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REVIEWS

A light life together: photosensing in the plant microbiota

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Abstract
Bacteria and fungi of the plant microbiota can be phytopathogens, parasites or symbionts that establish mutually advantageous relationships with plants. They are often rich in photoreceptors for UVA–Visible light, and in many cases, they exhibit light regulation of growth patterns, infectivity or virulence, reproductive traits, and production of pigments and of metabolites. In addition to the light-driven effects, often demonstrated via the generation of photoreceptor gene knock-outs, microbial photoreceptors can exert effects also in the dark. Interestingly, some fungi switch their attitude towards plants in dependence of illumination or dark conditions in as much as they may be symbiotic or pathogenic. This review summarizes the current knowledge about the roles of light and photoreceptors in plant-associated bacteria and fungi aiming at the identification of common traits and general working ideas. Still, reports on light-driven infection of plants are often restricted to the description of macroscopically observable phenomena, whereas detailed information on the molecular level, e.g., protein–protein interaction during signal transduction or induction mechanisms of infectivity/virulence initiation remains sparse. As it becomes apparent from still only few molecular studies, photoreceptors, often from the red- and the blue light sensitive groups interact and mutually modulate their individual effects. The topic is of great relevance, even in economic terms, referring to plant-pathogen or plant-symbionts interactions, considering the increasing usage of artificial illumination in greenhouses, the possible light-regulation of the synthesis of plant-growth stimulating substances or herbicides by certain symbionts, and the biocontrol of pests by selected fungi and bacteria in a sustainable agriculture.

Keywords Biological photoreceptors · Phytochrome · LOV-domain · Plant–microbe interaction

1 Introduction

In the same environment in which plants receive their energy from light through photosynthetic activity, and from which they collect light inputs through photosensory proteins, also a large variety of microorganisms is thriving: they constitute the plant microbiota [1]. Some species of fungi and bacteria are well known and dangerous phytopathogens, but many are plant symbionts or commensals, and we see increasing evidence for their positive effects on plant growth and fitness, nutrient recycling and protection against pathogens [2, 3]. In other cases, microbes associated to plants influence the production of secondary metabolites in medicinal or aromatic plants, or synthesize antibiotics, pesticides, and herbicides [4].

There is an increasing number of reports describing the impact that light has on plant–microbe association, not only via the photoreceptors of plants, but also through bacterial and fungal photosensory proteins that regulate the lifestyle of these microorganisms [5, 6]. Prominent examples include the phytopathogenic bacteria *Pseudomonas syringae* and *Xanthomonas citri*, whose photoreceptors influence growth patterns, motility, biofilm formation, and down-regulate virulence towards plants [7, 8].

Plants-associated bacteria and fungi share with their hosts red-/far red-light (RL/FRL) and blue light (BL)-sensing domains/modules, chiefly phytochromes (Phy), and flavin-binding photoreceptors of the LOV (Light, Oxygen, Voltage) and cryptochrome/photolyase (Cry/PHR) superfamilies [9–11]. BLUF (Blue Light sensing Using Flavins) [12, 13] proteins and retinal-binding receptors ('microbial rhodopsins') [14] are definitely less represented, at least in

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the limited group of organisms taken into consideration in this work (vide infra) (Tables 1, 2).

In some cases, the number of candidate photoreceptors in members of the plant microbiota is relatively small: considering the phytopathogen *Pseudomonas syringae* pv. *tomato* DC3000, genes encoding two biliverdin IXα- (BV) binding bacteriophytochromes (*Pst*BphP1 and *Pst*BphP2) and a LOV protein (*Pst*LOV) could be identified, all of them molecularly characterized [15–17]. In other plant-associated bacteria the number of photoreceptors is large, possibly due to their ability to live as facultative phototrophs: plant symbionts belonging to Methylobacteria have genes encoding on the average for two BphPs, six LOV- and three BLUF proteins [18]. These pink-pigmented facultative methylotrophic (PPFMs) bacteria normally thrive on leaves [19], where they consume methanol and other C1 compounds produced by plants, in turn promoting plant fitness by the production of phytohormones and iron-chelating compounds, by fixing nitrogen, by the uptake of metabolites, and by providing defense against infections [20]. Therefore, they are considered as biofertilisers and plants probiotics in the frame of sustainable agriculture [21]. Nevertheless, even though it was recently demonstrated that Methylobacteria photoreceptor candidates are functional [18], there are no reports on the effect of light in vivo, most importantly on possible roles of photoreceptors during the symbiosis with plants: we are, for example, not aware whether light affects the consumption of methanol or the production of phytohormones.

Also for fungi the role of photoreceptors during interaction with plants is scarcely known. Light regulates many aspects of fungal life and development, including circadian clock entrainment, hyphal growth, carotenoid and melanin synthesis, spore germination, development of structures for sexual and asexual reproduction, rate of growth, and directional development (phototropism) of reproductive structures [22]. Furthermore, fungal photoreceptors are involved in nutrient uptake, stress responses, pathogenicity, and secondary metabolism [23]. Given the rich photobiology of fungi, it is anticipated that photoreceptors may influence the pathogenicity against plants or the beneficial effects that some fungi have for agriculture such as the ability to control insect pests [24].

The plants-microbes-light interplay is definitely extremely complex, also because plants have their own photoreceptors that trigger a large variety of responses aiming to optimize photosynthesis, plant growth, fitness and the need to cope with other environmental factors (e.g., temperature, humidity). In plants, light regulates photomorphogenesis, levels of phytohormones, synthesis of secondary metabolites, or the release of volatile compounds triggering biosynthesis of plant defence molecules; all of these processes in turn affect the plant–microbe interaction [25]. Abiotic effects of light include changes in temperature and water status of plant parts, an important aspect also with respect to the evergrowing use of artificial lighting in greenhouses [6]. It is thus mandatory to disentangle light effects mediated by plant photoreceptors and those triggered by resident microorganisms during plant–microbe interaction. Examples for this complexity are the light effects on Peronosporaceae (oomycetes), wide spread phytopathogens causing downy mildew in diverse agricultural plants. In these oomycetes, RL can inhibit sporulation, e.g., in *Peronospora belbahrii*, such that exposure to this light quality during night-time effectively inhibits damages to basil plants [26]. However, RL is also

Table 1 Summary of photoreceptors types and number of genes encoding for the specified photoreceptors (as X) in plant-associated bacteria for which a role of light has been described; see Table S1 for the specific strains

Species	Feature	BphP[a]	LOV[a]	BLUF[a]	Cry/PHR[a]	Rho[a]
Agrobacterium fabrum	Phytopathogen	XX	none		X	
Azospirillum brasilense	Plant colonist	XX	none		X	
Bradyrhizobium sp.	Plant colonist	XXX	X		X X	
Bradyrhizobium sp.	Plant colonist	XXX	X		X	
Bacillus amyloliquefaciens	Plant colonist		X			
Bacillus thuringiensis subsp. *kurstaki*	Entomopathogen				X	
Pseudomonas aeruginosa	Phytopathogen	X			X	
Pseudomonas amygdali pv. *tabaci*	Phytopathogen	X X	X		X	
Pseudomonas cichorii	Phytopathogen	X	X		X	
Pseudomonas syringae pv. *tomato*	Phytopathogen	X X	X		X	
Pseudomonas syringae pv. *syringae*	Phytopathogen	X X	X		X	
Rhizobium leguminosarum pv. *viciae*	Plant colonist	X	X		X	
Xanthomonas campestris pv. *campestris*	Phytopathogen	X	X		X	
Xanthomonas citri subsp. *citri*	Phytopathogen	X	X	XX	X	
Xanthomonas oryzae pv. *oryzae*	Phytopathogen	X			X	

[a]: *BphP* bacteriophytochrome, *LOV* Light, oxygen and voltage protein, *BLUF* blue light sensing using flavins protein; *Cry/PHR* cryptochrome/photolyase, *Rho* rhodopsin; see Table S1b–e for details

Table 2 Summary of photoreceptors types and number of number of genes encoding for the specified photoreceptors as X in plant-associated fungi for which a role of light has been described; see Table S2 for the specific strains

Species	Features	BphP	LOV	BLUF	Cry/PHR	Rho
Alternaria alternata	Phytopathogen	X	XX		XXXX	XXX
Beauveria bassiana	Plant symbiont; Entomopathogen	X	XXX	X	XXXX	
Botrytis cinerea	Phytopathogen	XXX	XXXX		XX	XX
Cercospora zeae-maydis	Phytopathogen	X	XXXX		XXXX	XXX
Colletotrichum acutatum	Phytopathogen	?[a]	?[a]	?[a]	?[a]	?[a]
Cordyceps militaris	Entomopathogen	X	XXX		XXX	
Emericella nidulans	Saprophyte; model system	X	XX		X	X
Fusarium asiaticum	Phytopathogen		XX			
Fusarium fujikuroi	Phytopathogen	X	XXXX		XXX	XX
Fusarium graminearum	Phytopathogen		XXX			
Fusarium oxysporum f. sp. *lycopersici*	Phytopathogen	X	XXXX		XXX	XXX
Magnaporthe oryzae	Phytopathogen	X	XXXXX		XX	
Metarhizium acridum	Plant colonist; Entomopathogen	X	XXX		XXX	
Metarhizium robertsii	Plant colonist; Entomopathogen	X	XXX		XXX	
Neurospora crassa	Saprophyte; model system	X	XXX		XX	X
Sordaria fimicola	Plant colonist; Dung fungus;		X			
Trichoderma atroviride	Plant colonist	X	XX		XXX	
Trichoderma harzianum	Plant colonist	X	XX		XXX	
Trichoderma reesei	Plant colonist	X	XX		XXX	
Tuber borchii	Plant symbiont /parasite	X	X		X	
Tuber melanosporum	Plant symbiont /parasite	X	X			
Ustilago maydis	Phytopathogen	X	X	X	XXXX	XXX
Venturia inaequalis	Phytopathogen	XXX	XXX		X	XX
Zymoseptoria tritici	Phytopathogen	X	XXX		XXX	XX

[a]No genome project available; see Table S2b-f for details

reported to increase the in-vitro germination capacity of *Peronospora effusa* that causes downy mildew in spinach [27]. In these microorganisms, though, photoreceptors are still to be identified and functionally characterized.

In this work we review, after a brief summary of the molecular properties of photoreceptors present in the plant microbiota, the current knowledge about the influence of visible light on the microorganisms traits that have or might have an effect on plant–microbe interaction, limiting our considerations to bacteria and fungi. Whenever possible, the photoreceptors related to given phenomena are indicated. In conclusion, we propose possible directions for the future developments of this topic.

2 Photoreceptors in the plant microbiota

Due to the many facets that plant-microbes interactions provide, we have chosen to consider and search photoreceptors candidates only in plant-associated bacteria and fungi for which light-regulated responses have been reported, be they correlated or not to individual photosensory proteins (Tables 1, 2, S1 and S2). For the widespread Methylobacteria, the reader is referred to a recent publication keeping in mind that so far no light-dependent response has been reported for this genus [18]. Photoreceptor candidates in the selected microbes belong to the following classes (Table 1): BV-binding, RL/FRL Phy proteins (BphP = bacteriophytochromes; FphP = fungal phytochromes); BL-sensing LOV, Cry/PHR (PHR, PHotoRepair) and BLUF proteins; microbial rhodopsins (Rho), covering a wide spectral range. In the following, we provide a basic functional description for the various photoreceptor classes.

Phy-proteins are characterised by covalently bound open-chain tetrapyrrole chromophores (bilins) that undergo double bond photoisomerisation [28]. This photochemical reaction forming the 'photoproduct' causes a shift of the absorption maxima of the parental ('dark') state to longer wavelengths. Most plant- and bacteria-derived phytochromes show dark states with absorption maxima around 650—665 nm (RL-absorbing, Pr state referring here to canonical plant- and cyanobacterial-derived phys)

and photoproducts with absorption maxima in the range of 710—730 nm (FRL-absorbing, Pfr). So-called bacteriophys that carry biliverdin XIα as chromophore undergo switches between 700 (Pr) and 750 nm (Pfr). Exceptions from the rule are the 'bathy'-Phys, in which the parental state shows a long wavelength-absorption (Pfr) that is switched into a RL-absorbing Pr form. Exceptions to this Pr-to-Pfr conversion are cyanobacteriochromes that again photoisomerize and show photochromicity, but cover the entire UVA-visible/near infrared spectral range [29]. Phy proteins that show a three-domain module (PAS-GAF-PHY, PAS = Per Arnt Sim, GAF = cGMP-specific phosphodiesterases, cyanobacterial adenylate cyclases, and formate hydrogen lyase transcription activator FhlA, PHY = Phytochrome-specific domain [30]) are named 'canonical' Phys. This three-domain arrangement instrumental to maintain the spectral, photochromic and photochemical properties. Different to plant and canonical cyanobacterial phytochromes that carry the chromophore-binding cysteine within the GAF domain, BphPs and FphPs bind the BV chromophore through a cysteine residue located very close to the N-terminus in the PAS domain, however, also these phytochromes embed the bilin chromophore in the GAF domain [28]. Their Pr and Pfr forms absorb maximally at ca. 700 and 750 nm, respectively, irrespective of the dark state being the Pr state or the Pfr state, as is the case in the 'bathy'-phytochromes [31]. Both BphP and FphP phytochromes undergo similar light triggered reactions, starting, for both Pr and Pfr forms, with the ultrafast photoisomerization of the bilin chromophore in the ps time range, followed by several, in some proteins relatively few intermediates that thermally interconvert into each other and finally result, within several hundred ms, in the formation of the photoproduct [32]. The overall process, in some BphP, runs with a low quantum yield (Φ) of 2% (PsBphP1 of *P. syringae* [17]) and maximally with Φ = 20% for a BphP of *M.radiotolerans* [18]). Bacterial and fungal phytochromes accomplish their regulating function through a signaling domain located in the C-terminal part of the protein (Figs. 1, 2). Most frequently found, in fact exclusively for the cases discussed in this paper, is the two-component signaling system, composed of histidine kinases (HKs) and their interacting, cognate response regulators (RRs) [33]. RRs can be present as independent proteins, their encoding genes often arranged in an operon with the Phy-encoding gene, but RRs are also found fused to the C-terminal end of HK-bearing Phy. The process of activation and functioning is fully conserved in these systems such that, upon activation of the HK by the sensor module, here the light-sensing part of the photoreceptor, a conserved histidine in the HK domain is phosphorylated employing the γ-phosphate of a non-covalently bound ATP. Only in this phosphorylated state, the RR forms a complex with the activated HK and

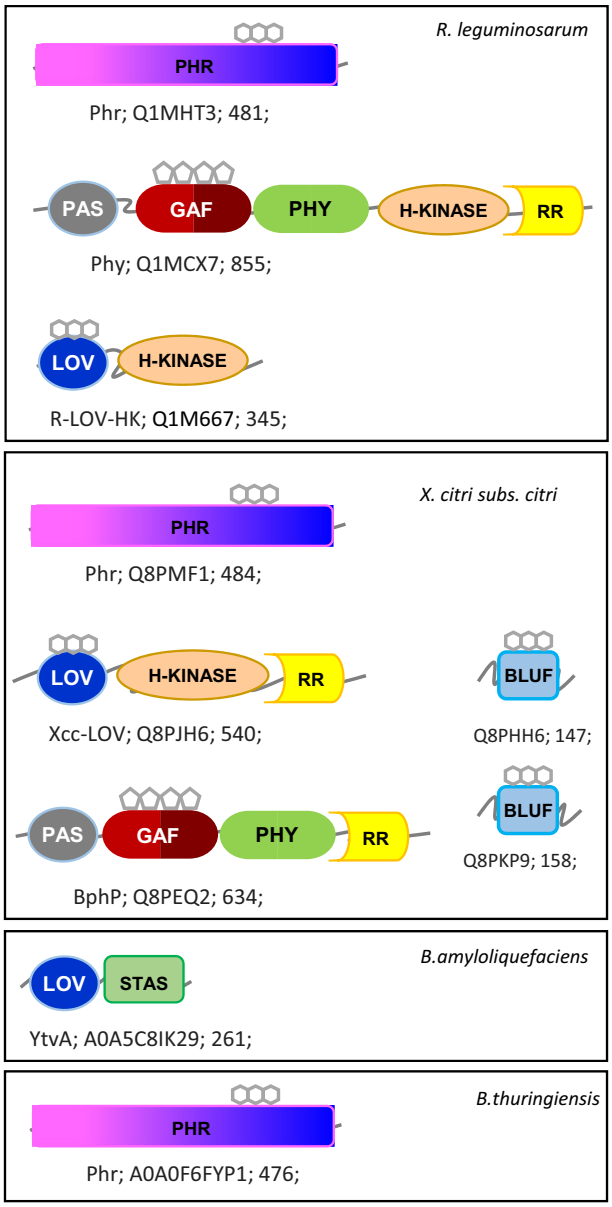

Fig. 1 Photoreceptor systems of selected bacteria interacting with plants; see Table S1 for details on the single organisms. The conventional names (if existing), protein codes (UniProt), and number of amino acids are given for each protein. Flavin chromophore (in LOV, Cry/PHR and BLUF domains) and BV in phytochromes are schematically represented

takes over the phosphate group that is then covalent bound to one conserved aspartate of the RR. After phosphate transfer, the complex falls apart and the now activated RR performs its function by, e.g., regulating flagellar activity for taxis or modifying the gene expression program [34]. In some cases, no effector domain is present, but a second PAS domain is found instead (Tables S1 and S2). We note that some BphPs bear instead effector domains that regulate the turnover of the second messenger molecule cyclic

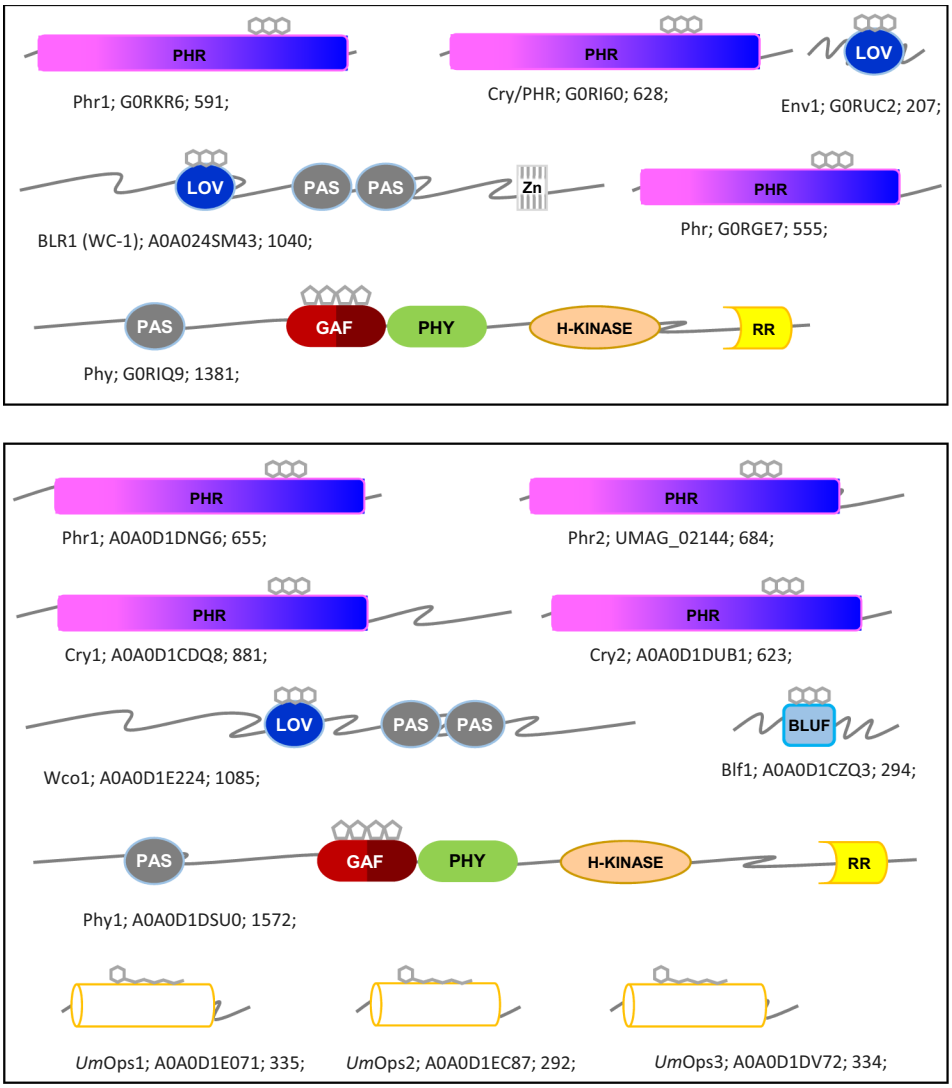

Fig. 2 Photoreceptor systems of selected fungi related to plants; see Table S2 for details on the individual organisms. Top, non pathogenic, bottom, plant pathogenic fungi. The conventional names (if existing), protein codes (UniProt), and number of amino acids are given for each protein. Flavin chromophore (in LOV, Cry/PHR and BLUF domains), BV in phytochromes and retinal in rhodopsins are schematically represented

dimeric guanosine monophosphate (c-di-GMP) [35], but they are not present in the organisms listed here.

LOV domains incorporate FMN (flavin mononucleotide) or FAD (flavin adenine dinucleotide) as chromophores within a PAS-like α/β fold comprising ca. 110 aa [36]. They are widespread in the three domains of life, from plant to archaea, from bacteria to fungi, but are not present in animals [37]. In the dark-adapted state, the chromophore is embedded non-covalently in fully oxidized form absorbing maximally at ca. 450 nm (LOV_{450}) and showing a bright green fluorescence. BL illumination induces formation of a covalent FMN-Cys adduct in the short μs time scale which is strongly blue shifted (LOV_{390}) with loss of fluorescence. LOV_{390} recovers thermally, in the dark, to LOV_{450} within few seconds, minutes or even many hours [36].

LOV-based photoreceptors constitute a variegate superfamily, with diverse associated effector/regulatory domains [37]. In our list of plant-associated bacteria (Table S1) we note chiefly LOV-linked histidine kinases (HK) of the two-component system, RR, and STAS (Sulphate Transporter and AntiSigma factor antagonist) domains [38]. In fungi (Table S2), the typical members are VVD (Vivid), made up of a standalone LOV domain with flanking regions (referred to as short-LOV), and WC-1 (White collar-1) proteins that bear PAS domains and Zn-finger domains to interact with DNA in transcription factor complexes [23].

Members of the Cry/PHR (Cryptochrome/photolyases) superfamily comprise: i. PHR photoenzymes that exploit BL to repair ultraviolet-(UV) generated photoproducts in DNA; ii. Cry proteins, originally discovered in plants and insects and characterized as photosensors without PHR activity; iii. bifunctional Cry proteins that possess photorepair and photosensing activity, such as the Cry-DASH clade (Drosophila, Arabidopsis, Synechocystis, Human) [39, 40]. Common to all Cry/PHR photoreceptors is the PHR region (ca. 480 aa) that hosts the FAD chromophore and most often a second chromophore functioning as an antenna and transferring energy to FAD. Cry proteins may have a

C-terminal extension involved in signalling [41]. To repair pyrimidine dimers produced in DNA by UV radiation, the FAD molecule of PHR must be in the fully reduced hydroquinonic form $FADH^-$, the functionally crucial reaction is a photoinduced electron transfer to the di-pyrimidine dimer [42]. Cry photo-induced reactions are, to some extent, still a matter of debate. A major question is the redox state of the bound FAD in vivo. Few systems have been studied in detail and the picture emerging is continuously developing, with diverse mechanisms being proposed; the vast majority of action spectra for Cry-regulated photosensory responses indicate that the dark-adapted state contains fully oxidised FAD, in agreement with their main role as BL receptors, although exceptions do exist [43]. Intramolecular photoinduced electron transfer chains from aromatic amino acids to the fully oxidised or semi-reduced FAD are held as the basis of Cry photochemistry [44]. In this manuscript we will not predict the function of Cry/PHR proteins, trying to distinguish between their activity as photoenzymes or/and photosensors, unless it is clear from experimental reported data.

BLUF domains (ca. 100 aa) are α/β folds with a structural arrangement reminiscent of ferredoxin [12]. They bind non-covalently a fully oxidised FAD chromophore. Their photocycle involves two conserved residues (a tyrosine and a glutamine) that via ultrafast electron transfer reactions promote hydrogen bond rearrangement around the FAD chromophore. As a result, a transient species is formed absorbing bathochromically by few nm to the dark-adapted state, but without an evident change of the FAD redox state [12]. BLUF proteins are solely present in bacteria, euglenoids, and some fungi (vide infra), and are less variegate than LOV proteins as for effector/regulative domains linked to the photo-sensing unit [13]. Importantly, some BLUF proteins bear effector domains that regulate the level of cyclic nucleotides that act as second messengers (cAMP, cGMP, c-di-GMP) [38]. The majority of bacterial BLUF domains, however, do not show any linked effector domain fused to the same protein (referred to as "short-BLUF").

Microbial rhodopsins (Rho) are based on the same seven-helix membrane-intrinsic protein structure as present in visual animal rhodopsins, although their functions are highly divergent [45]. The retinal chromophore is bound via a protonated Schiff base to a lysine residue located in the seventh helix, but, different to animal Rho, these proteins incorporate the all-*trans* isomer that photo-isomerises (in most cases) into its 13-*cis* isomer. Photoisomerisation of the retinal occurs on the ps time-scale, followed by formation of several transient species and closure of the photocycle typically on the ms-to-s time range. Many microbial rhodopsins are able to actively transport ions (pumps, like bacteriorhodopsin, halorhodopsin, and proteorhodopsins) or act as light-gated ion channels (channelrhodopsins) or photosensors (e.g., sensory rhodopsins) [45]. Recent years have seen identification of enzyme-rhodopsins, where Rho proteins are fused to effector domains that in turn activate a signal transduction chain [46]. In the list of microorganisms considered here Rho photoreceptors were solely detected in fungi, not in bacteria.

3 Light-regulation in the plant microbiota

3.1 Photoresponses and photoreceptors in plant-associated bacteria

Perhaps one of the most prominent features of bacterial photosensing proteins is the finding that they perform light-independent functions besides serving as photoreceptors [5, 7]. To clarify this aspect, it is useful to consider information available for some well-known plant pathogens of the genera *Xanthomonas* and *Pseudomonas*. *X. citri* subsp. *citri* (*Xcc*) is the causal agent of citrus canker, causing significant agricultural losses worldwide [47]. This gammaproteobacterium possesses one BphP, one LOV protein, two BLUF proteins, and a PHR (Table 1, Table S1). The LOV protein, *Xcc*LOV has a typical LOV + HK + RR architecture (Fig. 1) and shows the canonical spectral features of LOV photochemistry [48]. The activity of the HK domain is enhanced upon BL illumination, but only down-regulated and not supressed in the dark. Studies with knock-out mutant strains devoid of *Xcc*LOV evidenced that this photoreceptor promotes bacterial adhesion to leaves, but opposite, protects hosts from necrosis in a light-dependent manner. Other effects are light-independent: *Xcc*LOV is instrumental for formation of flagella, it inhibits swarming motility and formation of the EPS (extracellular polymeric substance). Finally, some effects are detected in the dark, but influenced by BL in a complex manner, e.g., timing of biofilm formation, protection of *Xcc* against oxidative damages, limitation of damages to plant tissues and of host defence responses [7, 49]. *Xcc* is considered a hemibiotrophic pathogen, i.e., it relies on metabolites derived from plant cells to survive. In this view, the observation that a photoreceptor somehow protects the infected plant from massive damages might make sense. In *Xanthomonas campestris* pv. *campestris,* light negatively regulates *Xcc* virulence towards plants and FRL inhibits the virulence systems of this bacterium. Light also inhibits xanthan production and biofilm maturation, phenomena probably triggered by a low Pfr:Pr ratio of the bathy phytochrome *Xcc*BphP [50]**.** The results obtained with these two Xanthomonads indicate that photoreceptors influence processes that in turn affect interaction with the plant host, although investigation is by far not complete. Another important hemibiotrophic foliar pathogen is *Pseudomonas syringae* pv *tomato* DC3000 (*Pst*), for which interaction with plants can be conveniently studied in the model system

Arabidopsis thaliana [51]. *Pst* is the causal agent of bacterial speck in *Lycopersicon esculentum*, producing severe loss of crops worldwide [52]. As mentioned in the introduction, *Pst* is equipped with the two RL/FRL sensing, BV binding *Pst*BphP1 and *Pst*BphP2 and the flavin binding, BL sensing *Pst*LOV (Table S1). Deletion mutants showed that these photoreceptors limit and delay leaf colonization and damages to infected *A. thaliana* plants; furthermore, they down-regulate swarming motility [8, 53, 54]. The locus encoding *Pst*LOV is part of a genomic island, active during infection, that was proposed to be acquired by the bacterium through horizontal gene transfer [55]. The dominant regulatory function of *Pst*LOV on the expression of genes encoding principal and alternative sigma factors and their downstream targets could be documented using *Pst*LOV-knock-out mutants that exhibited de-repressed, enhanced reactivity. Many of these genes (and their gene products) are linked to general bacterial growth, virulence, and quorum sensing [55]. Recent work evidenced BL up-regulation of secretion system genes and RL down-regulation of coronatine, a bacterial toxin that induces stomata opening. In addition, light-treated *Pst* cells showed a larger virulence at dawn than at dusk, possibly due to an increased level of stomata opening [56]. Study of the molecular properties of the two BphPs in *Pst* revealed clear differences in their regulatory role for the bacterium. Both proteins show a very similar modular arrangement of PAS-GAF-PHY-HK domains (*Pst*BphP2 carries motifs for a second, yet somewhat corrupted HK [54]). However, while *Pst*BphP1 is readily loaded with its BV chromophore by its genuine heme oxygenase (arranged in an operon), its ortholog, *Pst*BphP2, is hardly furnished with the BV chromophore under conditions of heterologous expression in *Escherichia coli*, even if the gene encoding *Pst*BphP2 is cloned precisely at the position of its P1 orthologue. This failure of chromophore incorporation, however, has to be considered an expression-prone artefact, as could be demonstrated by comparing the biological properties of *Bst*BphP1- or *Bst*BphP2-knock-out mutants with those of the WT cells. Δ*Bst*BphP1 cells showed a stronger swarming activity, whereas Δ*Bst*BphP2 cells were negatively affected in their growth capacity and, in addition, these cells showed a remarkably different dendritic swarming behaviour [54]. The double phytochrome-knock out mutant cells reproduced the effect found for the deletion of only *Bst*BphP2, and triple mutant cells (Δ*Bst*BphP1, BphP2, and ΔLOV) levelled in between the enhanced growth of the LOV-mutant and the diminished growth of *Bst*BphP2. These findings for *Pst* on reduced motility concur with similar studies in *Agrobacterium fabrum* (formerly *A. tumefaciens*) for which a dependence on the spectral quality of the incident light was found [57]. The different swarming behaviour of the individual *Pst* knock-out mutants was investigated in greater detail by Moyano et al. [8]. These authors could identify an increased flagellin concentration in the ΔBphP1 and ΔBphP2 mutants (ΔLOV mutants were not investigated in this assay). Interestingly, a larger concentration of flagellin was also found for these two mutants, when the bacteria were kept in the dark. These two knock-out mutants reduced the capability to adhere to tomato leaves. This finding concurs with more detailed in vitro investigations of the WT- and mutated bacteria aiming at the concentration and capability to develop biofilms. Again, the BphP-mutants nearly lost the capability to adhere to a glass surface, and this property could be only partially rescued when the mutated strain was complemented for the mutated gene. The wide variation of *Pst* functional properties in response to light, as evidenced by the various knock-out mutants, identify the photoreceptors as major regulatory elements for the expression of a large number of genes. Other effects of RL treatment include enhanced resistance of tomato plants to *Pst* [58] and the delay of the programmed death of *Pst*-infected tobacco leaves [59], although a link to specific photoreceptors was not established in these last two cases.

Further studies on the virulence of *Pst* towards *Arabidopsis thaliana*, again employing individual knock-out mutants clearly demonstrate a regulatory function of the photoreceptors. SEM (scanning electron microscopy) experiments were performed to identify the distribution of bacteria in leaf tissue distant from the position of bacterial cells injection [53]. This investigation revealed a much wider distribution of bacterial cells in leaf tissue, especially in apoplast regions near the xylem vessels, but only under conditions, if leaves where infiltrated with the knock-out mutants. The stronger deleterious activity of photoreceptors-devoided *Pst* became also evident when the hypersensitive response (HR) was followed. Observing the formation of chlorosis and of necrotic spots, when followed up to 72 h, showed yellowing of the entire infiltrated leaf especially for the ΔLOV and ΔBphP1 mutants.

The related strain *Pseudomonas syringae* pv. *syringae* B728a (*Pss*) exhibits additional features important for plant infection and virulence, such as ice nucleation activity and production of the phytotoxin syringomycin; additionally, it can exploit both the leaf surface and the apoplast as habitats, preferentially infecting bean plants [60]. *Pss* has the same ensemble of photoreceptors as *Pst*, and, similarly to the latter organism, studies with knock-out mutants evidenced that *Pss*BphP1 attenuates spread of infection and virulence towards plants, but concomitantly favours survival of *Pss* immediately after leaf colonization [61]. WL represses swarming motility of *Pss,* an effect mainly due to RL/FRL, while this repression is counteracted by BL, underscoring a cross-talk between photoreceptors [62] already emerged with *Pst* [54].

Initial results with other phytopathogenic Pseudomonads indicate a role of light, possibly mediated via bacterial

photoreceptors, in infectivity and virulence towards plants: light suppresses the population of *P. amygdali* pv. *tabaci* (formerly *P. syringae* pv. *tabaci*) in leaves via accumulation of reactive oxygen species (ROS), in particular H_2O_2 [63]; for *P. cichorii* JBC1 was demonstrated that RL and GL down-regulate infectivity towards tomato seedlings, but also in this case a link to specific photoreceptors (Table 1) remains to be identified [64].

Pseudomonas aeruginosa (*Pa)* is a dangerous opportunistic human pathogen, but some strains are also capable of infecting roots causing plant mortality; it was found that formation of biofilm is a key factor for *Pa* pathogenicity [65]. Light represses biofilm formation and the expression of virulence genes, with FRL being more efficient than other wavelengths, but also BL and RL show effects [66]. This light-response proceeds via the phosphorylation of a response regulator (AlgB) by the bathy-phy PaBphP and is intertwined with quorum sensing, also converging on AlgB. Recently it was reported that WL delays maturation of biofilm, indicated by wrinkling, due to low levels of c-di-GMP: this effect is most pronounced with BL, and RmcA was identified as the putative photoreceptor [67]. RmcA bears a PAS domain predicted to bind a Flavin, but lacks the reactive cysteine of LOV domains and has no resemblance to other flavin-based photosensors. The PAS domain is fused to a tandem GGDEF-EAL module (domains named after a conserved sequence motif), whereby GGDEF and EAL act potentially as a cyclase and a photodiesterase (PDE) activity regulating the turnover of c-di-GMP within the cell [68]. RmcA shows a PDE activity (EAL is active), but it is still to be demonstrated that the stimulus sensed by the PAS domain is light [67]. It should be mentioned here, however, that photoactivation of LOV domains void of the canonical cysteine has been demonstrated, with the intermediate formation of a flavin radical, indicating that apparently adduct formation is not absolutely essential to accomplish this function [69, 70].

An EAL sequence, however, exclusively reduced to these three amino acids without other signatures of a common EAL domain, has recently been identified within a helix between the N-terminal PAS and the GAF domain of the bathy-phy from *Xanthomonas oryzae* pv. *oryzae* (*Xoo*BphP) and of similar proteins with the architecture PAS-GAF-PHY-PAS [71]. *Xoo*BphP is reported to possess PDE activity, which is higher in the dark-adapted form when the protein is in a stable Pfr state. Diverse physiological responses appear to be dependent on the light-modulated PDE function of *Xoo*BphP: the authors propose a model according to which during daylight (Pr/Pfr equilibrium) the higher levels of c-di-GMP promote formation of biofilms, EPS formation, and sessile lifestyle, thus protecting the bacteria from environmental stress. During the night or under RL (when the Pfr state accumulates) the lower level of c-di-GMP favours motility and expression of virulence factors [71]. Indeed, infection of plants with WT- *Xoo* showed that blight lesions are larger when bacteria are pre-incubated in the dark or under RL with respect to WL. Significantly, deletion of *Xoo*BphP or introduction of the mutation C13A (the BV chromophore cannot bind to *Xoo*BphP) result in reduced virulence effects of *Xoo* [71], somehow contrasting with the data obtained for other Xanthomonads and Pseudomonads illustrated above, for which photoreceptors seem to have a protective role towards infected plants (vide supra).

From genuine phytopathogens to bacteria being both friend and foe: *Agrobacterium fabrum* strain C58 (formerly *Agrobacterium tumefaciens*) is a good example of the latter category. *A. fabrum* is a soil bacterium able to live as a non-pathogenic rhizosphere colonizer or, alternatively, as a plant pathogen causing crown-gall disease. A wound on the plant can guide *Agrobacterium* spp. to the wounded site by diverse plant-generated compounds, among which the most important is hydroxycinnamic acid (HCA) [72]. The signalling compounds emitted by the plant are received by the bacterium through a two-component signal-system, composed of a canonical HK and RR couple, here called VirA and VirG, then starting the virulence program of the bacterium. Plant tumour development is induced by several (*vir*) genes, all located on a specialized tumor-inducing (TI) plasmid [73]. Approximately 30 genes are under control of a master-regulator. Upon infection, this T-region is first duplicated, then excised from the plasmid by action of an endonuclease, brought into the nucleus of a plant cell (carrying a nuclear localization signal) by a complex multi-protein process, and there randomly inserted into the plantal DNA. The bacterial DNA encodes enzymes for synthesis of auxin, cytokinin, and opine, the latter compound a nutrition source for the bacterium. The BphPs Agp1 and Agp2 from the *Agrobacterium fabrum* strain C58 have been extensively studied at the molecular level and partially in vivo [74–76]. Agp1 is a canonical BphP, where the dark-adapted state is in the Pr form, while Agp2 is a bathy-phy, stable in the dark as the Pfr form [77]. A starting investigation of Agp1 and Agp2 evidenced their physiological role during DNA exchange (conjugation): both BphPs positively regulate conjugation in the dark, to the extent that in the double knock-out mutant $agp1^{-}/agp2^{-}$ conjugation is fully inhibited [78]**.** Conversely, RL and FRL up-regulate conjugation (ca. 3.5 fold) in the WT strain. More important with respect to plants are the results of plant root infection: formation of root tumours by *A. fabrum* is strongly down-regulated by RL, with respect to dark conditions, and almost totally repressed in the $agp1^{-}/agp2^{-}$ mutant (both in dark and under RL) [79]. This latter result indicates that plant phyproteins, possibly present in the roots, do not have significant effects on light-regulation of tumour formation.

Absence of Agp1 and/or Agp2 also affect swimming, inter-bacterial competition, and the expression of diverse proteins, but in many cases without light regulation [79].

Amongst the beneficial bacteria, some plant growth-promoting, nitrogen-fixing species have been investigated with respect to their photoreceptors (Table 3). The phytochrome *Ab*BphP1 of the non-phototrophic *Azospirillum brasilense* is necessary for survival on minimal media under RL; the knock-out mutant is also more sensitive to photooxidative stress, but this protection mechanism operated by AbBphP1 is not related to carotenoid synthesis [80]. At least nine proteins are up-regulated in response to RL, among others chaperonins involved in protein refolding after photodynamic damages. Recently it was demonstrated that light is detrimental for growth and motility, with BL causing the most dramatic effects [81]**.** Although a link to specific photoreceptors or phototoxic molecules was not established, such observations may have an impact on the usage of this strain in agriculture.

The BL receptor R-LOV-HK of *Rhizobium leguminosarum* pv *viciae*, another nitrogen-fixing, non-phototrophic bacterium has multiple roles in this organism that all can affect root colonisation. Through this photoreceptor, BL down-regulates EPS, biofilm formation, and flagella production; furthermore, bacterial proliferation in plant roots is reduced, but the number of N_2-fixing nodules is increased: these effects might be important to optimize root colonization and nitrogen fixing at different soil levels [82]. There are two more nitrogen fixing strains considered here. They belong to *Bradyrhizobium spp*. that express photosystems and grow as phototrophs [83]: *Bradyrhizobium* is especially important in agriculture, given that commercial legumes can establish symbiosis with species belonging to this genus [84]. In some countries, *Bradyrhizobium* strains are even used as inoculant to optimize soybean productions [85, 86]. This genus comprises three main phylogenetic supergroups represented by *B. japonicum*, *B. elkanii*, and the photosynthetic *Bradyrhizobium* species/strains [87]. Among

Table 3 Photoresponses in plant associated bacteria

Species	Light/photoreceptor regulation	Photoreceptor
Agrobacterium fabrum	Dark up-regulates and RL/FRL down-regulate conjugation [78]	Agp1;Agp2
	WL inhibits tumor formation [79]	–
Azospirillum brasilense	BL/WL inhibit growth and swimming motility [81]	–
	Control of photodynamic stress and survival in RL [80]	*Ab*BphP1
Bradyrhizobium sp. ORS278	FRL enhances photosystem synthesis [89]	*Br*BphP1
Bradyrhizobium sp. BTAi1	RL/FRL control synthesis of peripheral LH complex synthesis [91]	BphP3B_{BTAi1}
Bacillus amyloliquefaciens	RL/GL enhance growth and production of lipopeptide; BL supresses bacterial growth [93, 94]	–
Bacillus thuringiensis	Strong photoreactivation of UV-induced DNA damages [96]	PHR
Pseudomonas aeruginosa	WL represses biofilm formation and virulence [66]	*Pa*BphP
	WL/BL inhibit biofilm wrinkling [67]	RmcA[a]
Pseudomonas amygdali pv. *tabaci*	WL supresses bacteria population in leaves via ROS [63]	–
Pseudomonas cichorii	RL and GL down-regulate infectivity [64]	–
Pseudomonas syringae pv. *tomato*	Negative regulation of virulence and leaf colonization, down-regulation of swarming motility [8, 53, 54]	*Pss*BphP1; *Pss*BphP2; *Pss*LOV
	RL enhances bacterial of growth into leaves [191]	*Pss*BphP1
	RL enhances resistance of tomato plants to *Pst* [58] RL delays the programmed death of infected tobacco leaves [59]	–
Pseudomonas syringae pv. *syringae*	RL/FRL/WL repress swarming motility, counteracted by BL [62]	*Pss*BphP1; *Pss*LOV
	Negative regulation of virulence and leaf colonization; enhancement of survival immediately after leaf colonization [61]	*Pss*BphP1
Rhizobium leguminosarum pv. *viciae*	BL inhibits bacterial proliferation, EPS, biofilm and flagella formation; promotes formation of N_2 fixing nodules [82]	R-LOV-HK
Xanthomonas campestris pv. *campestris*	WL/FR negatively regulate virulence, virulence factors, xanthan production, biofilm maturation [50]	*Xcc*BphP
Xanthomonas citri subsp. *citri*	Negatively regulates virulence, motility and EPS formation; promotes flagellum formation and adhesion to leaves [7, 192]	*Xcc*LOV
Xanthomonas oryzae pv. *oryzae*	Light/dark control of motility, infectivity, and virulence factors via tuning c-di-GMP levels [71]	*Xoo*BphP

⁻: indicates that the photoreceptor(s) responsible for a given photoresponse has (have) not been identified

[a] Photoreactive cysteine is missing

symbiotic bacteria, *Bradyrhizobium* sp. ORS278 is a special case emphasising the close relationship with the host plant as for photosensing. In this organism the first bathy-phy named *Br*BphP1[88] was discovered: *Br*BphP1 controls the synthesis of the photosynthetic system, up-regulated by FRL with a maximum efficiency at 750 nm [89]. Beyond a canonical BphP (*Br*phP2), this bacterium also bears a PCB binding module with $\lambda_{max} = 610$ nm. The encoding gene was inherited by horizontal gene transfer (HGT) together with the enzymatic apparatus to synthesize the chromophore, which, similar to the phytochromes from plants and cyanobacteria, is bound to a cysteine within the GAF domain; this special photoreceptor, with unknown functional role, is switching between a dark-state absorbing in the orange range (Po) and a photoactivated red absorbing form (Pr) with an absorption maximum around 670 nm [90]. In the related *Bradyrhizobium* sp. BTAi1, the RL/FRL ratio controls the synthesis of the peripheric light harvesting complex [91]. Both strains are phototrophic and are equipped with three BphPs, one LOV protein, and one/two BLUF photoreceptors (Tables 1, Table S1). This is in sharp contrast with the non-photosynthetic rhizobia discussed above, and even with *B. japonicum* which solely possesses a gene for a BphP, no LOV and no BLUF proteins [10]. These observations, together with the few experimental data available, suggest that in nitrogen fixing, root nodulating bacteria at least some photoreceptors are linked to phototrophic life. A similar suggestion has been recently made for Methylobacteria that mostly reside in the phyllopshere, possess photosystems, and are packed with photoreceptors, with the exception of *M. nodulans* that colonizes roots and has no photosynthetic potential [18]. An important difference with *Bradyrhizobia* does exist, though: *M. nodulans* has given up (or not acquired) BL receptors, but BphPs.

To conclude this section dedicated to bacteria we briefly mention the few known light-effects on the gram-positive, non-phototrophic *Bacillus amyloliquefaciens* and *Bacillus thuringiensis*. The former is associated to roots, acts as biofertilizer through nitrogen fixation and phosphate solubilisation, and can control infections by producing a lipopeptide toxin and by triggering plant defense responses against phytopathogens [92]. Recently it was shown that RL/GL enhance bacterial growth and production of the lipopeptide, while BL supresses bacterial growth [93, 94]. The only photoreceptor candidate for the latter response is a LOV protein, analog to *B. subitlis* YtvA [95], but a physiological link was not established; alternatively, BL growth suppression can be a phototoxic effect. Interestingly, *B. amyloliquefaciens* has no genes encoding for Cry/PHR proteins and, accordingly, does not show photoreactivation of UV-induced damages to DNA [96]. On the contrary, a strong photoreactivation is observed for *B. thuringiensis* [96]. This bacterium produces insecticidal toxins during the sporulation phase of growth and is, therefore, used in agriculture and in transgenic plants as a biocontrol agent [97].

4 Photoresponses and photoreceptors in plant-associated fungi

Given the prominent role that light has on the life cycle of fungi, we present an image illustrating as a paradigm the reproduction and morphogenesis patterns of the filamentous plant pathogen *Botrytis cinerea* (*Botryotinia fuckeliana*), an ascomycete that is the causal agent of grey mould disease in many agricultural plants [98]. *B. cinerea* has a a necrotrophic lifestyle, attacks all aerial parts of a plant and also rotting fruits, producing grey conidiophores and conidia typical of the diseases (Fig. 3).

Filamentous fungi colonize plant tissue in the form of vegetative mycelia and, for dispersal and survival, they produce conidiospores (asexual) and ascospores (sexual); in this fungus light serves as an important cue for making lifestyle decision [99]. Studies with *A. thaliana* evidenced that *B. cinerea* penetrates the plant during night (dark), in the form of a vegetative mycelium [22]. The evolution of the mycelium into conidia (asexual reproduction) for dispersal (summer cycle) or into a hard mass called sclerotium (winter cycle) is determined by light quality and quantity. The sclerotia are formed only in constant darkness and they are meant for survival, since they mostly germinate asexually giving origin to mycelia and conidia; but sclerotia are also a prerequisite for sexual reproduction: when in spring they meet microconidia of the opposite mating type, they are fertilized and, in the light, they give origin to the sexual structures (apothecia). Formation of sclerotia is inhibited by WL and BL. Light is, therefore, a cue to decide between two choices: dispersal by formation of the asexual conidia in the light, or survival in the dark by forming sclerotia [100]. Formation of conidia is stimulated by WL, near UV, and FRL, while it is inhibited by RL and BL. BL thus ultimately inhibits development both of sexual or asexual spores [100]. Further photoresponses of *B. cinerea* include positive phototropism of conidiophores towards BL and negative phototropism of conidial germ tubes [101]. The complex array of photoresponses in *B. cinerea* relies on a large number of photoreceptors (Table 2 and Table S2) [100], whose known roles will be discussed later in this section.

Much of the molecular and physiological information on fungal light response derives from studies with the saprophytic ascomycetes *Neurospora crassa* and *Emericella nidulans* (*Aspergillus nidulans*). In *N. crassa* the clock proteins White Collar 1 and 2 (WC-1 and WC-2) interact to form the transcriptional factor White Collar Complex (WCC) that in its dimeric forms promotes the expression of target genes with a circadian rhythmicity [102]. Among

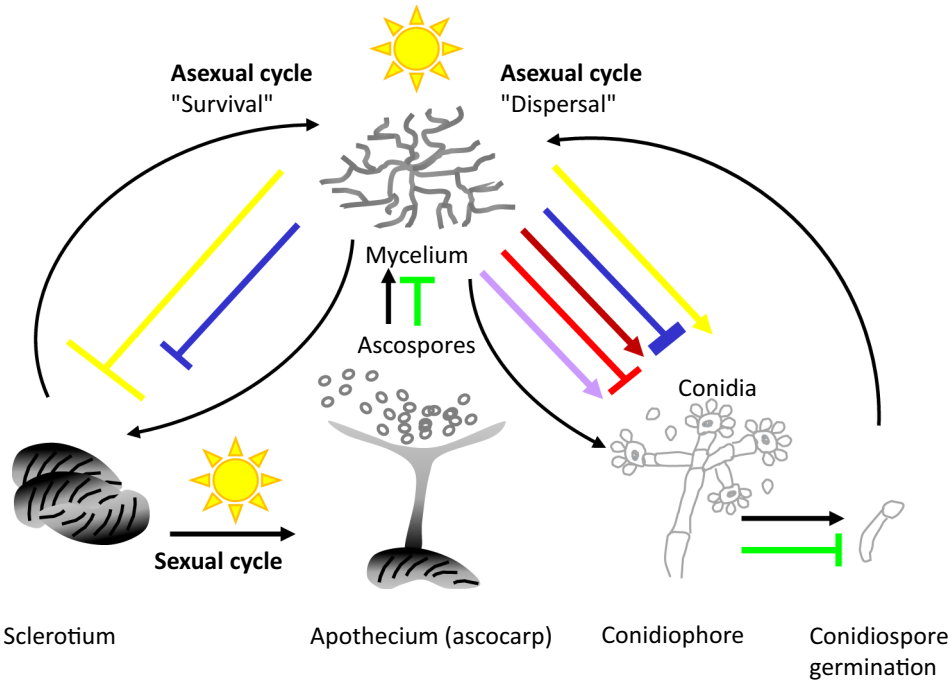

Fig. 3 Life cycle of *B. cinerea* and influence of light. Sclerotia are vegetative structures formed in the dark, but also a prerequisite for fertilization and sexual reproduction. Note that the sexual structures (apothecia) need light to develop. Asexual reproduction via conidia is prompted by WL, FRL, and UV light, while RL and BL are negative factors. Adapted from ref. [100]

many other proteins, production of the clock protein Frequency (FRQ) is activated by WCC: as FRQ accumulates, it inhibits the activity of WCC, generating a feedback loop and the intrinsic rhythmicity of the clock. The WCC complex acts also as a BL-regulated transcription factor through the photosensing LOV domain of WC-1. Orthologues of WC-1 are widespread in Ascomycota and Basidiomycota and are present in all species reported here (Table S2). In *N. crassa,* the gene for another BL sensor, Vivid (VVD, a short-LOV protein), is up-regulated by the WCC dimer; VVD undergoes BL-induced homodimerization and competitive WC-1/VVD heterodimerization, which disrupts the WCC dimer reducing transcriptional response [103, 104]. In this way VVD permits photoadaptation to increasing intensities of BL. Photoadaptation involves BL-induced sequestration of WCC by VVD, but also induces VVD instability in the dark and its accumulation in the light [105]. A further BL effect in *N. crassa* is the induction of carotenoids yielding the development of an orange color: this is more intense in *vvd* deletion mutants, implying again attenuation of WC-1 effects by VVD [106]. Besides acting on the transcriptional level, the WCC complex controls gene expression through chromatin modification and has a regulative function also in the dark [107]. A variation of this mechanism has been proposed for *Trichoderma reesei* (Fig. 4): this ascomycete is a plant colonist, industrially used for cellulase production since many decades [108]. The WCC complex is formed by Blr1 and Blr2 and Envoy (ENV1) which is a VVD-like protein [109] that under oxidative stress conditions does not exert inhibition on the WCC complex, underscoring cross-talk with other signal transduction chains; indeed, BL-induced conidiation (asexual reproduction) occurs under BL and O_2 [110]. In addition, photoactivated ENV1 inhibits pheromone production and female fertility in the light [111].

The physiological roles of the other photoreceptors of *N. crassa* are less characterized, but available data give some promising hints: the phytochrome PHY-2 was recently shown to participate in the light-induced repression of sexual reproduction [112], while no clear function has been assigned to the Cry protein [105]. During sexual development the expression of the *N. crassa* rhodopsin (NOP-1) is upregulated; an extended transcriptomic analysis strongly indicates that NOP-1 act in concert with oxidative stress to inhibit sexual development, through its GL-driven proton-pumping activity [113].

The saprophyte *E. nidulans* is used since many years as a model for cross-talk among multiple photoreceptors, where mainly RL regulates development and metabolite production [105]. Although normally not associated to plants, *E. nidulans* is closely related to phytopathogens and mycotoxin producers [5]. Light effects are mediated by a complex network, where the main actors are the phytochrome FphA, the LreA/LreB complex (orthologue of *N. crassa* WCC, LreA is an LOV protein) and VeA, a master regulator of development and secondary metabolism; these proteins form a complex in the nucleus [114]. Both BL and RL upregulate conidia formation and repress ascocarps (cleistothecia) production, but the largest inhibitory effect is found under RL via FphA, while the LreA/LreB complex is suggested to have a positive effect. Light exerts a similar inhibitory effect on the synthesis of the mycotoxin sterigmatocystin, again mainly via FphA, while LreA/LreB has again a stimulatory function

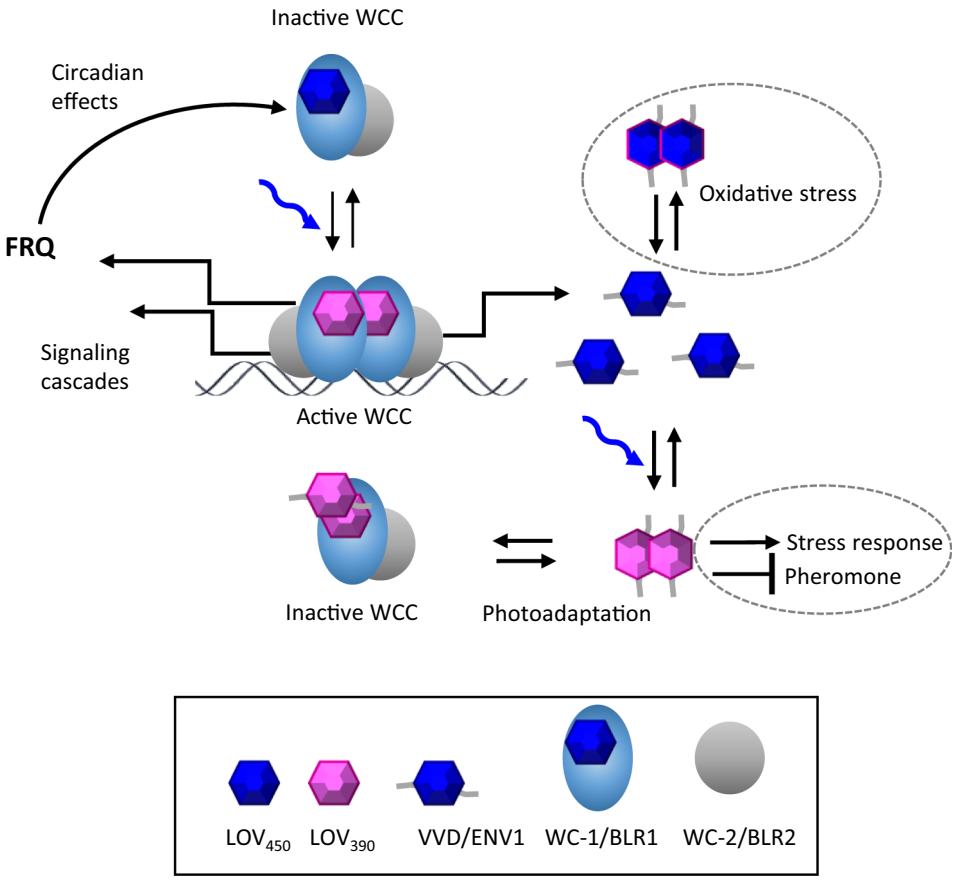

Fig. 4 In the circadian clock of *N. crassa* WC-1 and WC-2 form the transcriptional factor WCC, that promotes expression of many genes, among which also the clock protein FRQ and for VVD. As FRQ and VVD accumulate, they inhibit WCC, generating feedback loops (adapted from ref. [23]). Photoadaptation provided by VVD is based on competitive homo-heterodimerization. In *T. reesei* (dotted forms) the VVD-like protein ENV1 is involved also in protection against oxidative stress: under these latter conditions ENV1 is sequestered in a dimeric form, competitive with its interaction with the WCC complex that remains active [110]. Additionally BL represses pheromone synthesis [111]

[115]. Most interestingly and indicative of FphA photochromicity and activity is the fact that RL-induced conidiation is reversed by FRL [116, 117]. FphA is also involved in temperature, osmolarity, and stress sensing signalling [118, 119]. Through FphA, light upregulates NO levels and the expression of *agaA* (arginase) and *fhbB* (flavohaemoglobin B) [120]. The multiple effects of FphA are mediated and fine-tuned by interactions with the LreA/LreB complex and with VeA [115]. Recently, a global regulator, possibly involved in light-induced chromatin remodelling and interacting with FphA, was identified and named RlcA (regulator of light sensing and chromatin remodelling) [121]. The WC-1 like protein LreA acts mainly as a BL-triggered inhibitor of sporulation [122], while LreB physically interacts with FphA [115]. Not withstanding the major role played by FphA in light regulation, the key enzyme for BV production, heme oxygenase, has not yet been found in this fungus [123].

A similar light regulation as in *E. nidulans* has been described for *Alternaria alternata*, a food contaminant and plant pathogen causing leaf spots, rots, and blights on many plant parts, producing diverse health-endangering mycotoxins, e.g., alteraniol and altertoxins [124, 125]. BL inhibits asexual sporulation, while RL reverses this effect underscoring interplay between different photoreceptors with LreA taking a prominent role; deletion mutants in FphA and LreA showed a reduced sporulation in the dark, suggesting also light-independent roles for these photoreceptors: in the *fphA* mutant conidiation was reduced by 86% in the dark with respect to the WT strain [126]. The deletion mutants *lreA* and *fpha* also showed the highest degree of resistance to oxidative stress, independent of light, due to upregulations of catalase and superoxide dismutase, indicative of cross-talks with other stress sensing systems. Both RL and BL sensing are in close interplay with high-osmolarity glycerol (HOG) mitogen-activated protein (MAP) kinase pathway. Importantly, BL and GL stimulate production of the mutagenic toxin alternariol, an effect due to the LOV protein LreA [126]. Until now it was not possible to detect any light effect on the virulence of *A. alternata*, an aspect particularly relevant, because *Alternaria* species cause at least 20% of crop losses of all fungal-mediated diseases, as it infects a broad variety of agricultural plants [125].

This observation brings us back to the phytopathogen *B. cinerea*. This filamentous fungus carries genes enconding for three phy proteins (*Bc*phy1, *Bc*phy2, *Bc*phy3), four LOV proteins (*Bc*wcl1, *Bc*vvd1, *Bc*lov3, *Bc*LOV4), two Cry/PHR (*Bc*cry1, *Bc*cry2), and two rhodopsins (Bop1, Bop2). *Bc*wcl1 is WC-1-like LOV protein with a Zn-finger domain, making part of the WCC complex with *Bc*wcl2. A basic function of this BL photoreceptor is repression of both conidia

and sclerotia development; furthermore, it is crucial for light-induced transcription of genes encoding for the other photoreceptors, for enzymes in the carotenogenesis pathway, for stress proteins, and for transcription factors [22]. More than 400 genes are regulated in BL by the action of the WCC complex and related transcription factors [127]. Another BL receptor essential for light-repression of conidiation is *Bc*Cry2, while *Bc*Cry1 acts as a PHR [128]. The WCC complex is also required for coping with excessive light, oxidative stress, and for achievement of full virulence towards plants [127]. Many of the light responses mediated by the WCC complex rely on the transcription factor *Bc*LTF1, especially important to cope with the oxidative stress caused either by light or by the plant defence response during infection [129]. Out of the three phy proteins, *Bc*phy3 is required for normal sclerotia formation, vegetative growth and phytopathogenicity, although the role of RL/FRL is not clear [130]. As mentioned above, RL represses and FRL promotes conidiation, pointing to the photochromicity typical of phytochromes (Fig. 3). Importantly, FR reduces resistance to *B. cinerea* but increases fruit mass in tomato, indicative of the double aspect of light during plant-pathogen interaction [131]. Although many aspects of the light-life of *B. cinerea* remains to be clarified at the molecular level, it is clear that this organism is becoming a model to understand the role of light and fungal photoreceptors during plant-pathogen interaction. Recently a LOV protein containing a RGS (regulator of G-protein signaling) domain has been identified in *B. cinerea* and other fungi (Table S2), indicated as *Bc*LOV4 [37]. These fungal RGS-LOV proteins are associated with anionic plasma membrane phospholipids, when photoactivated with BL [132], and are now being used to engineer systems for optogenetic applications [133].

Other well-known phytopathogens and mycotoxin producers are members of the *Fusarium* genus [134] that includes four species complexes for which light regulation has been investigated (Table 4): (i) *F. asiaticum* and *F. graminearum* strains which cause head blight in wheat, barley, and other small grain cereals [135, 136]. (ii) *F. fujikuroi* strains that cause the bakanae disease in plants by producing the phytohormone gibberellin. As a consequence, the plants grow long without control and eventually die; *F. fujikuroi* can also contaminate maize and other cereals through the production of fumonisin mycotoxins [137]. (iii) *F. oxysporum* strains, root associated fungi that can be pathogenic, neutral or even beneficial for fighting other plant infections [138]. As they are known to infect the roots of more than 100 agronomical plants, *F. oxysporum* phytopathogenic strains cause extensive damages, from wilting to necrosis, to an extent that they are ranked among the top 10 fungal phytopathogens as for their economic importance. Many Fusarium strains are also opportunistic pathogens for animals including humans [139].

In contrast to the situation in *E. nidulans* (see above), the phytochrome of *F. graminearum*, *Fg*Fph, does not play a role in the sexual development of this organism, while the WCC complex (*Fg*Wc-1/*Fg*WC-2) acts as a negative factor for perithecia formation and has a positive effect on photoreactivation [140]. The observed effects on sexual development are quite puzzling, because light has, as a whole, a positive effect on this process. Other light effects in *F. graminearum* are the upregulation of carotenoid synthesis (by BL) and the down-regulation of trichothecene mycotoxins production [141]. In the related *F. asiaticum*, BL upregulates carotenoids and induces UV-C resistance, while *Fa*WC-1 is required for sexual fruiting body maturation and ascospore formation [142]. BL has a positive effect also in *F. fujikuroi* on carotenoid production, via VvdA, WcoA (WC-1), possibly involving activity of the phy protein PhyA [143, 144]. In this organism, the synthesis of the green pigment bikaverin is repressed by a cryptochrome (CryD) [145], and one of the two rhodopsins, the proton pumping CarO, retards spore germination from light-formed conidia in a GL–dependent manner [146]. Importantly, the pumping activity of CarO is enhanced by a plant hormone, the auxin indole-3-acetic acid (IAA); the presence of CarO also strongly diminishes the severity of disease symptoms and the expression of this photoreceptor is strengthened by light, also when the fungus has already entered the plant [147]. To finish with this genus, in *F. oxysporum f. sp. lycopersici,* BL upregulates expression of photolyase and carotenoids; the BL receptor WC-1 does not affect pathogenicity on plants, but is required for infecting animals [148]. Recently it was reported that during infection of plants WL/BL sharply increase ethylene production in *B. cinerea*, *F. asiaticum*, *A. alternata*, and other pathogenic fungi. The authors have proposed to exploit this phenomenon for non-invasive detection of fungal infections [149].

Many phytopathogenic fungi produce photosensitisers, such as hypocrellin and cercosporin that act as photoactivated phytotoxins [150]. A well-known example is *Cercospora zeae-maydis,* the causal agent of gray leaf spot in maize [151]. In this fungus BL represses conidiation, upregulates cercosporin synthesis and photolyase expression via the LOV proteins CRP1 (WC-1); CRP1 is also essential for tropism towards stomata and induction of foliar necrosis [152]. Therefore, for *C. zeae-maydis* a BL receptor of the LOV superfamily is strictly correlated with its pathogenic effects towards plants and, again, upregulation of PHR hints to enhancement of photoprotection.

Further light regulation has been described in other phytopathogenic Ascomycota. In *Colletotrichum acutatum*, causal agent of the destructive anthracnose in many agricultural plants [153], RL/GL reduce mycelial growth, while BL impairs conidial germination, enhances virulence against pepper, and the amount of melanin [154].

Table 4 Photoresponses in phytopatogenic and model fungi

Species	Light/photoreceptor regulation	Photoreceptor
Alternaria alternata	BL inhibits sporulation, RL reverses this effect; BL/GL up regulate the mycotoxin alternariol; photoreceptors diminish resistance to ROS [126]	LreA (WC-1) FphA
Botrytis cinerea	BL represses conidiation and sclerotia development. Increases resistance to (photo) oxidative stress and virulence; light regulation of > 400 genes among which those for the 11 photoreceptors, carotenoid synthesis and for conidiation [22, 127]	*Bc*WCL1 (WC-1)
	BL repression of conidiation[128]	*Bc*Cry2
	RL represses and FRL promotes conidiation; BL represses conidiation; GL represses growth of mycelia [100]; BL promotes phototropism of conidiophores [101]	
	FR reduces resistance to *B. cinerea* but increases fruit mass in tomato [131]	
	Promotes sclerotia formation, vegetative growth and pathogenicity [130]	*Bc*phy3
Cercospora zeae-maydis	BL represses conidiation, upregulates the light-activated toxin cercosporin and PHR; CRP1 is essential for tropism towards stomata and induction of foliar necrosis [152]	CRP1 (WC-1)
Colletotrichum acutatum	RL/GL reduce mycelial growth; BL impairs conidial germination, enhances virulence and amount of pigments [154]	?
Emericella nidulans	RL and BL favour asexual reproduction and inhibit sexual reproduction via FphA; LerA favours sexual reproduction [115] BL, RL and FRL delay conidiospore germination[118] WL represses production of the mycotoxin sterigmatocystin; FphA inhibitor, LreA stimulator [115] FphA involved in temperature sensing, osmosensing and stress-sensing signalling [118, 119] WL upregulates NO; FphA upregulates and LreA represses *agaA* and *fhbB*[a]. The global nuclear regulator RlcA interacts with FphA [121]	FphA LreA (WC-1),
Fusarium asiaticum	BL upregulates carotenoids and induces UV-C resistance; *Fa*WC-1 required for sexual fruiting body maturation and ascospore formation [142]	*Fa*WC-1
Fusarium fujikuroi	BL upregulates carotenoids and affects mycelial development [143]	VvdA
	BL upregulates carotenoids [144]; CryD represses the synthesis of the pigment bikaverin and the production of macroconidia [145]	CryD, WcoA (WC-1)
	RL upregulates carotenoids [144]	PhyA (?)
	GL retards spore germination from light-formed conidia [146]; pumping activity enhanced by IAA [147]	CarO
	No pumping activity, unknown function [147]	OpsA
Fusarium graminearum	WL required for sexual development; FgWc-1 negatively regulate sexual development and favours photoreactivation; BL upregulates carotenoids; light represses production of a mycotoxin [140, 141]	FgWc-1, FgFph?
Fusarium oxysporum f. sp. *lycopersici*	BL upregulates PHR and carotenoids; WC-1 does not affect pathogenicity in plants, is needed for infecting animals [148]	WC-1
Magnaporthe oryzae	Light-dependent disease suppression during the dark-phase [156]	MGWC-1
Neurospora crassa	Clock protein; forms with WC-2 the WCC transcription factor; BL upregulates carotenoids [23]	WC-1
	Downregulates carotenoids; [106]photoadaptation via WCC sequestration [104]	VVD
	Contribute to repression of sexual development in the light [112]	Phy-1, Phy-2
	Contribute to repression of sexual development in the light; coupling with oxidative stress [113]	NOP-1
Ustilago maydis	GL-driven proton pumps [164]	*Um*Ops1,*Um*Ops2
	Highly expressed during corn infection [165]	*Um*Ops3
	WL/BL/RL stimulation of basidiocarps (sexual reproduction) formation, with RL more effective than BL; Phy1 needed to form basidiocarps [163]	Wco1a (WC-1), Wco1b[a]; Phy1
	BL-induction of > 50 genes via WC-1 among which Cry/PHR proteins contributing to UV tolerance [162]	Wco1a (WC-1)
Venturia inaequalis	NIRL stimulates spore release [158]	?
Zymoseptoria tritici	WL, RL and BL affects largely gene expression; upregulation of Cry, NOP-1, and genes for oxidative stress, metabolism and transportation [160]	?

[a]: *agaA* arginase, *fhbB* flavohaemoglobin B

In *Magnaporthe oryzae*, the causal agent of rice blast [155], it was observed that the BL receptor MGWC-1 is responsible for disease suppression during the dark-phase in alternating light–dark cycles; this occurs immediately after host–pathogen contact [156]. *Venturia inaequalis* causes apple scab worldwide [157]. In this fungus, near infrared light (NIRL) stimulates spore release, an important step for disease spread; importantly, artificial illumination during the night resulted in an increase of almost 50% of released ascospores [158]. The photoreceptor responsible for these effects has so far not been identified. *Zymoseptoria tritici* is one of the most damaging pathogen of wheat worldwide [159]. In *Z. tritici* WL, RL, and BL largely affect gene expression: the genes for the photoreceptors Cry and NOP-1 (rhodopsin) are upregulated by light, as well as those for oxidative stress, metabolism, and transportation [160].

The sole phytopathogenic basidiomycete for which photoreceptors and photoresponses have been characterized is *Ustilago maydis*, the causal agent of corn smut disease in maize. This organism is often used as a model system for fungi-plant interaction [161]. *U. maydis* has a biphasic lifestyle: as a saprophyte it shows a yeast-like morphology and is haploid, but on a suitable surface and under the influence of pheromones two cells can fuse (sexual reproduction) and the resulting diploid is the pathogenic form that grows as a filamentous fungus [161]. The fruiting body (sexual structure) is named basidiocarp. *U. maydis* is equipped with one LOV protein (Wco1a), one phytochrome (Phy1), one BLUF protein (Blf1), two photolyases (PHR1, PHR2), two cryptochrome (Cry1, Cry2), and three rhodopsins (*Um*Ops1, *Um*Ops12, *Um*Ops3) (Table S2). More than 50 genes are induced by BL via the WC-1 protein Wco1a, among which Cry/PHR proteins contribute to UV tolerance [162]. WL/BL/RL stimulates formation of basidiocarps, with RL being more effective than BL; indeed, Phy1 is needed to form basidiocarps, also independent of light [163]. The first two rhodopsins are GL-driven proton pumps [164], while *Um*Ops3 is highly expressed during corn infection, therefore, considered to be an important photoreceptor for this process [165]. Quite unfortunately, the function of Blf1 is not known [9, 162], as BLUF photoreceptors are quite rare in plant-associated fungi.

Tuber spp. comprise hypogeous ascomycetes that can form a symbiosis with plant roots, the ectomycorrhizae [166], and can become parasite of non-ectomycorrhizal plants [167]. *Tuber melanosporum* and *Tuber borchii* possess genes encoding canonical WC-1/WC-2 systems sensing BL and genes for phy proteins (Table 2, TS2). In both fungi, BL inhibits mycelial growth, a key feature of symbiosis establishment, while the phytochromes were reported to be non-functional (Table 5) [168, 169].

Sordaria fimicola is a dung fungus, normally non phytopathogenic that can live as endophyte and reduce growth and fecundity of plants [170]. In *S. fimicola* BL effects via *Sf*WC-1 include phototropism and carotenoids synthesis, regulation of rhythmic zonation of ascocarps and of fruiting-body development [171].

Some fungi associated to plants are entomopathogenic, i.e., they parasitize insects that damage plants and are thus considered beneficial as biocontrol agents and probiotics [172–174]. Taking *Metarhizium robertsii* as an example, this fungus is insect-pathogenic, establishes mutualistic

Table 5 Photoresponses in plant-associated, non phytopathogenic fungi

Species	Light/photoreceptor regulation	Photoreceptor
Beauveria bassiana	BL upregulates conidiation; VVD serves for virulence towards insects [178]	VVD
	RL/FRL down-regulate conidiation. Regulates growth, conidiation and multistress tolerance; *Bb*phy diminishes resistance to ROS [179]	*Bb*phy
Cordyceps militaris	BL upregulates conidia, carotenoids and cordycepin	*Cm*WC-1
	BL upregulates cordycepin and downregulates carotenoids [182]	*Cm*VVD
Metarhizium acridum	WL upregulates PHR and increases photoreactivation ability [176]	?
Metarhizium robertsii	WL, BL, GL, RL influence resistance of conidia to osmotic stress and to UV. Conidia formed in the dark are more resistant [174]	
Sordaria fimicola	BL induces phototropism and carotenoids; regulation of rhythmic zonation of ascocarps and fruiting-body development [171]	*Sf*WC-1
Trichoderma atroviride	BL induces conidiation [185]	BLR1 (WC-1)
	PHR-like action; BL and RL regulation of gene expression [186]	CRY1
Trichoderma harzianum	BL induces expression of PHR1 and of pigmented, resistant spores [187]	
Trichoderma reesei	BL + O_2 induce conidiation [110]	BLR1 (WC-1)
	Integrates BL, redox and nutrient sensing and photoadaptation; regulates growth and pheromone production, needed for female fertility in the light[111]	ENV1
Tuber borchii	BL inhibits mycelial growth [168]	Tbwc-1
Tuber melanosporum	BL inhibits mycelial growth [169]	?

interactions with plants and stimulates plant root development [175]. In this organism light (WL, BL, GL or RL) influences resistance of conidia to osmotic stress and to UV, i.e., conidia formed in the dark are more resistant [174]. In the related *M. acridum*, WL upregulates expression of a photolyase and increases photoreactivation ability [176]. Scientific reports for these fungi are still sporadic and light-effects have not been related to any specific photoreceptor. The entomopathogen *Beauveria bassiana* is being increasingly used to control insect pests in the field and is under inspection for its ability to promote plant growth, the possibility that strong inoculation of its spore at the roots level might affect the plant microbiota and for the question of its persistence in the environment [177]. In *B. bassiana* BL upregulates conidiation and, importantly, the BL sensor VVD is required for virulence towards insects [178]. RL/FRL instead down-regulate conidiation and the Blphy photoreceptor participates in growth, conidiation and multistress tolerance; interestingly the presence of *Bb*phy diminishes resistance to ROS [179].

The ascomycete *Cordyceps militaris* is under investigation especially for its ability to produce cordycepin, a potent herbicide that inhibits plant growth, and as an entomopathogen [180]. In *C. militaris* light controls the expression of more than 1000 genes, almost 60% of which via the LOV protein *Cm*WC-1 [181]. Genome inspection revealed the existence of other five photoreceptor candidates (Table 2 and Table S2): one phytochrome, one LOV-domain protein, *Cm*VVD, and three members of the CRY/PL superfamily [182]. Inactivation of the gene for *Cm*WC-1 results in impaired production of conidia, carotenoid and cordycepin, as well as morphological modification of hyphae [181]. *Cm*VVD has thus a role both in photoadaptation (as in *N. crassa*) and in the BL-induced upregulation of *Cm*WC-1; furthermore, *Cm*VVD has a positive effect on cordycepin synthesis, while it downregulates the production of carotenoids [182].

Fungi belonging to the genus Trichoderma are used in agriculture as biocontrol agents against other, pathogenic fungi and also because they participate in preserving plant health and protection against infections [24]. *Trichoderma reesei* is an endophyte that promotes the growth of the wheat *Solanum surattense* under salt stress [183]. *T. reesei* represents a model organism, because it exhibits a large variety of physiological phenomena. It has been found, as an example given, to degrade plant cell walls and is even employed in industry for the production of cell wall degrading enzymes [184]. In addition, and most interesting for this paper, it shows quite a range of light-induced responses: BL induces conidiation when oxygen is present, a response mediated by BLR1 (WC-1) [110]. As mentioned above, the VVD-like protein ENV1 integrates BL, redox, and nutrient sensing with photoadaptation; ENV1 also regulates growth and pheromone production, needed for female fertility in the light [111]. In *T. atroviride* BL also induces conidiation via BLR1 [185]. In this fungus the photoreceptor CRY1 has a PL-like action, but also regulates the expression of genes in a BL- and RL-dependent way [186]. The RL-effect observed for the Cry protein in *T. atroviride* appears contradictory; however, RL regulation has been previously reported for a CRY protein from the green alga *Chlamydomonas reinhardtii* and this effect has been ascribed to the presence of neutral radical state of the bound flavin chromophore [43]. Finally, in *T. harzianum* BL induces expression of the photolyase PHR1 and of pigmented, resistant spores [187].

5 Conclusions and perspectives

Entering the field of plant–microbe interactions revealed a multi-faceted research area exhibiting variations of this interplay ranging from probiotic over symbiotic up to clearly plant pathogenic scenarios; on top, some of these microbes are also known as animal-/human-pathogens. This research is growing, but currently still in its infancy, partially due to the often missing molecular characterization of the individual photoreceptor proteins, not to speak of only sparse information on the interaction of the plant-dwelling microbes and their plant hosts. The lack of information, but also the wealth of data extracted from genome-wide surveys, as performed here, allow stunning and intriguing insights into this complex plant-microbes network. Considering the large number of bacteria and fungi carrying photoreceptors, intense work is required, as some of these microbes have been identified to cause significant economic loss.

Information on bacterial photoreceptors, their function and biochemical properties, and their impact on the bacterial behavior and plant-directed activity is more profound than for their fungal orthologs, with some notable exceptions. Pictures emerge, however, for both groups, highlighting two important aspects: (i) Photoreceptors are placed high on the regulatory pyramid, and (ii) photoreceptors are part of a maze of interacting proteins, be they other photoreceptors or, e.g., hormone receptors, in some cases in a concurrent activity, in other cases counteracting with each other. Several interesting aspects seem to emerge for plant-pathogenic bacteria such that the photoreceptors keep the game under control. In other words, these light-sensitive proteins seem to control infectivity and virulence to a level that generates not too much harm to the plant host. This becomes particularly evident when the photoreceptor genes are interrupted causing remarkably increased infectivity and in-leaf distribution of the bacteria, eventually causing tissue collapse and plant death. Nearly no information could be compiled on the downstream processes like signalling cascades or the

molecular mechanisms of gene expression control that eventually result in a bacterial or fungal attack against a plant host [7].

The more complex lifestyle of fungi allows expecting even more sophisticated interactions with plants. From the data collected in this work no general picture emerges that can answer the question: do fungal photoreceptors affect fungi-plant interaction, in particular pathogenicity towards plants? It is clear that light and photoreceptors affect fungal reproductive traits, but only in few cases a correlation with specific features connected to virulence and or infectivity could be established, mentioning only the production of mycotoxins, hormones and other metabolites (see Table 4). It is also emerging that photoreceptors have an impact, mostly positive, on the resistance to stressors (e.g., UV radiation, ROS, osmotic stress) also by promoting the production of protective pigments and PHR proteins; these aspects certainly deserve more attention, in that they may have an impact on fungal survival rate under severe conditions. This is also true for non-phyto-pathogenic fungi used for the biocontrol of insect pests (see Table 5) for which again it is difficult, with the few data available, to answer the question: do photoreceptors influence the pathogenicity towards insects? To our knowledge, the answer is at hand only for the case of *Beauveria bassiana*, for which the BL receptors VVD was found to control virulence towards insects [178].

One aspect that came to light—still for only few reported cases—is the finding that the presence of photoreceptor genes is instrumental for the invading activity of bacteria and of fungi also in the dark. These observations point to the need of an intact region in their genome not allowing an interruption of transcriptional read-through. In these reported cases, the photoreceptor genes are located within (or are part of) a virulence 'island' or a plasmid carrying virulence-activating genes. Whether light activation adds to this 'dark activity', remains still an open question.

Light sensing in the plant microbiota has many more unexplored aspects; we cite here Methylobacteria, ubiquitous inhabitants of the phyllosphere belonging to pink-pigmented facultative methylotrophic (PPFMs) alpha-proteobacteria that exploit C1 compounds synthesised by the host plant, in turn producing phytohormones that promote plant growth [188]. Methylobacteria possess genes for an impressive number of photoreceptors, chiefly belonging to LOV and BphP proteins, whose preliminary investigation demonstrated the expected light-triggered reactions [18]. The functional role of Methylobacteria photoreceptors is fully unknown but, given the high potential of these organisms as plant probiotics and for biotechnological applications [21, 188], the relevance of their photosensors in vivo should be definitely investigated. Last but not least we note that photoreceptor proteins of microbes living under variable environmental conditions, might show peculiar properties suitable for applications [31, 189]. As an example and again referring to Methylobacteria, a LOV protein from M. radiotolerans has turned out to be an efficient photosensitiser for singlet oxygen formation after insertion of a single mutation, concomitanly showing an astonishing resistance to denaturation with urea [190].

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