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Seeing the Light: The Roles of Red- and Blue-Light Sensing in Plant Microbes

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Abstract

Plants collect, concentrate, and conduct light throughout their tissues, thus enhancing light availability to their resident microbes. This review explores the role of photosensing in the biology of plant-associated bacteria and fungi, including the molecular mechanisms of red-light sensing by phytochromes and blue-light sensing by LOV (light-oxygen-voltage) domain proteins in these microbes. Bacteriophytochromes function as major drivers of the bacterial transcriptome and mediate light-regulated suppression of virulence, motility, and conjugation in some phytopathogens and light-regulated induction of the photosynthetic apparatus in a stem-nodulating symbiont. Bacterial LOV proteins also influence light-mediated changes in both symbiotic and pathogenic phenotypes. Although red-light sensing by fungal phytopathogens is poorly understood, fungal LOV proteins contribute to blue-light regulation of traits, including asexual development and virulence. Collectively, these studies highlight that plant microbes have evolved to exploit light cues and that light sensing is often coupled with sensing other environmental signals.

INTRODUCTION

Photosensory proteins: proteins that detect light

Photosensing: the activity of detecting and responding to light

Chromophores: molecules responsible for light absorption

Visible spectrum: wavelengths from ~390–700 nm

Phytochromes: photosensory proteins that detect red light (~620–700 nm) and far-red light (~700–800 nm)

LOV proteins: photosensory proteins that detect blue light (~450–495 nm)

Photoperception: the ability to perceive light

Light scattering: dispersal of light away from a path because of a physical barrier

Light pervades our environment on Earth. It serves as a major driving force for evolution and adaptation. Plants have evolved to maximize the capture of light, and this capture fosters a light-rich environment for the resident microbes on and in plant tissues. The wide distribution of photosensory proteins among microorganisms, animals, insects, and plants suggests roles for light sensing in behaviors far beyond photosynthesis. Plants, for example, use light to bolster their defenses against microbes (47, 93), and the resident microbes may exploit light cues to colonize and fine-tune their pathogenic and mutualistic interactions with their host. This review focuses on the molecular mechanisms of red-, far-red-, and blue-light sensing and the role of photosensing in the biology of plant microbes. In particular, we explore recent developments in photosensing by two protein classes that are common in plant-associated bacteria and fungi, namely the bacteriophytochromes and LOV (light-oxygen-voltage) domain–containing proteins.

Photosensory proteins provide a critical link between sensing light and transducing light signals to evoke a response. Aromatic amino acids allow proteins to absorb near-UV light, whereas chromophores allow proteins to absorb specific wavelengths in the visible spectrum. Photosensory proteins include phytochromes, rhodopsins, xanthopsins, and flavin-binding proteins, with the latter including cryptochromes and LOV and BLUF (blue-light sensing using flavin) domain–containing proteins. Among these, phytochromes and LOV domain–containing proteins (hereafter, called LOV proteins) are of particular note for their wide distribution among plant-associated bacteria and fungi (44, 71). Phytochromes respond primarily to red and far-red light, whereas LOV proteins respond to blue light. The selective attenuation of blue, red, and far-red light as sunlight penetrates plant tissues provides opportunities for diverse photoperception responses by microbes. Increasing evidence of integrated pathways responding to red or far-red light and blue light highlights the importance of detecting distinct light qualities. However, our current understanding of photosensory pathway outputs, especially in the context of plant-microbe interactions, is limited.

Light can influence many microbial traits, including the morphology and reproduction of fungi (33). Although light often represses sexual reproduction and favors asexual reproduction in fungi, these effects are highly nuanced for specific fungi, with distinct wavelengths often differentially affecting fungal phenotypes. Photoregulated sporulation can optimize dispersal by enabling spore release at an optimal time for widespread distribution and in a particular direction (e.g., toward the open air). Moreover, photoregulation of secondary metabolites such as mycotoxins and melanin (33) can enhance protection from co-occurring stresses that occur during the day, such as low water availability, ultraviolet radiation, oxidative stress, and high temperature (34). The role of photosensing in the virulence of phytopathogenic bacteria was recently reviewed (see 56). Here, we discuss the current knowledge on how photosensing affects the growth and behavior of plant-associated bacteria and fungi, including those that are phytopathogenic.

MICROBES HAVE AMPLE ACCESS TO LIGHT WITHIN PLANT TISSUES

Plants concentrate, attenuate, and conduct light throughout their tissues. When direct light hits a leaf, the curved surface of an epidermal cell can function like a lens, concentrating light on the tissues below (116). Light that penetrates leaves scatters as it passes through cell walls, organelles, and intercellular air spaces (118). The more extensive air spaces in the spongy mesophyll layer of leaves promote greater scattering than the air spaces in the packed, columnar cells of the palisade layer. Similar to light that shines into an inwardly mirrored ball, light that penetrates leaves is concentrated due to internal reflection and light scattering; this enables leaves to function as light traps (115). In the absence of absorption, plants can increase the incident light within their tissues by three to fourfold (115).

Light is absorbed as it passes through photosynthetic tissues, generating gradients specific to distinct wavelengths. Absorption by chlorophylls, carotenoids, and other pigments generates blue- and red-light gradients in which the wavelengths decrease exponentially as the light penetrates deeper into the tissue (22, 43, 118, 121). In contrast, little far-red light (>700 nm) is absorbed by plant photosynthetic pigments (20), resulting in linear decreases with increasing depth into tissues. Differences among plant species in the nature and distribution of their pigments affect these gradients, as illustrated by blue light decreasing by 50% in spinach (*Spinacia oleracea*) leaves within the top 125 μm (117) and by 90% in alfalfa (*Medicago sativa*) leaves within the top 50 μm (114). Owing to these differences in absorption, far-red light should increase in abundance relative to blue and red light in the interior of photosynthetic tissues.

Light quality: the spectral composition, or wavelengths, of light

Light intensity: the strength of light, measured as the number of photons that hit a unit area per unit time [$\mu mol/(m^2 \cdot s)$]

Temporal gradients in light quality and intensity are generated daily and seasonally. Red and far-red light shine from dawn to dusk. In contrast, blue light is most abundant at mid-day when the scattering of these short wavelengths by the earth's atmosphere is at its lowest, although complex changes can occur in the hour after dawn and the hour before dusk (108). The intensity and quality of light reaching the earth's surface are affected by atmospheric moisture, pollution, phase of the moon, and season (103, 108). Just as plants cue into light gradients to regulate activities such as germination (73), stomatal opening (100), and defense (5, 124), resident plant microbes may exploit temporal changes in light quality and intensity to alter specific behaviors.

Spatial differences in light intensity may occur throughout a plant. Light may be intensified below the major and minor leaf veins because of minimal absorption by cells along the veins (114) and below water droplets because of their function as lenses (11). Light penetrates deeper into upper-canopy than lower-canopy leaves because of the influence of angle and diffusivity on light penetration (118), and deeper into water-infiltrated leaves because of the elimination of intercellular air spaces and consequent reduction in light scattering (118). Light also reaches belowground tissues because stems and roots act as bundles of optical fibers that efficiently conduct light over long distances (63, 104). Although light is conducted primarily by the vascular tissue, it also spreads into the adjacent pith and cortical tissues, allowing belowground tissues to transmit light (105), and particularly far-red light (104). Collectively, these spatial distribution patterns highlight opportunities for microbial photosensing within leaves, stems, and roots, and possibly even in the rhizosphere. Moreover, the lack of absorption of far-red light by pigments, and thus its availability for optical redistribution, indicates that far-red light may be a particularly prevalent signal for plant-associated microbes.

PHYTOCHROMES ENABLE RED- AND FAR-RED-LIGHT SENSING

Phytochromes have been characterized in plants (102), algae (90), fungi (44), and bacteria (24, 91). All phytochromes bind a linear bilin tetrapyrrole chromophore, with the structure of the chromophore differing among phytochrome families. Plant and green algae phytochromes (Phy family) bind phytochromobilin, whereas cyanobacterial phytochromes (Cph1 and Cph2 families) bind phycocyanobilin; these chromophores bind at the same conserved cysteine location (91). In contrast, fungal phytochromes (Fph family) and bacteriophytochromes (Bph family) bind biliverdin IVα via a conserved cysteine that is distinct from that found in plants and cyanobacteria (50). Structural similarities support a close relatedness between fungal and bacterial phytochromes (7) and suggest that the Fph and Bph families arose from a single proteobacterial progenitor (29). These phytochromes work in concert with heme oxygenases that linearize heme to form the associated bilin chromophore (77). Whereas heme oxygenases are known in bacteria because of their propensity to be coexpressed with bacteriophytochromes (**Table 1**), they have yet to be identified in fungi (4, 7, 10).

Table 1 Properties of selected phytochromes

Organism	Organism type	Name	Absorbance[a]	Phytochrome type[b]	Operon[c]	Reference
Arabidopsis thaliana	Plant	*PHYA*	665/730	Normal	NA	123
A. thaliana	Plant	*PHYC*	661/725	Normal	NA	26
A. thaliana	Plant	*PHYE*	670/724	Normal	NA	26
Avenae sativa	Plant	*PHY*	666/730	Normal	NA	113
Aspergillus nidulans	Fungus	*An*Fph1	707/754	Normal	NA	7
Synechocystis spp.	Bact (C)	Cph1	656/703	Normal	NA	84
Deinococcus radiodurans	Bact (NP)	*Dr*BphP1	698/750	Normal	*bphO-bphP1-bphR*	6
Rhodopseudomonas palustris	Bact (NP)	*Rp*BphP2	710/750	Normal	*bphP2-bphP3-RR1-RR1-RR3*	38
Agrobacterium fabrum	Bact (P)	*Af*BphP1	702/749	Normal	*bphP1-RR1*	48
A. fabrum	Bact (P)	*Af*BphP2	698/755	Bathyphytochrome	*bphP2*	48
Agrobacterium vitis	Bact (P)	*Av*BphP2	700/750	Bathyphytochrome	*bphP2*	95
Azospirillum brasilense	Bact (P)	*Ab*BphP1	710/750	Normal	*bphP1-bphR-his*	57
Bradyrhizobium spp.	Bact (P)	*Br*BphP1	676/752	Bathyphytochrome	*ppsR-bphP*	37
Pseudomonas syringae pv. *tomato*	Bact (P)	*Pst*BphP1	690/760	Normal	*bphO-bphP1*	6
Xanthomonas campestris pv. *campestris*	Bact (P)	*Xcc*BphP	688/752	Bathyphytochrome	*bphO-bphP*	9, 83
Xanthomonas oryzae pv. *oryzae*	Bact (P)	*Xo*BphP	683/757	ND	*bphP*	21

[a]Absorbance maximum is shown for the Pr and Pfr forms, respectively.
[b]Normal phytochromes have the Pr form as the ground state following assembly with a biliverdin; in bathyphytochromes, some of this Pr form is nonphotochemically converted to a Pfr-like ground state.
[c]Structure of the operon, where *bphO* denotes a heme oxygenase–encoding gene and *bphR* and *RR* denote response regulator genes.
Abbreviations: Bact (C), cyanobacterium; Bact (NP), non-plant-associated bacterium; Bact (P), plant-associated bacterium; NA, not applicable; ND, not determined.

Pr: the red-light-absorbing form of a phytochrome

Pfr: the far-red-light-absorbing form of a phytochrome

Histidine kinase (HK) domain: a protein domain that is autophosphorylated at a histidine residue, generally in response to an environmental signal

Phytochromes act as photosensors by reversibly interconverting between two stable conformations when the chromophore is stimulated by light. These conformations, a red-light-absorbing Pr form and a far-red-light-absorbing Pfr form, interconvert via the *cis*/*trans*-isomerization of a double bond in the bilin chromophore. This structural refolding, along with a recently elucidated proton translocation (27), regulates the activity of the output domain. In addition to an N-terminal domain that binds the chromophore, fungal, cyanobacterial, and bacterial phytochromes generally have a C-terminal histidine kinase (HK) domain, and plant phytochromes have an HK-related domain (44, 91, 92). The HK domains are similar to those in two-component systems (TCSs), suggesting an HK phosphorelay system for transducing light signals to a response regulator. Some response regulators are encoded in the same operon as bacteriophytochromes, but for the many that are not (**Table 1**), the response regulators have not yet been identified.

The phytochromes of plant-associated bacteria and fungi generally respond to longer red and far-red wavelengths than plant and most cyanobacterial phytochromes (**Table 1**). This shift toward far-red wavelengths reduces overlap in the absorbance spectra of these phytochromes with chlorophyll (6), therefore potentially improving their access to red and far-red wavelengths in photosynthetic plant tissues. Moreover, the phytochromes of many plant bacteria are more sensitive to far-red light than those of nonplant bacteria. Following autocatalytic binding of the bilin

chromophore, most bacteriophytochromes assume the Pr form as the ground state (Pr*), which means that Pr* is thermally stable in the dark (**Figure 1**). For bacteriophytochromes of many plant bacteria, however, Pr converts to a Pfr ground state (Pfr*) in the dark, and the Pr* and Pfr* forms establish an equilibrium mixture that may be dominated by Pfr* (37, 48, 111). Bacteriophytochromes that form this Pfr* ground-state form have been designated bathyphytochromes (48). Whereas phytochromes that have only the Pr* form in the dark may require red light for initial photoactivation, the Pfr* ground state of bathyphytochromes enables initial photoactivation by far-red light (**Figure 1**). This far-red-light responsiveness of bathyphytochromes in many plant bacteria (95) (**Table 1**) is consistent with far-red-light enrichment in plant tissues.

Two-component systems (TCSs): systems that enable sensing and responding to an environmental signal via phosphotransfer from an HK domain to a response regulator

Response regulator: a protein that mediates a response after receiving a phosphate from an HK domain

Absorbance spectra: profiles illustrating the wavelengths absorbed by substances, such as photosensory proteins or pigments

Ground state: the form of a phytochrome following synthesis and prior to exposure to light

Bathyphytochromes: phytochromes whose ground state is in the Pfr form

ROLE OF RED- AND FAR-RED-LIGHT SENSING IN PLANT BACTERIA

At present, red- and far-red-light-regulated phenotypes are known in only a few plant bacteria. We speculate that far-red-light sensing is particularly important to symbionts and phytopathogens that colonize interior tissue sites. Here, we discuss the current status of research on phytochromes in these organisms.

Phytochromes in *Bradyrhizobium*

A role for bacteriophytochromes in plant-associated bacteria was first found in a stem-nodulating symbiont of *Aeschynomene*, *Bradyrhizobium* sp. strain ORS27A. The genes encoding the *Br*BphP bacteriophytochrome and heme oxygenase colocalize with a cluster of genes involved in photosynthesis (37). This led to the discovery that *Br*BphP, which is a bathyphytochrome, contributes to far-red-light-mediated induction of the photosynthetic apparatus, including the photochemical reaction center and associated bacteriochlorophyll and carotenoids. Unlike most bacteriophytochromes, *Br*BphP lacks an HK domain; it transduces light signals by suppressing negative regulation by a coexpressed transcription factor, PspR, leading to derepression of the photosynthetic apparatus genes.

Stem nodules have chlorophyll in their outer layer; therefore, far-red light is likely more abundant than red and blue light in these nodules. Far-red-light sensing in *Bradyrhizobium* ORS27A may enable a shift in metabolism from chemoheterotrophy during growth in the soil to the more energetically favorable metabolism, photoheterotrophy, in stem nodules (37). The *Bradyrhizobium* sp. strain BTAi1 similarly uses a bacteriophytochrome to regulate the production of a light-harvesting complex, with this complex proposed to help protect from oxidative stresses associated with photosynthesis (45).

Bathyphytochromes are well-represented among members of the Rhizobiales family, including in the root-nodulating species *Rhizobium etli* and *Rhizobium leguminosarum*, and often co-occur with other phytochromes, including some with unusual spectral properties (95). The presence of bathyphytochromes in root-nodulating bacteria indicates that these bacteria may sense light signals, particularly far-red-light signals, that are conducted through the root system (104, 105).

Phytochromes in *Agrobacterium fabrum*

Not long after the discovery of bacteriophytochrome-mediated regulation of photoheterotrophy in *Bradyrhizobium* sp. ORS27A, the phytopathogen *Agrobacterium fabrum* (formerly *Agrobacterium tumefaciens*) C58 was found to produce two phytochromes. These include *Af*BphP1, which is a normal bacteriophytochrome, and *At*BphP2, which was the first recognized bathyphytochrome (48) and the founding member of a new family of HKs (49). The differences in the light-sensing

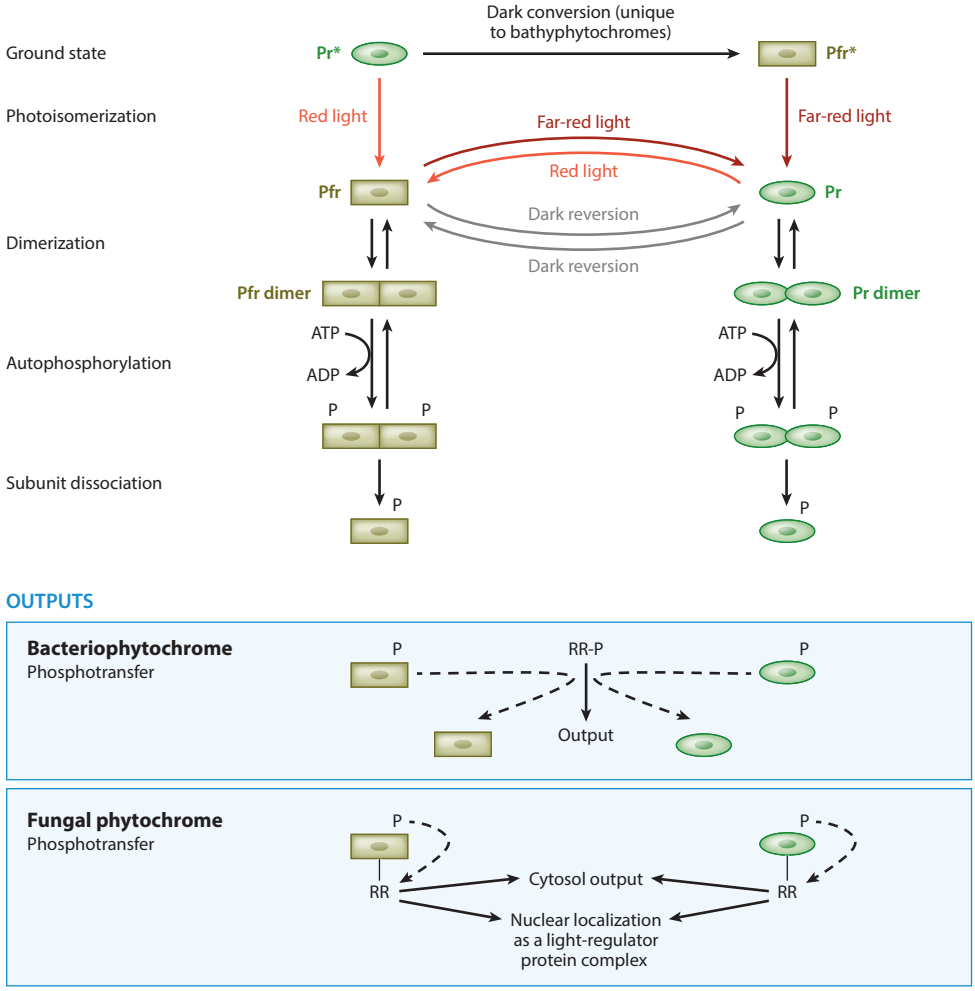

Figure 1

Model of mechanisms involved in light-mediated signal transduction by bacteriophytochromes and fungal phytochromes. Phytochromes exist in two forms, a red-light-absorbing form, designated Pr, and a far-red-light-absorbing form, designated Pfr. For normal bacteriophytochromes and fungal phytochromes, the ground-state (thermostable dark-state) form following assembly with a biliverdin is a Pr-like form, designated Pr*. For bathyphytochromes, some of the Pr* form is converted in the dark to a thermostable Pfr-like form, designated Pfr* (37, 99, 111). The photoactivated Pr and Pfr forms revert to their dark-adapted states by thermal reversion, designated dark reversion. The Pfr form generated by dark reversion of the Pr form appears to be distinct from the Pfr* form generated by dark conversion of Pr* based on observations with the bathyphytochrome *Pa*BphP (111). Bacteriophytochromes and fungal phytochromes behave as homodimers (6, 10, 111), with photoactivation occurring independently of dimerization (109) and *trans*-autophosphorylation occurring within the dimer and involving the histidine kinase A (HisKA) domain of these phytochromes. Autophosphorylation was strongly light-dependent in *Pss*BphP1 (74, 75) and weakly light-dependent in *Pa*BphP (111), in contrast to being light-independent, as in a previous model (92). The photosensory domains and response regulator (RR) receiver domains are generally on separate proteins for bacteriophytochromes; whether the Pr and Pfr forms of the bacteriophytochromes exhibit specificity toward distinct RR proteins is not yet known. The fungal phytochromes contain RR domains and mediate their output via activities in both the cytosol and the nucleus. Biliverdin is represented by small filled ovals, Pr-form phytochromes by large ovals, Pfr-form phytochromes by rectangles, and phosphorylated RR by RR-P.

capabilities of *Af*BphP1 and *Af*BphP2 were speculated to enable *A. fabrum* to simultaneously sense environments rich in red light and far-red light and thus fine-tune its responses to the environment (48). In *A. fabrum* C58, light reduces flagellar number, flagellar gene expression and protein production, swimming motility, attachment to roots, and tumor induction on cucumber plants; however, *Af*BphP1 and *Af*BphP2 are not involved in this regulation (80). Their biochemical properties have been extensively examined (58–60, 78, 79), but a biological role was found only recently: *Af*BphP1 and *Af*BphP2 contribute to light-mediated suppression of conjugation from a donor to strain C58 (2). The ecological advantages of this regulation are not known but may include minimizing light-mediated DNA damage (2), as single-stranded DNA is more susceptible to UV damage than double-stranded DNA.

Phytochromes in *Pseudomonas syringae*

A bacteriophytochrome from the foliar pathogen *Pseudomonas syringae* pv. *tomato* strain DC3000, *Pst*BphP1, was among the first phytochromes discovered to rely on a biliverdin chromophore (6). Interestingly, maximal production and photoactivity of *Pst*BphP1 requires coexpression with a heme oxygenase, designated BphO, suggesting that these proteins are translationally coupled (65) and that BphO enhances folding and chromophore incorporation into the bacteriophytochrome (99). Other phytochromes have also shown increased yields when coexpressed with chromophore biosynthesis genes (36, 61), suggesting that the formation of a BphO-BphP complex during biosynthesis may be common. At present, evidence for an effect of red light and *Pst*BphP1 on DC3000 behavior is equivocal. When DC3000 cells were exposed to red light prior to inoculation onto *Arabidopsis thaliana* leaves, this strain established populations that were larger, but not significantly larger, than when cells were exposed to white light, blue light, or the dark prior to inoculation (89). In contrast, two studies that examined DC3000 bacteriophytochrome mutants suggested that *Pst*BphP1 represses swarming (98) and growth in leaves (88), but these results, as well as results with the second bacteriophytochrome, *Pst*BphP2 (98), were equivocal given the nonquantitative nature of the analyses.

Recent results indicate that light functions as a global signal in *P. syringae* pv. *syringae* strain B728a and that the bacteriophytochrome *Pss*BphP1 is critical to this global regulation. Far-red light altered the expression of more than a quarter of the genes in B728a, with blue and red light each affecting many of these same genes (B. Hatfield, H. Dong, G.A. Beattie, unpublished data). Moreover, loss of *Pss*BphP1 eliminated regulation of the vast majority of these genes, and restoring *bphP1* expression restored their regulation. Phenotypic data are beginning to provide insights into the biological role of *Pss*BphP1. For example, *Pss*BphP1 strongly represses swarming motility under white light, red light, and far-red light and does so via a pathway that integrates red/far-red and blue light (122). This finding supports light-mediated attenuation of motility as a common theme in plant bacteria (8, 9, 80, 89, 98, 122). A closer look at how *Pss*BphP1 influences swarming motility shows that it delays the time of initiation of swarm tendrils on agar medium, and thus regulates the transition from a sessile to a motile state (75). Interestingly, *Pss*BphP1 responds to blue light, as shown for several plant phytochromes (18) and a cyanobacterial phytochrome (30, 120).

*Pss*BphP1 impacts the behavior of strain B728a at multiple stages of plant colonization. Similar to its impact on swarming motility, *Pss*BphP1 negatively regulates movement from soil and buried plant tissues to seeds (75), which is likely the first step in seed colonization, and negatively regulates virulence, as shown on bean pods following stab inoculation (75). These behaviors may be phenotypically linked to *Pss*BphP1-mediated repression of swarming motility. *Pss*BphP1 also enhances survival immediately following leaf inoculation but negatively impacts subsequent leaf

colonization (75). Using a swarming motility assay, we identified two components in the *Pss*BphP1 pathway: the downstream regulator Bsi (bacteriophytochrome-regulated swarming inhibitor) and an acylhomoserine lactone (75). Whereas Bsi was similar to *Pss*BphP1 in its influence on swarming motility, virulence, and movement in soil, Bsi did not influence leaf colonization (75). This finding demonstrates that *Pss*BphP1 contributes to leaf colonization by mechanisms beyond its effect on motility. The *Pss*BphP1 regulatory pathway is therefore branched and affects multiple stages of plant colonization (75).

Phytochromes in *Xanthomonas* spp.

Bacteriophytochromes have been characterized in strains of the pathogens *Xanthomonas oryzae* pv. *oryzae* and *Xanthomonas campestris* pv. *campestris*. Bacteriophytochromes in this genus have an N-terminal photosensory domain similar to that in other bacteriophytochromes, but of the bacteriophytochromes examined in 75 *Xanthomonas* spp., 97% had a PAS domain rather than an HK domain at their C terminus (9). PAS domains often function in sensing signals and mediating interactions with other proteins. Recent studies elucidated the crystallographic structure of the full-length *Xcc*BphP bacteriophytochrome (53, 83) and found that, as a bathyphytochrome, the thermodynamically stable ground-state Pfr form dominated over the Pr form by a ratio of 6:1 during incubation in the dark (9, 83). This Pfr ground-state form exhibited a 100% conversion to the Pr form when exposed to sunlight filtered through leaves (9), just as it does in far-red light (83), demonstrating that far-red light penetrates through leaves.

Far-red light functions as a global signal in *X. campestris* strain 8004 as well as in *P. syringae* strain B728a. The growth of 8004 under far-red light affects the expression of a quarter of the genes in its genome, and *Xcc*BphP affects the expression of almost 80% of the far-red-light-regulated genes as well as an additional 272 genes that are not light regulated (9). Among the genes and traits associated with virulence, *Xcc*BphP negatively regulates extracellular endoglucanase production and sliding motility but positively regulates xanthan and biofilm production, although the light dependence of this regulation varies among traits (9). *Xcc*BphP strongly impacts the virulence of this strain on *A. thaliana* (9). For example, exposure of cells to white light prior to inoculation into *A. thaliana* leaves reduced bacterial growth in planta, whereas exposure of *Xcc*BphP null mutant cells did not (9). Moreover, strain 8004 cells induced callose production and stomatal closure in leaves exposed to light, whereas an *Xcc*BphP null mutant did not (9). These findings support a model in which, like *Pss*BphP1 in *P. syringae*, the bacteriophytochrome *Xcc*BphP suppresses light-mediated activities contributing to virulence. Specifically, *Xcc*BphP downregulates traits contributing to bacterial growth in planta and upregulates traits that trigger basal plant defenses. As proposed by Bonomi and colleagues (9), this attenuation may minimize virulence trait expression to avoid light-enhanced plant defenses (3, 97); alternatively, it may maximize virulence trait expression on shaded leaves, thus exploiting the greater susceptibility of these leaves to pathogens (25).

Phytochromes in *Azospirillum brasilense*

The root-colonist *Azospirillum brasilense* Sp7 regulates carotenoid synthesis in response to light and has genes encoding two bacteriophytochromes. Although the bacteriophytochrome *Ab*BphP1 does not regulate carotenoid synthesis, it does enhance tolerance to the photosensitizing compound toluidine blue (57), demonstrating a role in tolerating stress generated by singlet oxygen. *Ab*BphP1 may function to provide photoprotection in soil-surface environments where sun exposure is high. Alternatively, it may enhance oxidative stress tolerance in the rhizosphere by responding to far-red light that has been conducted through the roots.

Challenges in Identifying Red-Light Pathway Components in Bacteria

Knowledge of the downstream components in phytochrome-mediated pathways could shed light on the cellular and ecological roles of these photosensory proteins. Unfortunately, most bacteriophytochromes in plant bacteria lack domains or cotranscribed genes that provide insight into their downstream signal components. Most of these bacteriophytochromes have HK domains, making them similar to the sensor kinase of bacterial TCSs. The response regulator component of TCSs generally have receiver (REC) and output domains, but many bacteriophytochromes lack a REC domain and are not clearly associated with a response regulator protein. Furthermore, for the bacteriophytochromes that have a fused REC domain or are co-transcribed with a protein with a REC domain, the REC domains lack output domains. These REC domains are generally most similar to the bacterial chemotaxis protein CheY, which functions by inducing phosphorylation-dependent conformational changes in target proteins that change their interactions with other proteins. Identifying phosphorylated target proteins in the absence of candidate proteins, however, is challenging, particularly for HK proteins (40). The propensity for plant and fungal phytochromes to function as protein complexes (86, 112) suggests that bacteriophytochromes may do the same, suggesting that protein-protein interaction approaches may be effective in identifying bacteriophytochrome-interacting proteins. In fact, bioinformatic prediction of HK-REC interactions (14) successfully identified a response regulator, SmpR, that is phosphorylated by *Pss*BphP1 in vitro, although evidence is lacking for a *Pss*BphP1-SmpR interaction in vivo (75).

ROLE OF RED- AND FAR-RED-LIGHT SENSING IN FUNGI

Fungal phytochromes exhibit greater similarity to bacterial phytochromes than plant phytochromes based on both their ability to bind a biliverdin chromophore and the inclusion of an HK domain in their structure. The presence of an HK domain and a C-terminal response receiver domain suggests that they originate from a bacterial hybrid kinase (7). Fungal phytochromes do not have a DNA binding domain and are not transcription factors; instead, their regulation is via both kinase activity in the cytosol and altered gene expression in the nucleus through interactions with other proteins (**Figure 1**). Fungal phytochromes are present in many ascomycetes (7) and basidiomycetes (62) but are absent in ascomycetous yeasts (44). Some ascomycetes and basidiomycetes have one phytochrome, whereas others have two or three; these appear to have resulted from duplication events (62, 119) with no clear evidence for subsequent subfunctionalization (119). Fungal phytochromes have been examined in only a few ascomycetes.

Phytochromes in *Aspergillus nidulans*

The first functionally characterized fungal phytochrome was that of *Aspergillus nidulans*. Although *A. nidulans* itself is not generally associated with plants, it is closely related to phytopathogens and aflatoxin producers. Like other fungi, *A. nidulans* uses light as a determinant of sexual versus asexual reproduction, secondary metabolite production, and germination (86, 94). In general, *A. nidulans* exhibits asexual reproduction (conidiospore production) in the light and sexual reproduction (cleistothecia production) in the dark. However, distinct wavelengths have distinct effects. For example, whereas red and blue light are both required for high-level conidia production, red has a much larger role than blue in repressing cleistothecia production. Also, far-red light activates the production of the mycotoxin sterigmatocystin, whereas blue light represses it (86). These distinct responses reflect the presence of both phytochrome and LOV proteins.

The *A. nidulans* phytochrome *An*FphA mediates suppression of sexual development in red light (7), but this phytochrome functions, at least in part, as a sensor for the absence of light. Following

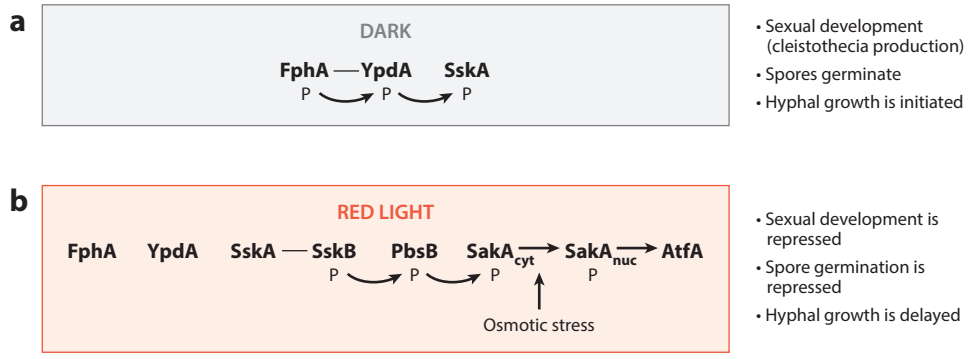

Figure 2

Model of the integration of light- and stress-responsive pathways involving a fungal phytochrome. YpdA, a histidine phosphotransferase protein, and SskA, a response regulator, are components in two-component systems. In the dark, the FphA-YpdA interaction activates FphA kinase activity, resulting in a phosphorelay through YpdA to SskA, and maintenance of SskA in a phosphorylated state (125). Red light disrupts the FphA-YpdA interaction, allowing for an SskA-SskB interaction that induces autophosphorylation of SskB, a MAP (mitogen-activated protein) kinase, with a phosphorelay through the additional MAP kinases PbsB and SakA and transmission of this response to AtfA, a bZIP transcription factor, via nuclear localization of phosphorylated SakA (125).

synthesis of Pr as the ground-state form, Pr exhibits autophosphorylation and transphosphorylation activities in the dark when particular response regulator domains are present (10). In fact, a physical interaction between *An*FphA and the histidine phosphotransferase protein YpdA in the dark triggers *An*FphA kinase activity and phosphotransfer to YpdA (**Figure 2*a***) (125), illustrating that this phytochrome is active in sensing the absence of light. The phosphorylated form of YpdA is predicted to maintain the response regulator SskA in a phosphorylated state (125), thus preventing SskA activation of a downstream stress-response pathway (**Figure 2*b***). The interaction with YpdA thus enables *An*FphA to function in the absence of light, whereas a light-mediated conformational change that disrupts the *An*FphA-YpdA interaction mediates its response to light (**Figure 2*b***) (125).

The co-occurrence of light with other environmental stresses like high temperature and low moisture suggests a biological rationale for coordinating photosensory and stress-response pathways. Recently, Yu and colleagues (125) screened for *A. nidulans* mutants that do not sense light and discovered that a key osmotic stress-sensing regulator is also central to light sensing. This regulator, SakA, exhibits light-dependent shuttling from the cytoplasm to the nucleus. Furthermore, although osmotic stress promotes nuclear shuttling independently of light, light-dependent nuclear shuttling and SakA phosphorylation both require the phytochrome *An*FphA (125). An emerging model shows that light-dependent activation of *An*FphA decreases the phosphorylation of YpdA and SskA, and this decrease enables SskA to interact with SskB and trigger a cascade of events that results in transcription factor AtfA binding and expression of genes involved in repressing sexual development and spore germination (**Figure 2*b***). This pathway requires *An*FphA but not the known blue-light-sensing proteins LreA and LreB; thus, the response of the pathway to blue light supports blue-light-sensing activities by the phytochrome *An*FphA (10, 94).

*An*FphA also functions in the nucleus as a complex with other proteins (86). Although the mechanisms by which this complex affects gene expression are still being elucidated, one mechanism is modulation of histone acetylation (41). In the dark, *An*FphA interacts with other proteins

to promote histone deacetylation, and the resulting chromatin condensation suppresses the expression of the light-induced *ccgA* (clock-controlled gene). In the light, these protein interactions promote histone acetylation and increase *ccgA* expression (41). Thus, *An*FphA regulation occurs by many routes, including phosphorylation-dependent events in the cytoplasm, and alterations in transcription factor binding and chromatin structure in the nucleus.

Holoprotein: a photosensory protein complexed with a chromophore

Phytochromes in Phytopathogenic Fungi

Phytochromes have been identified in diverse phytopathogenic fungi, including *Fusarium graminearum*, *Cochliobolus heterostrophus*, *Ustilago maydis*, and *Botrytis cinerea*. Inactivation of the *B. cinerea* phytochrome slows growth, increases susceptibility to cell wall stress, and reduces cell wall chitin content and virulence, with the disruption to chitin synthesis potentially explaining the slow growth and reduced virulence through increased susceptibility to plant defenses (42). These phenotypes, however, are not clearly influenced by light in the wild type or in a phytochrome-deficient mutant; thus, the possibility remains that the phytochrome functions as a developmental sensor more than, or in addition to, a light sensor. Pathogenic *Fusarium* spp. have a single phytochrome gene (1), and this gene is upregulated during late sexual development (119), but the impact of red light on the biology of these *Fusarium* spp. is not known. Phytochromes have yet to be characterized in other plant-associated fungi.

Beyond *A. nidulans* and *B. cinerea*, fungal phytochromes have been characterized in *Neurospora crassa* and *Beauveria bassiana*. *N. crassa* has genes for two phytochromes, Phy-1 and Phy-2, and although Phy-2 in particular contributes to light-mediated repression of sexual development, this repression is relatively subtle and was missed in early studies (119). In contrast, in *B. bassiana*, an entomopathogen used for the biocontrol of many insects, inactivation of the phytochrome *Bb*Phy significantly alters conidiation, growth, and stress tolerance (87). *Bb*Phy inactivation also reduces phosphorylation of Hog1, an ortholog of SakA, suggesting coordination of the phytochrome and SakA/Hog1 stress-response pathways in *B. bassiana* as in *A. nidulans* (125).

LOV PROTEINS ARE WIDESPREAD BLUE-LIGHT-SENSING PROTEINS

LOV proteins are the most widespread blue-light-sensing proteins among plants, fungi, bacteria, and archaea (68, 71). As with the phytochromes, their photochemistry is understood better than their biological roles. Following protein synthesis, a flavin compound, usually a flavin mononucleotide (FMN), inserts into the flavin-binding pocket of the LOV domain and forms a ground-state holoprotein. Exposure to blue light triggers the formation of a series of excited-state forms of the isoalloxazine ring of the flavin that culminate in a covalent bond between the flavin and a highly conserved cysteine residue in the LOV domain (67). The bond formation changes LOV domain–effector domain interactions and effector activity. The mechanisms for this signal transduction vary based on the domain structure but generally are not yet well understood. In the dark, the photoexcited adduct decays back to the noncovalent ground state, with a decay rate that varies from seconds to days among LOV proteins and is influenced by the environment (85).

ROLE OF BLUE-LIGHT SENSING IN PLANT BACTERIA

LOV proteins were first identified as phototropins in plants but are now known to include diverse families that vary in their associated effector domains. In bacteria, these effector domains include HK domains, GGDEF and EAL domains, which function as diguanylate cyclases and phosphodiesterases, respectively, and STAS (sulfate transporter and antisigma factor antagonist) domains,

which function primarily as antisigma factors. Among almost 500 bacterial LOV proteins examined, approximately a quarter lacked effector domains and half had HK effector domains (71). Like bacteriophytochromes, LOV-HK proteins are similar to the sensor kinase component of TCSs. Approximately half of the LOV-HK proteins have a fused C-terminal receiver domain (LOV-HK-REC), and all lack a fused output domain. The presence of a histidine kinase A (HisKA) domain, which includes a homodimerization region, suggests the formation of homodimers by LOV-HK proteins (15, 46).

LOV proteins in plant bacteria (pathogens, symbionts, and root and leaf colonists) most commonly have the domain structure LOV-HK-REC. In fact, among almost 500 bacterial LOV proteins (71), 61 had a LOV-HK-REC structure, and 91% of these were in plant bacteria. Conversely, proteins with this domain structure, or truncated versions of it (short-LOV and LOV-HK), were present in 88% of plant bacteria but only 14% of nonplant bacteria, illustrating a strong association between this type of LOV protein and plant bacteria. Moreover, a phylogenetic analysis of the LOV domains demonstrated a closer relatedness among those of plant bacteria than those of nonplant bacteria (74). Based on the similarity of LOV-HK-REC proteins to TCSs, the signal transduction pathway likely involves blue-light-activated autophosphorylation and phosphotransfer to the REC domain, but the lack of an associated output domain has thus far confounded the identification of downstream components in LOV protein pathways.

Many LOV proteins regulate the transition of bacterial cells between a single-cell, motile state and a multicellular, sessile state as well as between a pathogenic and an environmental (or epiphytic) lifestyle (39). Recent studies have found that regulation of motility and surface attachment by LOV proteins varies among plant bacteria; however, all the LOV proteins examined thus far in these organisms markedly affect the nature of the interactions between these organisms and plants.

LOV Proteins in *Pseudomonas syringae*

Our knowledge of the photochemistry of LOV-HK proteins, and particularly LOV proteins in plant bacteria, is based primarily on studies with *Pst*LOV, the LOV protein in *P. syringae* pv. *tomato* strain DC3000. *Pst*LOV shows a low level of autophosphorylation in the dark, blue-light-induced kinase activity, and a 94-min decay rate back to the noncovalent ground state (12, 17, 107). This long decay rate indicates that even transient photoactivation can have effects that last for hours. *Pst*LOV associates primarily with FMN (86%) as a flavin cofactor and secondarily with either flavin adenine dinucleotide (13%) or riboflavin (0.7%) (17). *Pst*LOV and *Pss*LOV in *P. syringae* pv. *syringae* strain B728a have also been examined for their cellular and ecological roles.

Blue light negatively impacts DC3000 virulence. Cells exposed to blue or white light prior to inoculation establish smaller populations and induce weaker symptoms in *A. thaliana* and tomato (*Solanum lycopersicum*) leaves than cells exposed to dark conditions, and these changes are lost when *Pst*LOV is inactivated (89). Moreover, LOV-mediated reductions in virulence are associated with increased adherence to leaves (89), consistent with blue light enhancing surface adherence and reducing entry. The negative impact of blue light on virulence is attenuated when cells are introduced via infiltration, which bypasses natural entry (89), supporting a model of blue-light-reduced bacterial entry into leaves. Other studies have also correlated loss of *Pst*LOV with increased virulence based on quantitative (76) and qualitative (88) assessments of growth in *A. thaliana* leaves exposed to white light.

The negative impact of blue light on DC3000 virulence may involve *Pst*LOV-regulated phenotypes observed in culture. Blue and white light inhibit swarming motility via *Pst*LOV, with white light reducing flagellar gene expression and inducing exopolysaccharide gene expression (89). These findings are consistent with *Pst*LOV regulating the transition between a motile state,

which involves swarming motility, and a sessile state (39), which involves producing the exopolysaccharide alginate. *Pst*LOV also regulates oxidative stress tolerance (76), a trait important during plant infection, suggesting a role for *Pst*LOV in regulating the transition between environmental and pathogenic lifestyles (39). Gene expression data in another study suggests that *Pst*LOV functions as a negative regulator of multiple global regulatory networks, including the HrpL, GacA-GacS, and RpoN networks (76); however, this negative regulation is not supported by the relatively limited impact of *Pst*LOV on virulence as compared to the large impact of the loss of these regulators (19). The influence of blue light and *Pst*LOV on growth in culture has varied among studies (76, 88, 89), suggesting that multiple environmental conditions interact with blue light to affect growth. Examples of such conditions may include nutrient-dependent effects on the cytosolic redox state and the presence of photosensitizing compounds.

*Pss*B728a shares 92.5% identity with *Pst*LOV but has a distinct cellular role. Whereas loss of *Pst*LOV increases swarming motility by DC3000 (89), loss of *Pss*LOV decreases swarming motility by B728a (122); regulation is blue- and white-light specific in both strains. Positive regulation by *Pss*LOV requires critical conserved residues in the HK and REC domains (122). *Pss*LOV regulation of swarming motility also requires the presence of the bacteriophytochrome *Pss*BphP1, with evidence indicating that *Pss*LOV relieves *Pss*BphP1-mediated repression. The mechanism by which this occurs is not yet clear, but although it occurs in blue and red light, it may occur differently in blue versus red light given that *Pss*BphP1 meditates repression of swarm tendril initiation only in red light (75). A null mutant of *Pss*LOV induces lesions on bean pods that are consistently, but not significantly, smaller than those of the wild type (75) and exhibits high experimental variation in the extent to which it is altered in leaf colonization (74). The variability in growth in culture and in planta observed for LOV mutants of both *P. syringae* strains suggests strong environmental influences on blue-light-dependent growth responses.

LOV Proteins in *Xanthomonas citri* subsp. *citri*

A LOV protein in *Xanthomonas citri* subsp. *citri* strain 99-1330 influences the host response to the pathogen. Similar to *Pst*LOV, *Xcc*LOV interacts primarily with an FMN cofactor and decays back to its ground state with a relatively long decay rate (87 min) (54). Following infiltration of 99-1330 into orange (*Citrus sinensis*) leaves, canker symptoms develop in the light and necrosis develops in the dark. Loss of *Xcc*LOV results in necrosis in the light and dark, suggesting that *Xcc*LOV contributes to light-mediated suppression of traits leading to necrosis (54). That is, *Xcc*LOV helps suppress a strong plant immune response that culminates in necrosis, similar to the function of phytobacterial effectors that suppress plant defenses to aid virulence.

*Xcc*LOV influences the host response without influencing the growth of the pathogen. A transcriptome analysis of orange leaves during infection showed greater repression of photosynthesis-related genes and induction of defense-related genes, sucrose and starch catabolism genes, and secondary metabolite genes in leaves infected with the *Xcc*LOV mutant than in those infected with the wild type (55). Furthermore, Kraiselburd et al. (55) documented greater membrane permeability, tissue degradation, and lignin deposition in leaves inoculated with the mutant than with the wild type. These results support a role for *Xcc*LOV in suppressing plant defenses and maintaining photosynthetic efficiency after infection. Interestingly, *Xcc*LOV does not influence bacterial growth in planta, irrespective of the light conditions; this is particularly surprising given the absence of an effect of the mutation on bacterial growth as late as 12 days postinoculation (dpi) (54) despite genetic and histological changes as early as 1 to 7 dpi (55). These results illustrate that the impact of *Xcc*LOV on plant symptomology did not influence the conduciveness of orange leaves to support the growth of this pathogen.

The loss of *Xcc*LOV affects many traits in *X. citri* subsp. *citri* (54). White light promotes adherence to orange leaves, polyvinylchloride, and other cells, as detected via cellular aggregation in biofilms, and this adherence depends, at least in part, on *Xcc*LOV (54). This adherence may be through *Xcc*LOV-mediated induction of a filamentous hemagglutinin-like adhesin (54). The finding that *Xcc*LOV, like *Pst*LOV, promotes adherence to leaves suggests that *Xcc*LOV could prevent entry into the leaf, but this is contradicted by the fact that *Xcc*LOV does not influence population sizes in leaves (54). Thus, the impact of light-enhanced adherence on *X. citri* subsp. *citri* interactions with citrus remains unclear. *Xcc*LOV also negatively regulates swarming motility and exopolysaccharide production, and positively regulates oxidative stress tolerance, twitching motility, and flagellin and flagella production, but regulation of these phenotypes is independent of light. Another pathogenic xanthomonad, *X. campestris* pv. *campestris*, has at least 11 potential blue-light-responsive proteins, four of which affect the size of lesions induced on cabbage leaves (72), illustrating the wealth of blue-light-responsive proteins that have yet to be investigated in phytopathogens.

LOV Proteins in *Rhizobium leguminosarum* bv. *viciae*

Blue light influences the symbiotic properties of plant symbionts. For cells of the nitrogen-fixing *R. leguminosarum* bv. *viciae* strain 3841, cells grown in white light prior to inoculation on pea plants (*Pisum sativum*) induce more red nodules, which generally support nitrogen fixation activity, and fewer white nodules, which lack nitrogen fixation activity, compared to cells grown in the dark. Moreover, nodules formed by cells grown in the light have more bacteria per nodule (8). This strain has a LOV protein, *Rlv*LOV, that differs from the LOV-HK-REC proteins in phytopathogens by lacking a REC domain and having an HK domain that is in the HWE HK family rather than the HisKA family (8). *Rlv*LOV also increases the competitiveness of strain 3841 for forming nodules; in fact, loss of *Rlv*LOV results in the almost complete inability to compete for nodule formation (8). The dramatic effects of *Rlv*LOV, and thus presumably blue light, on these symbiotic phenotypes may reflect sufficient blue-light conductance through plant roots to photoactivate *Rlv*LOV; alternatively, environmental factors other than blue light may activate *Rlv*LOV.

*Rlv*LOV influences multiple phenotypes in culture in a light-dependent manner. *Rlv*LOV is required for white-light-mediated repression of flagellar production and some flagellar genes (8). *Rlv*LOV is also required for repression of exopolysaccharide production and adhesion to polystyrene surfaces, with this regulation requiring a conserved histidine in the HK domain (8). Although motility is inhibited by high light intensities, it is not regulated by *Rlv*LOV (8).

Light represses nodulation in many legumes, and this repression is influenced by the quantity and quality of light (106). For the symbiosis between *Mesorhizobium loti* and *Lotus japonicus*, nodule numbers are reduced on blue-light-exposed roots compared to on shaded roots but not on red-light-exposed roots (101). Reduced nodulation correlates with fewer infection threads, possibly due to blue light inhibiting bacterial growth and reducing cell numbers for infection thread initiation. An *Mll*LOV protein contributed to blue-light inhibition of growth in culture, but its influence on nodulation was equivocal given that a null mutant induced more, but not significantly more, nodules than the wild type (101).

Challenges in Identifying Blue-Light Pathway Components in Bacteria

Knowledge of the downstream components in LOV protein–mediated pathways could provide insights into integrated pathways sensing blue light and other environmental signals and the cellular and ecological roles of LOV proteins. Similar to bacteriophytochromes, LOV proteins in

plant bacteria lack output domains and have REC domains that are most similar to CheY. Also, LOV proteins mediate responses not only to blue light but also to the cellular redox state because of the requirement for fully oxidized flavin before photoexcitation (85); conditions favoring reduced flavins can therefore make a LOV protein light insensitive (85). Similarly, the finding that *Pss*LOV attenuates phytochrome-mediated repression of swarming motility illustrates that red or far-red light can influence the detection of blue-light responses. Future studies will benefit from greater attention to cross talk among photosensory proteins, as discussed below. Despite these challenges, our understanding of blue-light sensing in plant bacteria, particularly by LOV proteins, is rapidly advancing.

White-collar complex (WCC): a fungal protein complex that regulates transcription in response to blue light

ROLE OF BLUE-LIGHT SENSING IN PLANT-ASSOCIATED FUNGI

Blue-light sensing in fungi is best understood through the lens of the well-studied white-collar complex (WCC) proteins in the nonplant-associated fungus *Neurospora crassa* (4, 44, 66). The WCC was so named because of the appearance of a collar of white hyphae beneath a layer of pigmented conidia in WCC null mutants. WCC comprises two proteins with DNA-binding domains, one with a LOV domain, WC-1, and one without a LOV domain, WC-2; together, these function as a transcription factor (44, 82). WC-1 was the first fungal photoreceptor to be cloned, and WCC is the only transcription factor known to be directly regulated by light (33). The WC-1 and WC-2 proteins are highly conserved and co-occur within a broad range of fungi, including ascomycetes, basiodiomycetes, mucoromycetes (formerly zygomycetes), and chytrids (33, 44). This distribution indicates a close functional linkage of WC-1 and WC-2 and a deep evolutionary origin for WCC homologs as photosensory proteins within the fungi. Given this origin, the absence of WCC in some fungi, such as the ascomycetous yeasts, likely resulted from gene loss, whereas the presence of multiple copies in others, like the mucoromycetes and chytrids, likely resulted from gene duplication, with some subsequent functional differentiation (44).

Blue-Light Sensing in *Neurospora crassa*, an Archetypal Model of Competitive Dimerization

Light regulation in *N. crassa* involves modulating the activity of the fungal LOV protein WC-1 via competitive dimerization (82). In the dark, the WCC protein complex binds light-responsive elements in the promoters of light-regulated genes. Blue-light activation of WC-1 induces a conformational change that favors WCC homodimerization and promotes transcription. The induced genes include transcription factors, circadian clock genes, and a gene encoding another LOV protein, VIVID (VVD). Blue-light activation of VVD enables it to bind competitively to light-activated WC-1, thus sequestering WC-1 and disrupting the WCC homodimers required for further transcriptional activation (70). This negative feedback loop contributes to photoadaptation (33). Blue light also induces WC-1 phosphorylation, causing WCC destabilization and ensuring that transcriptional activation is only transient (82). Many additional proteins modulate the activation of light-regulated genes, including via histone acetylation and methylation, and promote activation of gene cascades such that early light responses can be distinguished from late light responses (23). Blue light influences the regulation of carotenoid production, asexual and sexual development, and the circadian clock in *N. crassa* (23). The central role of WCC (33) and the minor role of phytochromes in *N. crassa* light regulation (23) illustrate the importance of this blue-light sensing.

Blue-Light Sensing in Phytopathogenic and Plant-Associated Fungi

Among phytopathogenic fungi, WC-1 homologs (WCHs) commonly affect asexual development in a light-dependent manner. In *Cercospora zeae-maydis* and *Botrytis cinerea*, the WCHs CRP1 and *Bc*WCL1 mediate light-dependent suppression of conidiation, respectively (16, 51), whereas in *Magnaporthe oryzae*, the WCH MGWC-1 enhances light-dependent conidial release (64). WCHs also influence light-dependent pigment and secondary metabolite production, as shown by the contribution of WC1 to carotenoid production in *Fusarium oxysporum* (96), CRP1 to phytotoxin (cercosporin) production in *C. zeae-maydis* (51), and WcoA to mycotoxin (fusarin) production in the plant-growth-promoting *Fusarium fujikuroi* (28). Some phytopathogenic fungi, including *F. oxysporum*, *C. zeae-maydis*, and *U. maydis*, require WCHs for photoreactivation, i.e., for light-mediated recovery from UV radiation–induced DNA damage, which is associated with increased expression of photolyase genes (13, 51, 96). Similarly, a WCH contributes to *B. cinerea* tolerance to oxidative stress (16).

Blue-light sensing also influences the virulence of several fungal plant pathogens. *C. zeae-maydis* requires open stomata for infection of maize leaves, and the blue-light sensor CRP1 regulates hyphal growth orientation toward stomata, appressorium formation, and foliar necrosis following a characteristic latent period (51). Blue-light sensing is also important to *B. cinerea* induction of gray mold disease, with *Bc*WCL1 enhancing virulence during a three-day incubation with, but not without, a light cycle (16). During *M. oryzae* infection of rice leaves, MGWC-1 antagonizes rather than enhances virulence in the light (52). In contrast to these foliar pathogens, loss of WC1 in the root pathogen *F. oxysporum* does not alter virulence, which is consistent with a greater role for blue-light sensing in aboveground tissues than belowground tissues.

Coupling of Blue-Light Sensing and Oxidative-Stress Sensing in Fungi

Trichoderma reesei, a close relative of *Trichoderma* species involved in the biocontrol of plant pathogens, requires blue light and oxygen for conidiation. It uses a slight variant of the WCC/VVD pathway in *N. crassa*. The *T. reesei* orthologs of WC-1, WC-2, and VVD, namely BLR1 (blue-light receptor 1), BLR2, and ENV1 (Envoy 1), respectively, also show blue-light activation of VVD (ENV1), which enables competitive binding and thus disruption of the BLR1-BLR2 heterodimer required for transcriptional activation of genes promoting conidiation (66). ENV1, however, can also form homodimers, and this homodimerization is strongly favored in the presence of oxygen (66). This is due to a distinctive cysteine residue in ENV1 that favors disulfide bond formation, resulting in irreversible homodimerization under oxidative stress conditions. ENV1 sequestration into homodimers removes ENV1 interference in BLR1-BLR2-mediated transcriptional activation, thus allowing gene expression only in the presence of both oxygen and blue light. Interestingly, the cysteine residue critical to this dual sensor response is specific primarily to plant pathogens in the Sordariomycetes family, including *F. oxysporum*, *Verticillium alfalfae*, *Colletotrichum gloeosporioides*, *Villosiclava virens*, *Claviceps purpurea*, and *Zymoseptoria tritici* (66), suggesting functional benefits to phytopathogenic fungi of coupling blue-light and oxidative-stress sensing.

CROSS TALK BETWEEN RED- AND BLUE-LIGHT-SENSING SYSTEMS IN PLANT MICROBES

Most plant pathogens have both red- and blue-light-sensing proteins, supporting potential integration of their responses. Among ~1,000 bacterial genomes examined that have at least one photosensory protein, approximately 22% have both phytochrome and flavin-based,

blue-light-sensing proteins, whereas among phytopathogenic bacteria, this percentage increases to approximately 77% (71). Among these pathogens, most of the *Pseudomonas* spp., *Xanthomonas* spp., and *Acidovorax avenae* and some of the *Agrobacterium* spp. for which genome sequences are available have both blue- and red-light-sensing proteins. In contrast, *Ralstonia solanacearum*, *Leifsonia xyli*, *Clavibacter michiganensis*, and *Pantoea* spp. have only blue-light-sensing proteins, with the latter three having BLUF rather than LOV proteins, and *Burkholderia* spp. and *Streptomyces* spp. have only red-light-sensing proteins (71). Many plant symbionts, including *R. leguminosarum* and some *Bradyrhizobium* spp., have both blue- and red-light-sensing proteins, as do the common leaf-associated genera *Methylobacterium* and *Sphingomonas* spp. (71).

Among the phytopathogenic fungi for which whole-genome sequences are available, 80% of the 20 ascomycetes examined and 75% of the 10 basidiomycetes examined have both phytochrome and flavin-based, blue-light-sensing proteins. In contrast, only 26% of the 23 ascomycetous and basidiomycetous human pathogens evaluated have both phytochrome and flavin-based, blue-light-sensing proteins (G. Beattie, unpublished data). Among potential symbionts, the fungal endophyte *Rhodotorula graminis* has phytochrome and LOV proteins, whereas the ectomycorrhiza *Laccaria bicolor* does not (62).

The bacterial pathogen *P. syringae* pv. *syringae* B728a integrates blue- and red-light-signaling pathways. A phytochrome negatively regulates swarming motility in response to blue, red, and far-red light, whereas a LOV protein suppresses this negative regulation in response to blue light (122). This same network regulates virulence in bean pods, possibly via its effect on motility (75). This network is similar in structure to an integrated *Arabidopsis* network in which phytochromes inhibit photomorphogenesis in response to blue or red light, and cryptochromes suppress this negative regulation in response to blue light (31, 122). This similarity suggests that this regulatory network structure is evolutionarily conserved.

The complex effects of blue and red light on fungal development and physiology (64, 69, 82, 86, 110) suggest integration of these light-responsive pathways in fungi as well. *N. crassa* has been an excellent model for characterizing the blue-light-responsive WCC pathway, as blue light regulates carotenoid production, conidiation, and other phenotypes, but this pathway was elucidated in the absence of red-light inputs because red-light-regulated phenotypes were not known. The suggestion that other photoreceptors alter WCC-mediated gene expression (81) led to the recent discovery that the *N. crassa* phytochrome Phy-2 regulates genes involved in sexual development (119). This model system is currently well-positioned to characterize a fungal network involving red- and blue-light signaling.

A. nidulans is currently the most developed fungal model of the molecular pathways involved in red- and blue-light signaling (33, 35). Investigations into *A. nidulans* as a model system for red-light sensing identified a central role for the blue-light-sensing WC-1 and WC-2 homologs, LreA (light response A) and LreB, respectively (86). The phytochromes *An*FphA, LreA, and LreB, which are all required for full conidiation, interact with each other and with the transcription factor VeA in a protein complex in the nucleus. Purschwitz and colleagues (86) elaborated a regulatory network in which LreA functions to keep gene expression low in the dark and *An*FphA relieves this repression in the light, in part, by increasing histone acetylation. This LOV protein–mediated repression and phytochrome-mediated derepression contrast with phytochrome-mediated repression and LOV protein–mediated derepression in the *P. syringae* pathway, demonstrating variation among these networks.

CONCLUSIONS

We have seen only a glimmer of the actual roles of light in modulating microbial behaviors when associating with plants. This is due, in part, to the complexity of light regulation, which can involve

distinct aspects of the light signals. Clearly, microbes can perceive differences in light quality, as reflected in red- and blue-light-specific responses, with integration occurring via a single photosensory protein such as *Pss*BphP1, which senses red and blue light (122); a protein complex such as *An*FphP1-LreA-VeA (86); or cross talk among separate pathways (41, 122). Microbes can also perceive differences in light intensity, as illustrated by light-intensity-driven differences in bacterial motility (89) and fungal development (7, 69, 86, 110). Most underappreciated, however,

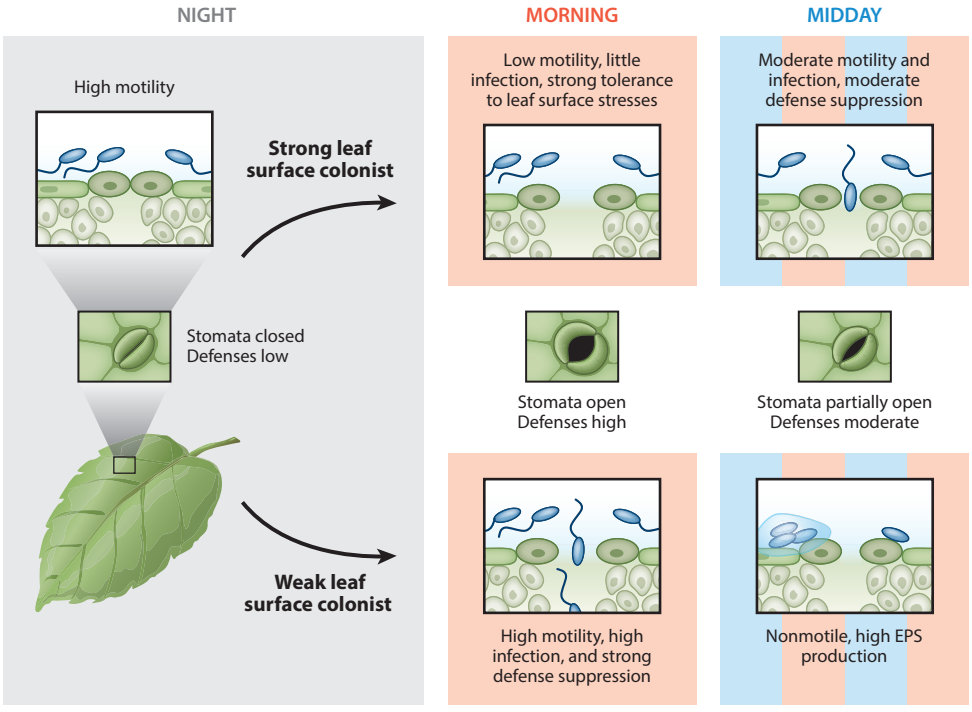

Figure 3

Model of light-sensing impacts on leaf colonists with distinct lifecycle strategies following bacterial immigration to a leaf surface. (*Left*) At night, bacterial cells are highly motile due to the absence of light-mediated repression of motility (8, 9, 80, 89, 98, 122). The stomata are mostly closed, preventing bacterial invasion, and the high surface moisture favors bacterial spread and growth. (*Middle*) In the morning, the solar radiation reaching leaves is richer in red light than blue light due to atmospheric blue-light filtering. The stomata open to promote gas exchange, and the basal defenses heighten to protect from invading microbes (5, 124). Bacteria that exhibit strong red-light-mediated repression of motility (122) exhibit minimal invasion, thus minimizing exposure to strong basal defenses. These leaf surface colonists can tolerate leaf surface stresses, such as low water availability (32), but may be weak at suppressing basal defenses. In contrast, bacteria that remain highly motile under high red light invade leaves through open stomata (89). These bacteria are likely highly effective at suppressing basal defenses, and therefore grow in the apoplast, but may be weak at tolerating leaf surface stresses (32). (*Right*) By midday, the blue light reaching the leaves has increased and the surface moisture, average stomatal aperture, and level of activation of the basal defenses have decreased. Bacteria that exhibit blue-light-mediated attenuation of red-light-mediated motility suppression (122) regain some motility, enabling them to invade through the stomata at a time when they have a better chance of suppressing the basal defenses. In contrast, leaf surface bacteria that are programmed for a blue-light-mediated switch from a motile to a sessile state (89) put their energy into tolerating the surface stresses, many of which peak at mid-day, rather than into invasion. Characteristics of a strong leaf surface colonist are modeled after *Pseudomonas syringae* pv. *syringae* strain B728 (122), and those of a weak leaf surface colonist, are modeled after *P. syringae* pv. *tomato* strain DC3000 (89).

is that microbes can perceive differences in light-dark cycling, as illustrated by the complex impacts of light-dark cycling on spore-release behavior in *M. oryzae* (64). The difficulty in studying, and fundamentally deconstructing, light regulation by microbes on plants is exacerbated by the coupling of light with other environmental signals, including temperature, water availability, and redox conditions. It is further exacerbated by the strong influence of light on the physiology, health, and defense responses of host plants (47, 93).

Interpreting the biological benefit of light-mediated networks in plant pathogens and symbionts therefore requires consideration of how light influences the plant host. For example, consider the *P. syringae* pv. *syringae* B728a regulatory network in which swarming motility is repressed by red light and derepressed by blue light. To predict the biological benefit of this network, we must consider that (*a*) stomata are required for *P. syringae* entry into leaves, (*b*) light induces stomatal opening, and (*c*) plant basal defenses are maximal early in the morning but then decline, based on studies with *A. thaliana* (5). A biological benefit of the regulatory network therefore may be to evade the plant basal defenses by suppressing motility in the early morning when stomata open but basal defense is high and attenuating this suppression as blue light increases at midday, thus enabling motility and entry when the basal defenses are lower. Light responses may also reflect differences in pathogen lifestyles on plants, as illustrated by a blue-light-mediated increase in motility by *P. syringae* B728a, which is a strong colonist of leaf surfaces (32), and by a blue-light-mediated increase in polysaccharide production and adherence to leaves by *P. syringae* DC3000 (89), which is a weak colonist of leaf surfaces (32) (**Figure 3**).

Here, we have summarized our current knowledge of light sensing in plant bacteria and fungi. Although far-red light is likely the most abundant light signal within plant tissues, surprisingly few studies have focused on far-red- and red-light-sensing photosensory proteins in plant microbes. The few studies performed thus far have identified roles for phytochromes in plant bacteria, including as major drivers of the global transcriptome, but have not yet established a role for these proteins as light sensors rather than developmental sensors in plant-associated fungi. Collectively, studies on blue-light sensing have demonstrated diverse blue-light responses mediated by LOV proteins in plant bacteria, but knowledge of these responses in plant fungi, and particularly phytopathogenic fungi, is lagging. The structural features of LOV proteins in many of these fungi, however, suggest that they coordinate responses to blue light and oxidative stress. Despite the potential complexity of light regulation, studies with these photosensory proteins are illustrating how photosensing in plant-microbe interactions is a field that is ripe for illumination.

SUMMARY POINTS

1. Plants can enhance the exposure of their resident microbes to light by capturing, concentrating, and conducting light throughout their tissues. Although red and blue light are absorbed by photosynthetic tissues, far-red light is not, allowing it to be redistributed and available as a particularly prevalent signal for plant-associated microbes.
2. Many plant-associated microbes have both far-red-/red- and blue-light-sensing proteins. This includes most plant-pathogenic bacteria and fungi, especially foliar pathogens.
3. Phytochromes are photoreceptor proteins that interconvert between red- and far-red-light-absorbing forms. Many plant-associated bacteria have an unusual form of phytochrome, a bathyphytochrome, which exhibits an initial photoactivation by far-red light and thus confers a heightened potential for far-red-light responsiveness.

4. Red-/far-red-light-regulated phenotypes are known in only a few plant bacteria. These phenotypes include phytochrome-mediated suppression of virulence in at least two foliar bacterial pathogens, with phytochromes serving as major global transcriptional regulators in these pathogens. Phytochromes also mediate suppression of motility and conjugation in phytopathogens and induction of the photosynthetic system in stem-nodulating bacteria.
5. Phytochrome-regulated molecular pathways that were elucidated in the model fungus *Aspergillus nidulans* show that fungal phytochromes can function as sensors of the absence rather than presence of light and can regulate pathways integrating light and environmental stress signals. Although exploring these pathways in phytopathogens is in its early stages, the phytochrome of at least one phytopathogenic fungus, *B. cinerea*, affects pathogenicity.
6. LOV-domain proteins are the most widespread blue-light-sensing proteins among plants, fungi, and prokaryotes. LOV proteins have marked effects on the interactions of phytopathogenic and symbiotic microbes with plants, as illustrated by fungal LOV proteins that repress or enhance virulence and by bacterial LOV proteins that repress virulence, suppress plant defenses, increase adherence to leaves, and enhance symbioses.
7. Blue-light-mediated molecular pathways elucidated in the model fungus *N. crassa* involve a complex of interacting proteins, including multiple LOV proteins; a cysteine residue in an ortholog of a LOV protein in *T. reesei* enables this protein to function as a dual sensor for blue-light and oxidative stress. This cysteine is conserved in orthologs in many phytopathogenic fungi, suggesting that these fungi similarly couple sensing of blue light and oxidative stress.
8. Photosensory proteins may help microbes evade light-driven plant defenses; however, these plant defenses can complicate identifying the impact of photosensing on plant-microbe interactions. Characterizing the molecular pathways involved in light sensing is further complicated by the lack of output domains in many photosensory proteins, the integration of responses to distinct wavelengths and potentially co-occurring conditions, and the ability of microbes to perceive distinct aspects of light, including light quality, light intensity, and light-dark cycling, as the primary signal.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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