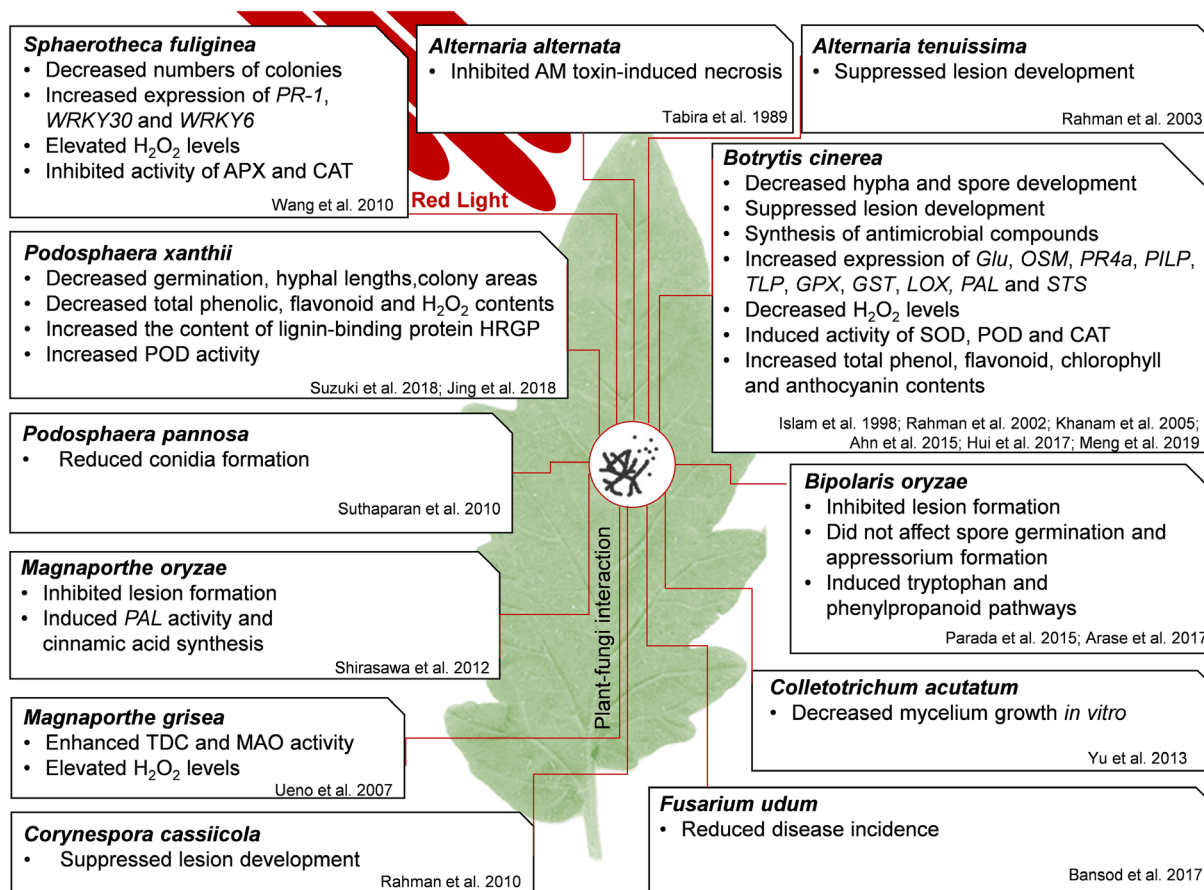


FIGURE 2 Effects of red light in plant–fungi interactions. APX: ascorbate peroxidase; CAT: catalase; *Glu*: β-1,3 glucanase; GPX: glutathione peroxidase; GST: glutathione-S-transferase; HRGP: hydroxyproline-rich glycoprotein; LOX: lipoxygenase; OSM: osmotin; MAO: monoamine oxidase; PAL: phenylalanine ammonia-lyase; PILP: protease inhibitor-like protein; POD: peroxidase; PR: pathogen-related; SOD: superoxide dismutase; STS: stilbene synthase; TDC: tryptophan decarboxylase; TLP: thaumatin-like protein [Colour figure can be viewed at wileyonlinelibrary.com]

Not only viruses and fungi but also the endoparasitic nematode *Meloidogyne incognita* causes significant yield losses in different crops, such as tomato, cucumber, celery and watermelon (Chitwood, 2002). The supportive effects of red light exposure in the systemic resistance of watermelon (*Cucumis melo* L.) against this root-knot nematode, are coordinated by both SA and JA, and are also regulated by changes in redox homeostasis, which were reported by Yang et al. (2018). The combined treatment (red light + root-knot nematode) resulted in significantly higher H₂O₂ levels, increased activities of SOD, CAT, APX and POD, moreover, higher glutathione and ascorbate contents in both the leaves and roots (Yang et al., 2018).

6.3 | Effects on the defence-related phytohormone signalling

Changes in ROS metabolism and redox homeostasis contribute to the biosynthesis and activation of defence-related phytohormones (Glazebrook, 2005; Vlot et al., 2009). Among these, elevated endogenous SA levels and highly activated SA signalling were observed in case of all biotic stressors under red light exposure. First of all, increased SA levels and SA-mediated *PR-1*, *PR-2* and *PR-5* expression have been observed under red light illumination in tobacco leaves exposed to cucumber mosaic virus (Chen et al., 2015).

Besides the cucumber mosaic virus, red light significantly influences SA signalling in bacteria-infected plants (Figure 3). Red light decreased the incidence of Gram-negative *P. cichorii* infection and reduced the bacterial burden in tomato (*S. lycopersicum*) seedlings and leaves after 4 days in comparison with white light illumination or keeping the plants in the dark. In addition, red light defended the tomato plants against this infection by upregulating the expression of defence-, SA biosynthesis- and signalling-related *phenylalanine*

ammonia-lyase and *PR-1a* genes. This upregulation effect was not observed at plants that were kept in the dark (Nagendran & Lee, 2015). The protective effect of red light illumination on rotting disease caused by *Pseudomonas putida* has also been described in soybean (*Glycine max* L. Merr.) seedlings. Red light increased resistance of plant against this bacterium after 5 days of infection. Elevated SA level, but not the accumulation of JA, was detected in infected hypocotyl after red light treatment. Moreover, upregulation of SA biosynthetic genes, such as *isochorismate synthase* and *phenylalanine ammonia-lyase*, and the SA response gene *PR-1* were also recorded after red light exposure (Dhakal, Park, Lee, & Baek, 2015). SA-dependent disease development was confirmed by investigating transgenic SA-non-accumulating *nahG Arabidopsis* plants under *P. syringae* infection (Islam, Babadoost, Bekal, & Lambert, 2008). Later, Yang et al. (2015) studied the protective effect of nightly red light treatment in tomato plant leaves. They found that red light illumination enhanced resistance against *P. syringae* pv. *tomato*, which was correlated with increased SA accumulation and the transcription of defence-related genes. They observed that 12 h of red light exposure at night upregulated biosynthesis genes of phytohormones (e.g., SA, auxin, JA and ET) and transcription factors responsible for defence hormone-related (e.g., SA and JA) gene expression and disease resistance (*WRKY18*, *WRKY53*, *WRKY60*, and *WRKY70*) (Yang et al., 2015). This article informs the potential application of nightly red light treatment to control *P. syringae* infection (Figure 4).

Effects of red light treatment on SA metabolism during fungal infection were investigated only by Wang et al. (2010). Red light illumination decreased the powdery colony number (*S. fuligine*) after 10 days of infection in cucumber leaves parallel with SA level elevation. In addition, the transcript levels of SA-regulated defence-related genes, such as *PR-1*, *WRKY30* and *WRKY6*, were also significantly higher as compared with those in white light-treated samples (Wang et al., 2010). These results allow the conclusion that SA is an

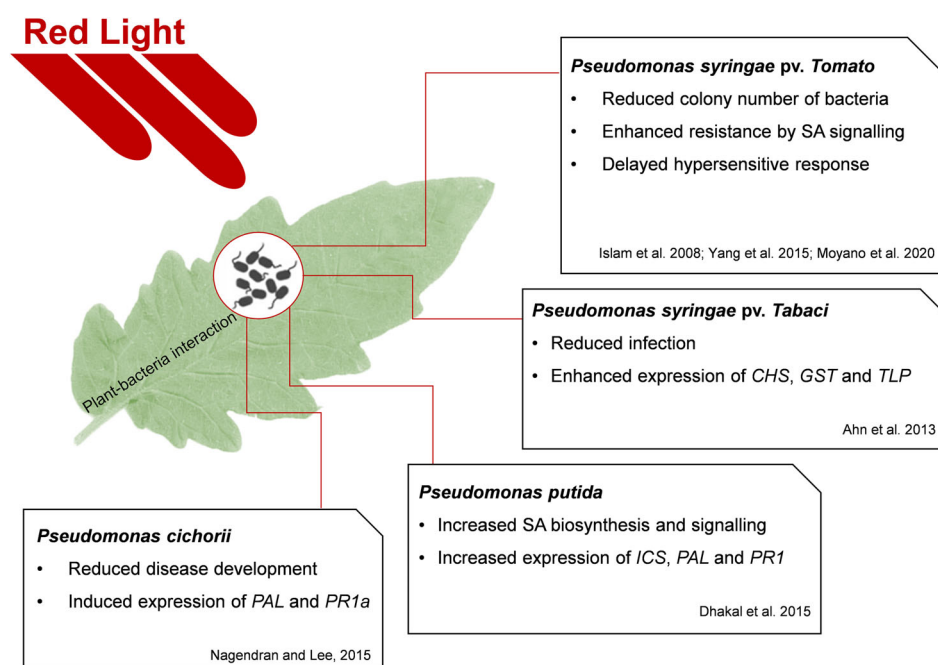


FIGURE 3 Effects of red light in plant–bacterium interactions *CHS*: chalcone synthase; *GST*: glutathione-S-transferase; *ICS*: isochorismate synthase; *PAL*: phenylalanine ammonia-lyase; *PR*: pathogenesis related; *SA*: salicylic acid; *TLP*: thaumatin-like protein [Colour figure can be viewed at wileyonlinelibrary.com]

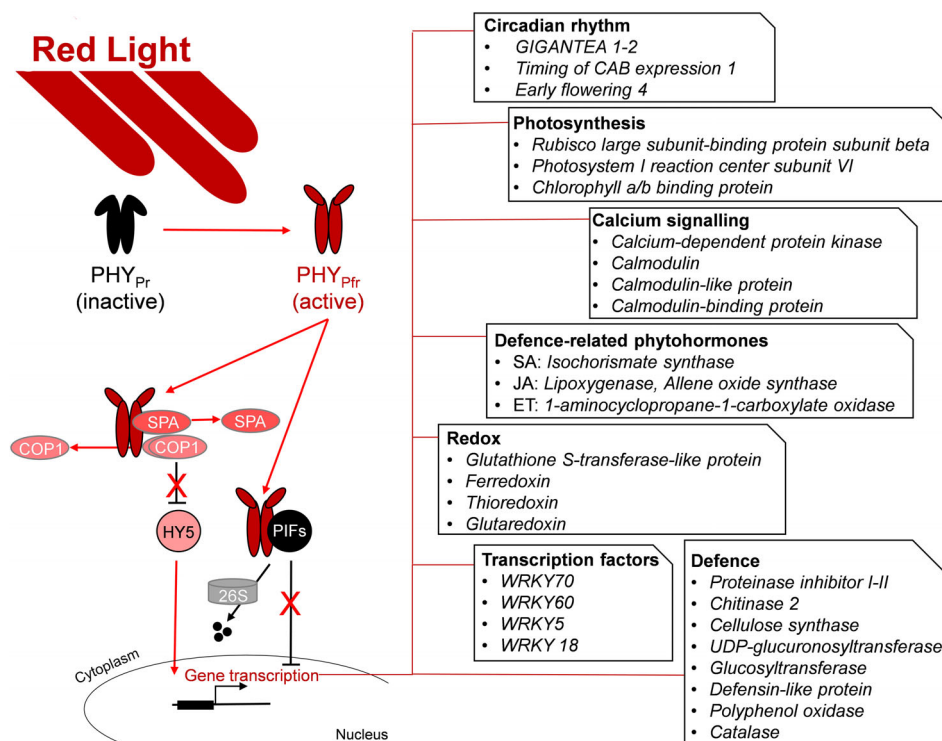


FIGURE 4 Nocturnal red light effects in plants. Red light activates phytochromes and the activated Pfr forms translocate into the nucleus where inactivate phytochrome-interacting factors (PIFs) by promoting proteasomal (26S) protein degradation and the constitutively photomorphogenic 1 (COP1)-suppressor of phyA-105 (SPA1) complex by causing its dissociation and subsequent nuclear exclusion of COP1. This contributes to the accumulation of key transcription factors (e.g., HY5) of light responses. Nocturnal red light elevates the expression of various circadian rhythm-, photosynthesis-, calcium signalling-, phytohormone biosynthesis-, redox- and defence-related genes, as well as, transcription factors based on the RNA-seq analysis (Yang et al., 2015) [Colour figure can be viewed at wileyonlinelibrary.com]

important element of the red light-mediated defence responses of plants against fungal pathogens.

The role of SA was also investigated in plant-nematode interaction under red light illumination. Four weeks of red light treatment for 12 h at night reduced the incidence of nematode infection in tomato plants also, and it elevated the root and shoot biomass. Significant increases in endogenous free SA levels, *PR-1* and *proteinase inhibitor protein 1* expressions were measured under red light exposure (Yang et al., 2015). It was found that the daily used red light-induced systemic resistance of watermelon against root-knot nematode is coordinated by SA and JA levels, and changes in redox homeostasis (Yang et al., 2018). Recently, it was found that red light enhances the expression of the JA biosynthesis-related gene, *allene oxide synthase* in the root-knot nematode-infected leaves and roots of watermelon, which implies that allene oxide synthase plays role in the JA-mediated red light-induced resistance against this pathogen (Zhou et al., 2019). Moreover, the induction (*ClabZIP6* and *ClabZIP56*) or repression (*ClabZIP37* and *ClabZIP57*) of several basic leucine zipper (*bZIP*) genes were also described in root-knot nematode infection under red light in watermelon leaves (Yang et al., 2019). The description of the molecular roles of these genes needs further study. The nocturnal effects of red light on the relation of SA-JA in other cases remained also unclear.

6.4 | Changes in antiviral and antimicrobial compounds

Although the positive effect of red light on SA-mediated *PR1* expression was observed in all biotic stress relation, similar data regarding other

antiviral and antimicrobial compounds are limited. Red light induced the accumulation of disease inhibitor polyphenols and flavonoids in strawberry leaves and muskmelon seedlings under *B. cinerea* (Meng et al., 2019) and *P. xanthii* (Jing et al., 2018) infection, respectively. In addition, red light elevated the activity and expression of phenylalanine ammonia-lyase, which involves in the biosynthesis of the phenolic compounds such as flavonoids, phenylpropanoids and lignin in plants (Sharma et al., 2019). This was observed in *P. cichorii*-infected tomato seedlings (Nagendran & Lee, 2015), *P. putida*-infected soybean seedlings (Dhakal et al., 2015), grapevine (*Vitis vinifera* L.) cultivars exposed to *B. cinerea* (Ahn, Kim, & Yun, 2015) and rice leaves treated with *M. oryzae* (Shirasawa, Ueno, Kihara, & Arase, 2012). The potential role of the phenylpropanoid or tryptophan pathways in red light-induced resistance was proven with the application of 0.5 mM aminoxy acetic acid or 0.1 mM *s*- α -fluoromethyltryptophan pre-treatments for 24 h before the infection with *B. oryzae* in detached leaves of rice plants. The application of both inhibitors reduced the resistance development in response to red light irradiation, suggesting that tryptophan and phenylpropanoid pathways are integral part of the red light-induced resistance against *B. oryzae* (Parada, Mon-nai, Ueno, Kihara, & Arase, 2015). The effect of red light illumination to elevate levels of other antimicrobial compounds in plants to combat fungal infections was also reported. The red light treatment triggered the accumulation of antimicrobial trans-piceid in ‘‘Kyoho’’ and resveratrol in ‘‘Campbell Early’’ grapevine leaves after 24 h of the application under *B. cinerea* infection (Ahn et al., 2015). In addition, antimicrobial stilbene biosynthetic enzymes were also up-regulated and showed two differential peaks at 12 and 48 h in ‘Campbell Early’ grapevine leaves under red light (Ahn et al., 2015). Therefore, these compounds could be also essential in plant defence.

6.5 | Hypersensitive response and cell death regulation

The red light exposure not only inhibits the infection development by inducing defence signalling mechanisms but it also attenuates or delays programmed cell death in the infected organs and plants to inhibit the diffusion of the pathogen. Continuous red light treatment for 96 h delayed the hypersensitive response in tobacco leaves infiltrated with *P. syringae* pv. *tomato*. As a consequence of attenuated hypersensitive response, lower electrolyte leakage and RUBISCO content were measured. Attenuation of programmed cell death markers such as DNA degradation and accumulation of nucleases, cysteine proteinases in red-light-exposed leaves in comparison with those leaves that were exposed to white light was also observed (Moyano et al., 2020). In addition, red light significantly inhibited *A. alternata* AM-toxin-induced necrosis within 36 h in apple (*Malus pumila* Mill. var. *domestica* Schneid.) leaf (Tabira et al., 1989). Moreover, red light treatment for 24 h before *A. tenuissima* infection suppressed lesion development in detached leaves of broad bean (Rahman, Honda, & Arase, 2003). The development of necrotic lesions by *B. cinerea* was significantly reduced after 48 h of infection when the leaves were illuminated with the red light. In addition, this treatment decreased the germination and hypha formation ability of *B. cinerea* spores (Islam, Honda, & Arase, 1998; Khanam, Kihara, et al., 2005; Khanam, Ueno, et al., 2005). Later, it was observed that the application of photosynthesis inhibitor (3-[3,4-dichlorophenyl]-1,1-dimethyl urea) suppressed the red light-induced resistance in broad bean leaflets. Altogether, these results indicate the presence of a red light-induced resistance mechanism against *B. cinerea* and dependence of the mechanism on host plant photosynthesis (Rahman, Honda, Islam, & Arase, 2002). *Corynespora cassiicola* is primarily found in tropical and subtropical regions and causes severe leaf spot disease in various plant species, including cucumber plants (Dixon, Schlub, Pernezny, & Datnoff, 2009). Rahman et al. (2010) found that red light treatment significantly suppressed *C. cassiicola*-induced lesion formation within 24 days in leaves of intact cucumber plants, providing a potential strategy to protect cucumber plants against this fungal pathogen under greenhouse conditions. Moreover, the formation of blast lesions caused by *M. oryzae* was significantly inhibited after 24-hours-long red light treatment in intact rice leaves (Shirasawa et al., 2012). Pre-treatment of pigeonpea (*Cajanus cajan* L. Millsp.) seedlings with red light showed a protective effect against fungal pathogens in the early plant developmental stage: 12- and 24-hours-long red light exposure reduced disease wilt of *Fusarium udum* (Bansod, Sakhare, Deshmukh, & Moharil, 2017). This finding suggests that red light treatment could be effective against fungal pathogens during early plant development.

6.6 | Effects on phytopathogens

Red light exerts a remarkable protective effect on the surface of host plants against bacterial and fungal infections. It was observed that red

light treatment significantly reduced the colony number of *P. syringae* pv. *tomato* on infected *Arabidopsis* leaves after 2 and 4 days of infection compared with white light treatment (Islam et al., 2008). Red light treatment decreased hypha formation and spore germination of *B. cinerea* (Islam et al., 1998), *C. acutatum* (Yu et al., 2013), *Podosphaera pannosa* (Suthaparan et al., 2010), *P. xanthii* (Suzuki et al., 2018) and *S. fuligine* (Wang et al., 2010) compared to white light. Interestingly, others found that red light irradiation did not affect the spore germination and appressorium formation of *B. oryzae* after 24 h of inoculation as compared with white light (Arase, Parada, Kihara, & Ueno, 2017). In contrast to these findings, the adverse effects of red light on muskmelon seedlings were described (Jing et al., 2018): Red light significantly increased the disease index and colony number of *P. xanthii* per leaf after 12 days. However, it can be concluded that these effects can depend on the infectious agents, genotype and the mode of the red light application (e.g., duration and intensity).

7 | CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Despite the fact that more comprehensive studies about the protective effect of red light in plants against pathogen infections have been conducted in the past 20 years, there are many gaps in the knowledge of red light connected signalling under different biotic stressors. We reviewed the current status of the physiological, biochemical and molecular aspects of red light-regulated defence mechanisms in different plant species, genotypes and organs, and we discussed interactions between plants and pathogens, such as viruses, bacteria, fungi and nematodes, especially focusing the role of ROS metabolism and phytohormones, especially SA under red light treatments.

Numerous studies have already proved that the application of red light increases biotic stress tolerance and improves plant growth and development, especially at night. Nocturnal red light exposure increases endogenous defence hormone levels, especially those of SA, and the expression of their related genes and transcription factors, such as WRKYs and bZIPs (Figure 4). However, red light induces other transcription factors, regulating the biosynthesis of defence hormones and their relation with clock genes remains obscured. In addition, based on electrolyte leakage measurements, the beneficial effects of red light in plant defence mechanism are manifested in the presence of various biotic stressors, such as viruses, bacteria, fungi and nematodes, through the alleviation of membrane damage. The reduced oxidative stress response and lipid peroxidation and enhanced detoxification and antioxidant capacity confirmed the positive effects of red light treatments. Moreover, increased photosynthetic efficiency and higher accumulation of defence-related compounds, such as polyphenol, flavonoid, chlorophyll and anthocyanin contents, also verified the beneficial effects of red light in infected plant organs. However, most of the discussed studies were conducted on detached plant organs, especially on leaves, which provide a reliable *in vitro* model plant system to study plant–pathogen interactions (Köhl, Kolnaar, & Ravensberg, 2019). Compounds involved in cell signalling, defence-

related enzymes and metabolites are produced by plants at different levels in vitro and in situ. Moreover, the long-term effects of infection and systemic acquired resistance, which is regulated by various phytohormones, especially SA, cannot be investigated in detached leaves in vitro because several parts of the intact plant, which could be sites of significant synthesis of defence-related compounds, are missing (Fu & Dong, 2013; Kachroo & Robin, 2013). Therefore, understanding the mode of action of red light under pathogen infection is essential to achieving optimal in situ disease control. Testing the effects of supplemented or nocturnal red light on intact plants under biotic stress conditions can support the development of novel plant or crop protection strategies. Furthermore, studying the impact of lighting techniques, such as conventional lighting or inter-lighting, on intact plants can also contribute to realizing these aims.

On the basis of the reviewed papers, it can be concluded that the application of only red light, especially at night, elevated endogenous SA levels and activated SA signalling in plants independently of biotic stressors. However, significant differences in hormone levels and SA signalling were observed in various plant species and organs, such as leaves, hypocotyls and roots. Changes in SA levels in these organs, especially in leaves, could be crucial for plants to survive a severe infection. However, the type of biotic stressors (e.g., biotrophic or necrotrophic herbivory) can also modulate the complexity of plant defence responses. Therefore, the application of red light as an environmentally friendly technology can prime SA under biotic stress without any chemical treatments. In addition, further analyses on SA-mediated signalling and other defence hormones, such as the JA-mediated signalling, are needed especially in plant–nematode interactions. The investigation of the co-operation of SA with other phytohormones, such as JA or ET, also requires further analyses, which can facilitate understanding the beneficial/priming effects of red light treatment in the development of local and systemic resistance in plants.

The fluctuation of phytohormone metabolism and signalling can be dependent on whether it is day or night and the dose and duration of red light treatments. Only a few studies have reported the impact of these parameters on the application of red light on plant species. Moreover, red light-induced plant defence shows distinct patterns, which can be altered by biotic stress in a time-dependent manner. Unfortunately, most of the studies determined the effects of red light only at one time point after red light exposure, although the effects may vary in time from some hours to a few days or weeks. Thus, the long-term effects of daily or nocturnal red light applications have to be analysed. Especially, the costs and benefits of the interruption of the dark period require further investigations. In addition, the timing of red light application, before or during the infection, and during seedling development, or in matured organs, also requires further study.

Understanding red light-induced defence activation represents an important future challenge. A deeper knowledge of the role of phytohormones during the process of infection can inform the design of novel strategies for environmentally friendly plant protection and food safety.

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AUTHOR CONTRIBUTIONS

All authors contributed to the writing and revising of the manuscript.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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