



Plant Archives

Journal homepage: <http://www.plantarchives.org>

DOI Url : <https://doi.org/10.51470/PLANTARCHIVES.2026.v26.supplement-1.414>

MOLECULAR PATHWAYS OF LIGHT PERCEPTION IN PLANTS AND THEIR MICROBIOTA: A REVIEW

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(Date of Receiving : 06-11-2025; Date of Acceptance : 22-01-2026)

ABSTRACT

Light is the main source of energy and informational signal of life on the earth. Plants have a complex photosensory system that allows them to maximize growth, development, defense and also the associated fungi and bacteria have their own set of photoreceptors to control motility, virulence and lifestyle. This is a synthesised review of latest knowledge about the molecular pathways involved in photo sensing in plants and their microbiota showing the new role of light as an important mediator in the intricate interactions between the two. The structure, physiological role, and signalling pathway of key plant photoreceptor superfamilies (Phytochromes, Cryptochromes, Phytotropins and UVR8) and their microbial counterparts (Bacteriophytochromes, BLUF, LOV and microbial opsins). Importantly, we discuss how the light environment, filtered and adjusted by the filtering of the canopy of plants, can serve as an ecological signalling hub, affecting the fitness, virulence, and beneficial position of the interacting microbiome. Further insights into this dialogue of light provide new biotechnological prospects of making crops more resistant and controlling host-microbe interactions toward sustainable crop production.

Keywords: Bacteriophytochromes, Plant Immunity, Microbiome, Virulence, Signal Transduction, Photo-sensing, Phytochromes, Cryptochromes, Phototropins and Photomorphogenesis.

Introduction

Light an Ecological Signalling Hub. Light reigns the terrestrial environment and is at the same time the vital energy base of photosynthetic life and a very instructive indicator (Franklin and Quail, 2010). Plants being obligate photoautotrophs are dependent on a highly sensitive photosensory apparatus to maximize resource capture and respond to seasonal variations as well as to trigger key developmental alterations (Kami *et al.*, 2010). A huge and intricate community of microorganisms, the plant microbiota, exists in the same environment including phytopathogens, symbionts, and commensals (Berendsen *et al.*, 2012). These microbes have a tremendous impact on the interaction between plants and them as well as whether this is beneficial, neutral, or antagonistic, and this is remarkably affected by the light environment (Hiltpold *et al.*, 2021). In the case of plants, the inputs of light

are handled by separate groups of photosensory proteins that cover the electromagnetic spectrum, which includes ultraviolet (UV) to far-red light (FRL) (Rockwell *et al.*, 2006). Photomorphogenesis, phototropism and photoperiodism rely on these receptors, which guarantee successful adaptation to the local ecological niches (Chen *et al.*, 2004). At the same time, numerous plant-associated bacteria and fungi also have their own and also diverse and specialized photosensory proteins (Purschwitz *et al.*, 2006). These microbial photo-receptors control the key events in the life cycle, such as growth, motility, biofilm formation, sporulation, and most importantly, virulence to the host plant (Idnurm and Crosson, 2009). The focal nexus that is taken care of in this review is the light-mediated communication that takes place at the plant-microbe interface (Veneault- Fourrey and Martin, 2011). Light that falls on a colony of microbial on the leaf surface or

inside the rhizosphere, is not pure sunlight; it gets filtered, dispersed and weakened by the plant host itself (Briggs and Christie, 2002). This altered light spectrum by the host is an environmental signal which plant and microbe sense, and which may cause antagonistic or synergistic interactions. The most important thing to harness these natural systems to improve crops and control diseases is to understand the functional dynamics of the photoreceptors of both interacting partners and their role in translating light cues into biochemical signals. The review will be made by initially describing the structure and the work of the major plant photosensory systems (Kami *et al.*, 2010). We will subsequently describe the key microbial families of photoreceptor including their regulatory functions in microbial lifestyle (Corrochano, 2019). Lastly, the combination of these ideas will entail an examination of the existing evidence that illustrates the direct association of light with the plant-microbe relationship, especially regarding the host immunity and microbial virulence (Berendsen *et al.*, 2012).

Plant Photoreceptor Toolkit: Signalling and Core Mechanisms

A variety of sophisticated photoreceptors, with each one selectively sensitive to a wavelength range, has evolved in plants, enabling them to accurately evaluate the light environment (Chen *et al.*, 2004). These receptors can be divided into four large families namely Phytochromes (Red light/Far-Red light), Cryptochromes and Phototropins (Blue light/UV-A light), and UVR8 (UV-B light) (Jenkins, 2017).

Phytochromes: Perceiving Red/Far-Red Light and Shading

The most famous examples of the photoreceptors involved in plant development are the phytochromes (PHYs), which regulate seed germination, shade avoidance, and flowering. They detect red light (RL, 600-700 nm), far-red light (FRL, 700-800 nm) with a covalently bound linear tetrapyrrole chromophore, phytychromobilin (P7B) (Li and Lagarias, 1992).

Signal Initiation and Photochemical Cycle

The PHY exist in two photointerconvertible forms, the inactive RL-absorbing form of the photo-interchangeable molecule (Pr) and the active FRL-absorbing form of the photo-interchangeable molecule (Pfr) (Butler *et al.*, 1959; Mancinelli, 1994). Pr absorbs RL and is transduced to the biologically active Pfr, whereas Pfr absorbs FRL or thermally decays to Pr. Photoequilibrium (PE), or the proportion of the ratio of the photo- to total- preciosity, represented as the proportion of P fr/P total is the most important input signal that plants utilize to determine the quality of

light (Smith, 2000). A PHY functional unit is usually a homodimer. PHYs are mostly cytosolic in the inactive state, which is denoted by Pr (Nagy and Schafer, 2002). When the photoconversion of a pulse occurs, on the photoconversion of the active component of a waveguide, Pr to Pfr, the active component of the photoconversion, Pfr, translocates to the nucleus (Kircher *et al.*, 1999; Nagatani, 2004).

Nuclear Signaling

The central PHY signaling cascade is associated with the direct response of nuclear-localized with transcription factors, in particular, Phytochrome Interacting Factors (PIFs) (Leivar and Monte, 2014). PIFs are simple helix-loop-helix (bHLH) transcription factors which typically mediate etiolation (dark-growth) and shade-avoidance reactions (Toledo-Ortiz *et al.*, 2003; Lorrain *et al.*, 2008). PIFs in the shaded area are stable and functional and stimulated the expression of growth-related genes in the dark (low PE environment) (Leivar *et al.*, 2008). In high RL conditions, accumulation of a rate estimator of the PIFs due to the accumulation of the ATP of the fr causes a direct interaction of PIFs with the ATP of the fr and as a result, ubiquitination of PIFs through the ATP of the fr occurs, and it is subsequently degraded by the 26S proteasome (Shen *et al.*, 2005; Al-Sady *et al.*, 2006). The degradation of this relieves PIF-mediated repression of photomorphogenic genes hence activating light responses (Leivar and Quail, 2011). Such a basic and efficient regulatory system enables the plant to quickly adapt its growth structure (e.g. stem extension, leaf relocation) to canopy dynamics, a critical process in competition and survival (Franklin and Whitelam, 2005).

Cryptochromes and Phototropins

The Blue-Light Brigade. Cryptochromes (CRYs) and Phototropins (PHOTs) sense blue light (BL, - 400-500 nm) (Briggs and Christie, 2002; Cashmore *et al.*, 1999). Both families use flavin adenine dinucleotide (FAD) as a chromophore, although they mediate distinctly different types of responses (Lin and Todo, 2005).

Growth Regulation and Cryptochromes (CRYs)

CRYs are homologous to microbial photolyases, but CRYs do not repair DNA but instead they are transcriptional regulators (Ahmad and Cashmore, 1993; Sancar, 2003). They mediate the inhibition of BL-induced stem elongation, cotyledon growth and flowering time (Guo *et al.*, 1998; Mockler *et al.*, 1999). CRYs, FAD, has a chromophore which photoreduces on absorbing BL and the protein changes its structure (Lin and Shalitin, 2003). The active CRY dimer

subsequently translocates to the nucleus where it has its main signalling activity in interacting with and regulating the activity of Basic Helix-Loop-Helix (bHLH) transcriptional factors (Yang *et al.*, 2000; Yu *et al.*, 2007). Among these key targets are Constitutive Photomorphogenic 1 (COP1) and Suppressor of PhyA (SPA) proteins (Wang *et al.*, 2001; Liu *et al.*, 2011). Active CRY interacts with the COP1/SPA complex, blocking its E3 ubiquitin ligase action (Lian *et al.*, 2011; Ponnu *et al.*, 2019). Because COP1/SPA typically directs positive regulators of photomorphogenesis toward degradation, CRY inactivation of COP1/SPA stabilizes these regulators (e.g. HY5), favouring the light-growth program (Osterlund *et al.*, 2000; Liu *et al.*, 2011).

Movement Responses and Phototropins (PHOTs)

PHOTs are protein kinases, associated with plasma membrane and that have a role of triggering prompt responses to directional and intensity variation of BL (Christie, 2007; Briggs, 2014). These are phototropism (directional growth), chloroplast movement and stomatology opening (Kagawa *et al.*, 2001; Inoue *et al.*, 2008). PHOTs have two LOV (Light, Oxygen, or Voltage) domains in each of which there is a FAD chromophore (Christie *et al.*, 1998; Crosson *et al.*, 2003). When the BL is absorbed, the FAD undergoes a photocycle during which the transient cysteinyl-flavin adduct is formed leading to a conformational change of the LOV domain (Kasahara *et al.*, 2002; Losi and Gärtner, 2012). This transition liberates a steric block on the C-terminal kinase domain leading to the activation and autophosphorylation of this domain (Harper *et al.*, 2003; Matsuoka *et al.*, 2018). The resultant activated PHOT in turn phosphorylates the downstream targets, e.g., the H⁺ATPase of stomatal opening, or proteins engaged in cytoskeletal rearrangement of directional growth responses (Kinoshita *et al.*, 2001; Inoue *et al.*, 2008).

UVR8

UV-B Light Sensing and Defense Preparation. The UV-B Resistance 8 (UVR8) is a special protein in that it can detect UV-B radiation and lacks a flavin or a tetrapyrrole (Rizzini *et al.*, 2011). Tryptophan residues are the major chromophore used by UVR8 (Christie *et al.*, 2012). UVR8 is an inactive homodimer that has stabilized by the electrostatic force between the Trp residues in the dark (Wu *et al.*, 2012). The UV-B light interruptions the interaction between the dimer resulting in the monomers quickly dissociating into active forms (Heijde & Ulm, 2012). The UVR8 monomer subsequently communicates with the

nuclear-based Constitutive Expresser of Pathogenesis-Related GENES 1 (COP1) (Favory *et al.*, 2009). This interaction facilitates the stabilization of the UV-protective genes transcription factor, as well as, most importantly, the defense-associated genes (Brown *et al.*, 2005). Light sensing is closely connected to pathogen resistance by the necessity of the UVR8 pathway in priming plant defense and secondary metabolite production in reaction to environmental stress (Demkura & Ballare, 2012; Jenkins, 2014).

Microbial Photosensory Systems: The Control of Lifestyle and Host Interactions

There are a huge number of bacteria and fungi that live together with plants and have their photoreceptors (Purcell *et al.*, 2017). These microbial sensors do not only control environmental adaptation, but are also important modulators of pathogenicity and symbiosis (van der Horst & Hellingwerf, 2004). The microbial photoreceptors are structurally and functionally varied with some being very spectacularly homologous to plant systems having distinct mechanisms of signaling (Bhoo *et al.*, 2001).

Bacteriophytochromes (BPhy):

The RL/FRL Sensors. Bacteriophytochromes (BPhy) are common microbial phytochromes and are present at least in part in some of the fungi (Rockwell *et al.*, 2006). They also perceive RL/FRL light, but with biliverdin IX alpha (BV) or other bilins as the chromophore as opposed to P gamma B in plants (Karniol & Vierstra, 2003).

Signalling Divergence Structure Divergence Structure

BPhy are typically used as the type of RL/FRL sensors, although their photochemical cycle does not always follow the canonical plant Pr / Pfr cycle, with many of them having a far-red absorbing dark state (Pfr) and a red absorbing light state (Pr) (Rockwell *et al.*, 2014). Structurally BPhy do not have C-terminal Ser/Thr kinase domain that plant PHYs have (Karniol *et al.*, 2005). They usually include instead a HPT (Histidine Phosphotransferase) or REC (Receiver) domain attaching them to two-component signal transduction systems (TCSTS) (Yeh *et al.*, 1997). BPhy sensor domain activates phosphorylation of its histidine kinase partner upon activation by light (Wagner *et al.*, 2005). The phosphate group is then relayed to a response regulator which then regulates the gene expression regarding photosynthesis, motility, or virulence factors (Giraud *et al.*, 2005). This TCSTS coupling has a more direct and commonly faster regulatory connection than the intricate nuclear

degradation mechanism of plant PHYs (Rockwell *et al.*, 2016).

Role in Phytopathogens

BPhy and other RL/FRL sensors are directly involved in virulence in a number of essential phytopathogens (Bonomi *et al.*, 2016). As an example, the fungal opsin NOP-1 in the fungal phytopathogen *Neurospora crassa*, though sensing BL, regulates the pathways associated with the developmental change, which depicts the complexity of light-regulation in these organisms (Wang *et al.* 2018). In a broader sense, the light-sensing fungi have been found to control the access to sexual reproduction and the transition between saprotrophic and pathogenic lives (Yu and Fischer 2019).

BLUF and LOV Receptors

Blue-Light. Microbes have light receptors that are highly varied with proteins containing LOV (Light, Oxygen, or Voltage) and BLUF (Blue Light sensor Using FAD) domains, each of which contain FAD as a chromophore, akin to plant PHOTs and CRYs, respectively, (Masuda & Bauer, 2002).

LOV-Domain Proteins

In bacteria such as *Pseudomonas syringae*, LOV-domain proteins are frequently linked to GGDEF and EAL domains that regulate the intracellular level of the second messenger (cyclic-di-GMP) (c-di-GMP) (Swartz *et al.*, 2007). Based on blue light absorption, the LOV domain undergoes allosteric changes to regulate the catalytic activity of the GGDEF (diguanylate cyclase) or EAL (phosphodiesterase) domains, increasing biofilm formation and surface adhesion and inhibiting motility (swimming/swarming) and expression of most virulence factors. Therefore, the perception of BL directly affects the choice of a sessile, colonization-oriented stance or a motile, invasive state of a bacterial cell- an important choice during the process of infection (Beattie *et al.* 2018).

BLUF-Domain Proteins

The BLUF-domain proteins have a FAD binding site that is conserved and regulate the processes like gene expression and protein activity in response to BL (Gauden *et al.*, 2005). Their action is based on a special displacement of a glutamine residue after absorbing photons leading to a structural cascade (Kraft *et al.*, 2003). BLUF proteins regulate gene expression that is related to light gathering and oxidative stress response, which is essential to endure on the plant surface in many bacteria (Losi & Gartner, 2012).

Uniqueness Microbial Sensors and Opsins

Opsins are a family of photoreceptors that bind retinal which are traditionally involved with animal vision, but are also present in an extremely diverse range of bacteria and archaea (Spudich *et al.*, 2000). Microbial opsins are generally simple transmembrane proteins of the type of seven helix, which after light absorption, are ion pumps or channel rhodopsins (Beja *et al.*, 2001). As an illustration, the proteorhodopsin of marine bacteria plays the role of a proton pump to complement the production of ATP, which suggests that it aids in energy acquisition (DeLong & Beja, 2010). Light-independent plants Opsins may regulate light-independent behaviour and metabolism in plant-associated microbes (Wang *et al.*, 2018). The interactions between opsins and the phytochromes of certain fungi (*N. crassa*) indicate the existence of a network of light-sensing interactions that combine various light wavelengths to optimize the commitment of developmental timing and ecological strategy (Yu & Fischer, 2019).

Light as an Intermediary Between Plants and Microbes

The light environment is not just a usual background of the plant and the microbiota, but it is a changing, host-regulated variable that becomes a special communication channel (Ballare, 2014). The plant canopy changes the light quality and quantity in the phylo sphere (leaf surface) and the rhizosphere (root zone) drastically and this changed light spectrum has a crucial effect on both host and microbe (Huang *et al.*, 2019).

The Light Spectrum of Plants and Microbes

A dense canopy of plants is a good effective absorber of RL, resulting in a large FRL/RL ratio in the light transmitted (or reflected) by other plants (Franklin and Whitelam, 2005). This large FRL/RL ratio is the prototypical signal of shading that triggers the plant to enter the elongation phase (activating *frl r* conversion) to enter flowering (Casal, 2013). Importantly, this same environment is host-filtered light that is perceived by the microbial community that inhabits this environment (Beattie *et al.*, 2018). The shaded lower leaves or the soil under the canopy will receive a certain pathogen or beneficial microbe and the signal will be low-RL, high-FRL signal (Kraiselburd *et al.*, 2017). They can activate or inactivate their own BPhy, or other photoreceptors, and subsequently produce a physiological response (e.g. increased motility, reduced virulence) which is directly related to the current physiological condition of the host (shade stress) (Endres and Schäfer, 2018).

The Signalling of Light in Plants

The photosensory network of the plant is closely connected with the immune system. The susceptibility of the plant to pathogens can depend on the light conditions that tend to activate or inhibit the defense pathways (Ballare and Austin, 2019).

Phytochrome-Defense Intersections

The PHY signalling pathway, especially the PIF transcription factors, is often a negative regulator of plant defense (Campos *et al.*, 2016). Defense responses which are frequently mediated by Jasmonate (JA) and Salicylic Acid (SA) signalling pathways are energetically expensive (De Wit *et al.*, 2013). At low RL/FRL (shade) the plant selects speed at the expense of defense in its development of stem elongation (PIF activity), which is termed shade-induced susceptibility (Cerrudo *et al.*, 2012). Under conditions of PHY's activity (high RL), PIFs are degraded and this usually de-represses major defense transcription factors, setting the plant up to defend itself. This process is a trade-off, where in high-shade competitive conditions the plant loses part of its defense to optimize the light uptake (D Wit *et al.*, 2013). The pathogens, detecting the same light ratio through their own BPhy, may take advantage of this plant weakness and increase their own virulence factors at the time that the plant is weakest (Kraiselburd *et al.*, 2017; Xue *et al.*, 2020).

Blue Light and UVR8: Protection Preparation

Unlike shade-avoidance, BL and UV-B cues can frequently be first-line inducers of defense pathways (Jenkins, 2014). UVR8 pathway is known to cause production of Phenylpropanoid compounds that are UV-B screens and strong antimicrobial agents (Demkura and Ballaré, 2012). Likewise, CRY-mediated BL signalling can help to express pathogen-related (PR) genes (Kaiserli and Jenkins, 2007; Rai *et al.*, 2019). This implies that, the quality of light is a pre-emptive cue: the high-intensity, direct light (which is rich in BL and UV-B) is an indicator of an exposed and stressful environment where defense is vital and the low RL is an indicator of a competitive and resource-limited environment where growth is important (Jenkins, 2017; Rai *et al.*, 2019).

Case Studies: Pathogen-Host Systems

The microbial photoreceptors have been shown to have a direct effect on pathogenicity as recorded by empirical data (Beattie *et al.*, 2018; Xue *et al.*, 2020).

Pseudomonas syringae (BL Sensors and Virulence)

One of the models bacterial phytopathogens is *Pseudomonas syringae* pv. *tomato* (Pst DC3000) (Xin

and He 2013) (Xin and He, 2013). Its LOV-domain blue-light receptor, PstB, has been found to control the intracellular levels of the second messenger, c-di-GMP (Beattie *et al.* 2018). In Darkness (Within Host Tissue): c-di-GMP is elevated. Bacteria are sessile biofilmers. This is essential in preliminary colonization and aggregate development, which is a major infection process. The Type III Secretion System (T3SS) effectors (one of the main virulence factors) is frequently expressed (McGrane and Beattie, 2017).

On Leaf Surface: There is low c-di-GMP. The bacteria motility (swimming/swarming) increases and the bacteria is dispersed, regulating virulence factors downwards (Beattie *et al.*, 2018). The proposed hypothesis of this response is that it is an adaptive response: the presence of BL on the leaf surface indicates an unfavourable, high-stress, or exposed environment, so the bacteria can either dissipate to new sites of infection or repress the energetically expensive virulence program until they are safely within the host tissue. This photo-controlled switch illustrates a direct environmental input on microbial pathogenicity which makes use of a host-relevant signal (BL) (Kraiselburd *et al.*, 2017).

Fabrum Agrobacterium (RL/FRL and Infection)

Its BPhy controls its growth, swimming, and interbacterial competition in the bacterial plant symbiont/pathogen *Agrobacterium fabrum* (formerly *A. tumefaciens*) (Xue *et al.* 2020). Particularly, BPhy-mediated signalling has been demonstrated to have an effect on: Infection Capability: Light conditions as sensed by the microbe has the ability to influence its capacity to adhere to the plant host and be able to successfully transfer its T-DNA (Karniol and Vierstra, 2003). Motility: The transition of a motile state to a sessile state, which is promoted by the RL/FRL environment, determines the speed and efficiency of colonization (Xue *et al.*, 2020; Bhoo *et al.*, 2001). These illustrations highlight the fact that the positive and negative associations are both dynamically regulated by the agreement between the signal of light and the photoresponse of the microbes (Kraiselburd *et al.*, 2017; Xue *et al.*, 2020).

Functional and Structural Dynamics of Photoreceptors

In a bid to have a clear picture of the interrelatedness of light signalling, the basic structure of proteins and their dynamics in functioning needs to be looked into in a deeper way (Winkelmann *et al.*, 2010). Structural biology has given detailed information on how photoconversion and relay of the

signal happens in plant and microbial systems (Rockwell *et al.*, 2006; Andel *et al.*, 2016).

Photoconversion at the Structural Level.

The PAS-GAF-PHY Domains and Phytochromes.

A conserved N-terminal photosensory core component of phytochromes (plant PHY) and bacteria (BPhy) incorporates γ -reactive adenosine dinucleotide (ADP)-generated by the FhlA domain contains γ -reactive adenosine monophosphate (AMP) and γ -reactive inositol monophosphate (AMP) domains; the N-terminal photosensory core also comprised of the γ -reactive diacylglycerol monophosphate (DAGT) domain (Accounts of Chemical Research 37) (Burgie & Vierstra, 2014). Light absorption induces cis-trans conversion of the C 15 C 16 double bond in the linear C 15 C 16 tetrapyrrole chromophore. This is the primary response that initiates a subsequent significant conformational alteration, which is then activated and diffused via the application of the domain of PHY and into the C-terminal effector domain. The plant PHYs The plant PHYs is believed to leave the nuclear localization signal and the surface of interaction of PIFs exposed to the P r fr switch (Li *et al.*, 2011). The conformational change is transduced to BPhy the C-terminal histidine kinase domain which alters its autophosphorylation capacity (Multamäki *et al.*, 2021).

Flavin Receptors and the LOV/BLUF Adducts

FAD/FMN chromophores are required by the blue-light receptors (PHOTs, LOV, BLUF). Their working principle involves creation of ephemeral chemical bond which is absent in tetrapyrrole sensors (Swartz *et al.*, 2007). LOV Domains: The triplet state of flavin chromophore is excited after the photons are absorbed by flavin chromophore. The carbon atom C4a of the flavin and the sulfur atom of one of the conserved cysteine amino acids of the LOV domain form the covalent bond rapidly (Crosson & Moffat, 2002). The result of this formation of cysteinyl-flavin adduct is a change in structure that causes the coupled effector domain (kinase, EAL, or GGDEF) (Ma *et al.*, 2002). This adduct is hydrolyzed slowly to return to the dark state, and this is an internal timer of the signal (Losi & Gärtner, 2012).

BLUF Domains

BLUF photoreceptors are activated by a covalent-free hydrogen-bonding change. The conserved residue of glutamine is also brought to relocate in the absorption of photons and the hydrogen-bonding network in the area of the FAD is rearranged (Gauden *et al.*, 2005). This is then passed on to the effector domain which is typically a phosphodiesterase of

cAMP, but in the absence of the covalent adduct (Andel *et al.*, 2016). This diversity in chromophore chemistry (isomerization, adduct formation, hydrogen-bond switching) demonstrates the immense evolutionary plasticity by which life has been able to adapt the specific wavelengths to a large range of signalling purposes (Zhou *et al.*, 2017).

Signal Transduction Cascades

A cascade of conversion Photon initial capture can be converted into a cellular response (e.g., change in gene expression or cytoskeleton dynamics) via a robust and generally complex cascade to turn light into a signal (Li *et al.*, 2011).

Plant Signal Integration

Plant photoreceptor signalling is densely cross-branched and the primary centre of the integration is the so-called \$COP1/SPA/HY5\$ regulatory hub, where the outputs of the inputs of the photomorphogenesis, that is, the input of the signal of the RL and the input of the BL are synchronized (Lau & Deng, 2012). This overlapping allows the plant to utilize the information involving the canopy shading (low ratio of RL/FRL) and open sky (high ratio of BL/UV-B) exposure as single and one developmental strategy (Jenkins, 2014). On top of that, these light signals are also involved in the classical hormone signalling pathways (auxin, gibberellin, brassinosteroids), and dictate the fate of the eventual growth (Leivar & Monte, 2014).

Microbial Signal Fidelity

Photoreceptors of microbes would rather the sensor domain be directly coupled with an enzyme or regulatory domain, which is fidelity based and transmission of signals rapidly (Purcell *et al.*, 2017). The complexity of signals is simplified by the ubiquitous nature of two-component systems (TCSTS) in BPhy and the direct control of the enzyme in LOV-GGDEF/EAL proteins (Malla *et al.*, 2024). This allows the microbe to quickly and locally alter its behaviour, such as triggering motility or the induction of the biofilm formation process or the expression of a virulence cassette in direct response to perceived quality of light in its immediate environment (Oliinyk *et al.*, 2017). These systems are critical to the functionality of the microbe in such a dynamic environment as the plant surface because they are fast and modular (Gomelsky & Klug, 2002).

Convergence and Divergence of Evolution.

The convergent and divergent evolution of plants and microbes is evidenced by the existence of distinct families of photoreceptors (Phytochromes/ Bacteriophytochromes, Cryptochromes/ Photolyases,

LOV/ PHOT) (Rockwell *et al.*, 2024). Phytochromes diverge (Phytochromes): The homologous photosensory core has completely different domains in the C-terminal effectors of the signal propagation (kinase/PIF regulators in eukaryotic cells, TCSTS in prokaryotic cells), showing varying evolutionary directions of signal propagation to the different cell systems (Multamäki *et al.*, 2021). Cryptochromes/ Photolyases: Cryptochromes in plants are non-functional photolyases which implies that they have originated as the ancient DNA repair enzymes in microbes (Sancar, 2003). In eukaryotes they have functionally conserved on transcriptional regulation of growth. Lateral Gene Transfer: Structural homology of several bacterial and fungal photoreceptors to their plant homologs may represent either a very ancient horizontal gene transfer history, or a very deep common ancestry, which only makes the evolutionary situation of photo sensing more difficult (Oliinyk *et al.*, 2017). Light has been a potent force as an effective selective force, and has caused parallel selection of powerful sensing systems across all the kingdoms of life (Rockwell *et al.*, 2024).

Future outlook and Biotechnology applications

The available literature solidly confirms light as a powerful regulator of the interaction between plants and microbes. Nevertheless, some urgent questions and research directions are still open, especially regarding the complexity of such interactions in the natural environment and the opportunity to apply them in practice.

Unpacking Complex Signalling Integration

As soon as the merger starts to unravel, it becomes time to cultivate recognizable products to draw in new customers and sales. Unwinding the Complex Signaling Integration Unloading the merger begins to unravel and as soon as it does, it is time to cultivate recognizable products to attract new customers and sales. One of the most significant problems is to see how the several light signals are merged by both partners at the same time. In the case of a plant, the RL, FRL and BL signals are combined to give one developmental response. Equally a microbe on a leaf surface will need to combine BPhy (RL/FRL) signal and LOV (BL) signals, frequently by cross-talk between the two pathways, the TCSTS and the c-di-GMP. Research that will be done in the future should be directed to: 1. Modeling Multi-Wavelength Input: Work on the quantitative models predicting the resultant host-microbe interaction in response to the aggregate spectral irradiance and not single wavelengths. 2. Profiling Transcriptional Networks:

Using high throughput transcriptomics and proteomics to chart the convergent and independent gene regulatory networks regulated by light in pathogens and symbionts in planta. 3. Exploring Soil/Rhizosphere Light: Phyllosphere light is well-known, however, light also gets into the soil to some degree. Photoreceptor-mediated activity of root-associated microbes is also a very poorly studied yet significant field of study in the light of the significance of the soil microbiome in nutrient cycling and stress tolerance (Wang *et al.* 2018).

Designing Light-Mediated Crop Resilience

The specific understanding of light-controlled virulence and host defense provides practical opportunities to the biotechnological application in food production sustainability.

Manipulation of Spectrum of light

The most direct one is to engineer the light environment in order to foster desirable interactions or inhibit unwanted interactions. As an illustration, covering with special purpose agricultural films or LED lights with a spectral composition that: • Reduces Pathogen Virulence: Weak activation of microbial LOV receptors (e.g. BL) causes high motility/low c-di-GMP and eventual down-regulation of virulence factors in phytopathogens. • Boosts Host Defense: Introducing UV-B light at sub-phytotoxic levels activates the UVR8 pathway, prepares the plant to respond to pathogens without expenditure of energy to activate constitutive defense.

Microbial Engineering with Specific Purposes

The genes of the microbial photoreceptor themselves are the best genes to be targeted by genetic engineering. Potentially, one could design a useful microbial strain (e.g. an nitrogen-fixing bacterium or plant growth-promoting rhizobacterium) to express its own photoreceptor that results in it:

Enhance Colonization: Only under certain light conditions that are conducive to initial host attachment should biofilm formation be up-regulated with the help of c-di-GMP.

Stimulate desirable Dynamics: Achieve the most production of plant growth hormones or antimicrobial products according to a pre-determined light signal, and when the benefit impact is provided at the most appropriate time and place.

Development of Phototransducing Biocontrol Agents

Natural co-evolution of host and microbe under pressure of light indicates the presence of light-

dependent strategies of biocontrol. As an example, certain strains of microbes may use light-controlled communication networks in order to detect the arrival of a pathogenic strain and to activate a competitive response. Future prospects should be to isolate and characterize microbial photosensors which control interbacterial competition, which will offer a novel category of intelligent biocontrol agents which can be triggered or suppressed by simple light signals.

Conclusion

Light is much more than a source of energy; it is an immense detailing informational medium that coordinates the elaborate ecological conversation between plants and their respective microorganisms. The precise molecular insights into photoreceptor functioning in both domains indicate a deeply complex, co-evolved signalling pathway. Plants combine spectral information in developmental and defense processes using their complex character of PHYs and CRYs as well as PHOTs and UVR8 and microbes use their BPhy, LOV, and BLUF systems to regulate fundamental life processes, such as colonization, motility, and virulence. The cross-talk mediated by light, which is faceted by the spectral filtering of ambient light by the host, is a special, dynamic and exploiting vulnerability to the infection process. It is due to translation of structural and functional knowledge into the regulatory framework of these photosensory systems that researchers can proceed to develop new biotechnological solutions that are environmentally controlled. The future of sustainable crop management perhaps will lie in our capacity to finely adjust the light environment in order to maximize the results of the fundamental, life-defining conversation that takes place at the interface of the plant and the microbe.

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