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Arabidopsis thaliana. (L.) Heynh Multifunctional Sensor Proteins and Signaling Networks Plant Photoreceptors

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Abstract

Light is a crucial environmental cue for the growth and development of plants as well as the production of photosynthetic energy. In order to recognize and process information from incoming light, plants employ sophisticated mechanisms. With the model plant Arabidopsis thaliana, five different types of photoreceptors have been found. (L.) ***Heynh*** *Photoreceptors play a specialized and/or recurring role in fine-tuning many aspects of the plant's life cycle. Unlike mobile animals, sedentary plants are highly flexible and can adapt and survive in changing environments. Plants adjust their direction in the right direction by following the different messages created by the light. It is not unexpected that light is connected to plant regulation in many ways, given that variations in the light environment are frequently synchronized with other environmental elements including temperature, abiotic stressors, and seasonal changes. physiology and growth. In fact, recent advances in plant photobiology have revealed large-scale connections between different photoreceptor signaling pathways and other internal systems, such as light Red hormones. In addition, some photoreceptors directly affect the perception of stimuli other than light, such as heat. Therefore, understanding signaling interactions is important for investigating photoreceptor function in plants. Here, we provide an overview of how different photoreceptors work in tandem with internal signals in plants to regulate a range of physiological and biochemical responses. Therefore, understanding the interplay of these interactions is important for studying plant photoreceptor function.*

Keywords: Photo morphogenesis, Photoreceptors, Sensory proteins, Signal integration, E3 Ubiquitin ligase

INTRODUCTION

Since plants are sessile, environmental conditions always affect the physiology and growth of plants. To adapt and survive environmental changes, plants have developed complex systems that identify external cues and convert them into internal signals. Light is one of the most important signals in many fields, affecting nearly every step of a plant's life cycle. Light is not only used as energy in the processing of carbon dioxide through photosynthesis, but also acts as a complex signal controlling plant physiology and growth. It is therefore important that plants interpret light through many photoreceptor actions (Figure 1).

To ascertain the plant's light environment, a range of specialized photoreceptors with various wavelength absorption spectra and biochemical

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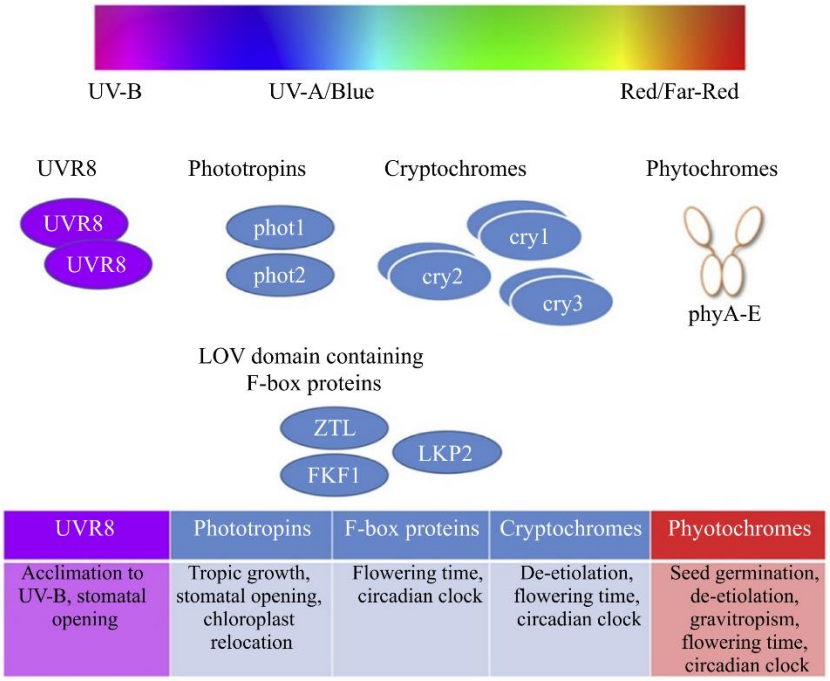
Figure 1. Flower of *Arabidopsis thaliana, Botanical name: Arabidopsis thaliana.* (L.) Heynh. *Vernacular name: Mouse Ear Cress is found in* parts of Asia.

characteristics are employed. There are at least five types of photoreceptors in plants to obtain detailed information from light of different wavelengths. Phytochrome (PHYA-E in the model plant Arabidopsis thaliana) detects red/infrared light (600–750 nm); -binding proteins for blue/UV-A light (320–500 nm) (such as ZEITLUPE, FKF1/LKP2); have identified a new role for receptors beyond light [2, 3]. Thus, emerging evidence supports the idea that photoreceptors are involved in direct sensing and/or modulatory responses to a variety of environmental stimuli, demonstrating their multisensory role. Here, the molecular mechanisms of photoreceptor light and their roles in various plant responses will be discussed, focusing on the red/far-red photoreceptor phytochrome signaling pathway.

Plants use photoreceptors of specific wavelengths to detect and interpret signals to control growth and development. The five phytochromes (phyA-E) found in Arabidopsis thaliana are sensitive to red light (650–670 nm) and far-infrared light (705–740 nm). Arabidopsis can sense blue light (UVR8 detects UV-B rays) as it has (cry1, ry2, and ry3) Three cryptochromes, (phot1, phot2) two phototrophins, and three LOV domain F-box proteins (ZTL, FKF1, and LKP2).

Molecular Mechanisms of Photoreceptors Action in Plants

Molecular mechanisms of photoreceptor action in plants Chromophores are used by phytochrome signaling photoreceptors in plants to absorb photons from incident light. Protein structure can alter when red/far-red light isomerizes the phytochrome receptor, which is covalently attached to the phytochrome tetrapyrrole ring [1]. Phytochromes can vary between two isomers: Pr and Pfr, representing weak and weak biological forms that respond to red and red light, respectively. Although monochromatic red/infrared light does not exist, many light sources represent different red/infrared light ratios [4]. For example, plants growing in the field will reduce the red light/far red ratio in natural light as nearby plants absorb red light. Red light activates all five phytochromes. However, due to its unique spectral properties, phytochrome A is only a red photoreceptor. Plant phytochrome signaling photoreceptors use chromophores to capture photons from incident light. Red/far-red light isomerizes the phytochrome receptor, which is covalently bonded to the phytochrome tetrapyrrole ring [5], changing the structure of proteins. Figure 2 Phytochrome performs this task by inducing various biochemical changes in the PIF transcription factor [6]. Early responses include sequestration [7], phosphorylation [8–10], polysubstitution, and subsequent degradation of PIF via the 26S proteasome-mediated degradation pathway [11–15]. Phytochromes are also directly affected by various mechanisms, with or without the COP1 (continuous photomorphotype 1)-SPA (PHYA-105 inhibitor) E3 ligase complex, an important negative factor in light. First, activated phytochrome can inactivate this activity by altering the COP1-SPA complex [16, 17]. An E3 ligase complex called COP1-SPA interferes with several of the light signaling pathway's active transcription factors to stop light-induced gene production in the dark (e.g. HY5, LAF1, HFR1, etc.) [18].



UVR8	Phototropins	F-box proteins	Cryptochromes	Phyotochromes
Acclimation to UV-B, stomatal opening	Tropic growth, stomatal opening, chloroplast relocation	Flowering time, circadian clock	De-etiolation, flowering time, circadian clock	Seed germination, de-etiolation, gravitropism, flowering time, circadian clock

Figure 2. Plant photoreceptors use spectrum wavelength selectivity to control a variety of physiological processes.

COP1-SPA creates a strong negative regulation of light cascades in plants by destabilizing positive factors. The activity of COP1 mainly depends on its binding partner SPA [19–21]. Light-activated phytochrome interacts with the complex and dissociates the COP1-SPA interaction, thereby inactivating the COP1-SPA E3 ligase, thereby stabilizing the active factor that promotes photomorphogenesis. Second, phytochrome can also remove COP1 from the nucleus by an unknown mechanism, thereby inactivating the COP1-SPA E3 ligase [22–24]. Based on these findings, it was concluded that reactive phytochromes can cause chemical/physical changes in many target proteins, especially the two negative regulators of light-positive vision (PIF, COP1-SPA complex). Some biochemical properties of phytochrome molecules (such as kinase activity, chelating activity) may explain some of the above changes in protein [25, 26] targets. However, many studies have also mentioned phytochrome-related enzymes (e.g. kinases, phosphatases, E3 ligases), whose function is to produce biochemical changes in phytochrome target proteins [27–32]. In general, the action of phytochrome depends on inhibiting negative control and activating positive control to initiate the lightening process.

Under constant light irradiation, phytochrome will be unstable throughout the 26S proteasome-mediated degradation process. This is a form of receptor desensitization, as demonstrated by many other receptor signaling cascades. Phytochrome A exhibits faster degradation kinetics, while phyB-E exhibits slower degradation kinetics [33, 34]. These two types of phytochromes may therefore provide unique mechanisms of action for many phytochrome-regulated responses in Arabidopsis thaliana.

In addition to glycolysis receptors, there are several levels that regulate phytochrome activity through post-transcriptional mechanisms. Phosphorylation is an important modification of phyA and phyB [35]. It has been reported that some serine, threonine, and even tyrosine residues of phytochromes are phosphorylated. By changing several facets of the molecule, phosphorylation frequently controls the activity of phytochromes. For example, phosphorylation of tyrosine 104 of PhyB abolishes the interaction between phyB and PIF [36] and affects the stability of phyB nuclear bodies. Phosphorylation of serine 598 of phyA in Avena sativa also inhibits the phyA-PIF3 interaction, whereas phosphorylation of serine 86 of phyB in Arabidopsis promotes phyB recovery

(discussed in section below) and reduces phyB production [38]. phyB [39] had lysine 996, a post-translational alteration known as sumoylation. The signal increases sumoylation and sumoylated phyB shows less activity.

In addition to the degradation receptor, there are several layers of regulation of phytochrome activity through post-transcriptional mechanisms. Phosphorylation is an important modification of phyA and phyB [35]. It has been shown that certain serine, threonine, and even tyrosine residues of phytochromes are phosphorylated. By changing several facets of the molecule, phosphorylation frequently controls the activity of phytochromes. For instance, the stability of the phyB nuclear body [36] is impacted by PhyB tyrosine 104 phosphorylation, which eliminates the connection between phyB and PIF [36]. Phosphorylation of oat (Avena sativa) phyA serine 598 [37] also inhibits the phyA-PIF3 interaction, whereas Arabidopsis phyB serine 86 phosphorylation promotes the recovery of phyB (discussed in the following section), thereby reducing phyB activity [38]. Another modification, called sumoylation, was discovered at PhyB lysine 996 [39]. While the signal increases the amount of sumoylation, sumoylated phyB shows a decrease.

An interesting molecular property of phytochrome is that it forms nucleosomes in light [40], phyB-GFP and phyA-GFP produced strong nuclear speckles [41, 42]. The amount of PhyB is generally related to the size and number of domains [43]. The phyB region was affected by the protein degradation site because smaller regions or mutants displaying less phyB indicate slow degradation of phyB itself or the PIF transcription factor. However, despite efforts to determine the molecular organization of phyB nuclear speckles, it has not yet been determined what the elements of these speckles are and how the formation of phyB speckles is achieved.

Cryptochrome Signaling Blue/UV-A photoreceptor cryptochrome (CRY) has flavin adenine dinucleotide (FAD) as its chromophore. Many molecular events are also required for the activation of cryptochromes, such as phosphorylation, dimerization, and photobody formation after photon sensing by FAD [44]. Cryptochrome molecules are rapidly phosphorylated in blue light. Phosphorylation of CRY is considered an important modification of its function. Rapid degrading of phosphorylated CRY2 occurs during receptor desensitization [45–51]. As homodimers, cryptochromes are also physiologically active. A recent study provides evidence that blue light-induced homodimerization is another important step in CRY activation [52].

Cryptochromes interact with the labeling process similarly to phytochromes. Cry2 initiates gene expression by interacting with CIB (CRY2-INTERACTING-BASIC-HELIX-LOOP-HELIX) [53, 54]. Recently, another group of cryptochrome-interacting proteins called BICs have been shown to be potent inhibitors of cryptochrome signaling. Under blue light, BIC (cryptochrome blue light inhibitor 1) interacts with cry2. It's interesting to note that nearly all CRY-mediated reactions are inhibited by BIC, including early molecular processes like dimerization, phosphorylation, and photobody formation. Consequently, transgenic plants overexpressing BIC exhibited a phenotype similar to cry1cry2 null mutants [52]. BIC activity itself is also modulated by CRY signaling, indicating feedback inhibition of the blue light signaling cascade [55]. The presence of active receptor desensitizing proteins indicates the importance of fine-tuning the plant light response.

Signaling via Phototropins The blue light receptors called phototropins are in charge of the well-known phototropic reactions in plants. Phototropin Signaling The phototropic response of plants is due to blue light receptors called phototropins. The phototropin molecule contains two flavin mononucleotides (FMN) as chromophores in the LOV (light oxygen voltage) domain [56]. Phototropin can directly phosphorylate many substrates, including phot1/photo2 itself, via its C-terminal serine/threonine kinase domain. To control downstream signaling, NPH3 (non-phototropic hypocotyl 3) may interact with Phot1 and PKS4 [57, 58]. Phototropin also plays an important role in blue light signaling between stomatal opening and chloroplast movement in response to light [59, 60].

ZTL/FKF1/LKP2 ZEITLUPE (ZTL) / FLAVIN-BINDING is a blue light receptor signaling Famiily, KELCH REPEAT, F-BOX 1 (FKF1)/LOV kelch Protein2 (LKP2) is type of another blue light receptor. Flavin-binding F-box proteins, ZTL and FKF1, transduce the signal primarily by altering the activity of the SCF E3 ligase complex [61].

Therefore, the target of SCF E3 ligase also changes its stability. Since ZTL itself is located within the internal clocks in plants, ZTL is mainly involved in the regulation of the circadian clock [62]. In Arabidopsis thaliana, it was discovered that FKF1 directly controls the amounts of the Dof domain transcription factor CDF1, which in turn controls the abundance of the powerful photoperiodic flowering inducer CO (CONSTANS). Under long-day conditions, this configuration results in photoperiod-dependent flowering [63].

UVR8 Signaling The recently discovered UV-B receptor UVR8 recognizes UV-B light in a different way than other photoreceptors. A series of aromatic tryptophan residue pairs on the UVR8 protein absorb UV-B light instead of a chromophore. Upon UV-B absorption, the resulting UVR8 dimers dissociate and the resulting monomer migrates to the nucleus and interacts with COP1 [64–67]. This interaction stabilizes HY5 by initiating UV-B-mediated gene expression. Recently, two UVR8-interacting genes (BES1/BIM1 and WRKY 36) were found to be involved in the UV-B signaling pathway [68, 70].

Although the five classes of photoreceptors in Arabidopsis have different biochemical mechanisms for interpreting environmental light, they share some common mechanisms. First, photon energy is converted into changes in the molecular structure of the photoreceptor, resulting in receptor activation. Second, activated photoreceptors transmit light information to proteins mainly through direct interaction, causing biochemical/physiological changes in the protein. Third, receptor desensitization/inactivation mechanisms exist to fine-tune signaling cascades. By using multiple photoreceptors with different but overlapping functions, plants can monitor their environment to ensure appropriate physiological responses.

REGULATION OF PLANT DEVELOPMENT BY PHOTORECEPTORS

Germination

Sensing the environment and deciding whether to bloom is an important decision for a plant's survival. This is especially true when soil covers the seeds and light is limited. Soaked seeds require signals that activate phytochromes to initiate the Arabidopsis germination process. The signal activates phytochromes, promotes synthesis in seeds of the germination-promoting hormone gibberellic acid (GA), and reduces levels of the germination-inhibiting hormone abscisic acid (ABA). In this particular reaction, the spatiotemporal regulation of phyA and phyB both play an important role in the different functions of the two phytochromes. PhyA expression is low and phyB expression is high [71] in dry seeds. Therefore, phyB is the first photoreceptor to detect growth-promoting signals. Approximately 48 h after cold stratification or water uptake, phyA levels increase and reach levels sufficient to promote seed germination [71]. Interestingly, due to its unique spectral properties, only phyA can be activated at very low light levels and thereby induce very low fluence response (VLFR)-mediated seed germination [72]. In nature, this gene appears to respond to very mild stimuli, resulting in physical regulation of phyA expression after a period of uptake.

Tissue-specific phytochrome control of seed germination is described in research. The precise phytochrome effect on seed germination can be ascertained by physically separating the coat between the seed and embryo. The plant hormone ABA [73] causes phyA-dependent germination in the embryo to be overridden by weak phyB function in the seed endosperm in red light-rich shade. With physiological control over photoreceptor expression and the unique functions of phyA and phyB, seed germination may be precisely regulated in response to quickly changing environmental conditions.

De-etiolation, transcription, and photoreceptor-mediated post-transcriptional regulation In this scenario, seedlings covered with soil need to be exposed to sunlight to initiate de-etiolation. Until then, the seeds must protect the shoot apical meristem (SAM) by retaining the apical hooks and closing the cotyledons. Hypocotyls grow rapidly in the soil. When seedlings are exposed to sunlight, they begin to undergo genetic changes called photomorphogenesis. Hypocotyl cells rapidly arrest, cotyledons open, and many light-induced genes begin to be expressed [74]. Photoreceptors in plants control the transition from dark to light, known as deetiolation. For example, phyAphyB mutants lacking the two major phytochromes in Arabidopsis are almost completely insensitive to signal-mediated inhibition of hypocotyl elongation and cotyledon opening [75]. At the molecular level, phyA plays an important role in early (approximately 1 h after irradiation) gene expression changes, while phyB is responsible for long-term light-induced gene changes [76].

The process of photoreceptor-mediated deetiolation may involve "a dual mode of negative and positive regulation" in the light signaling pathway. PIF (phytochrome-interacting factors) and COP1/SPA (constitutive photomorphogenesis 1/suppressor of phyA-105) E3 ligase, two critical negative regulators, cooperate to repress light-mediated gene expression in darkness. When light activates the signaling pathway, transcription factors degrade, thereby activating the COP1/SPA E3 ligase complex [18]. PIF and COP1/SPA synergistically protect against light exposure in darkness [77]. Upon light activation, phytochromes and cryptochromes interact with PIF (both phytochromes and cryptochromes) and CIB (cryptochrome only), altering their activities. Additionally, phytochromes and cryptochromes interact with the COP1/SPA complex, inactivating it and thereby stabilizing the HY5 transcription factor, which can regulate approximately 9000 genes (Figure 2) [78, 79].

Phytochrome responds directly to light and temperature information. Through coordination of photoreceptors, they control many types of responses, including biotic and abiotic stress responses, gravitropism, and various adaptations. At the molecular level, photoreceptors express key elements such as the E3 ligase COP1-SPA complex and transcription factors called PIF (PHYTOCHROME

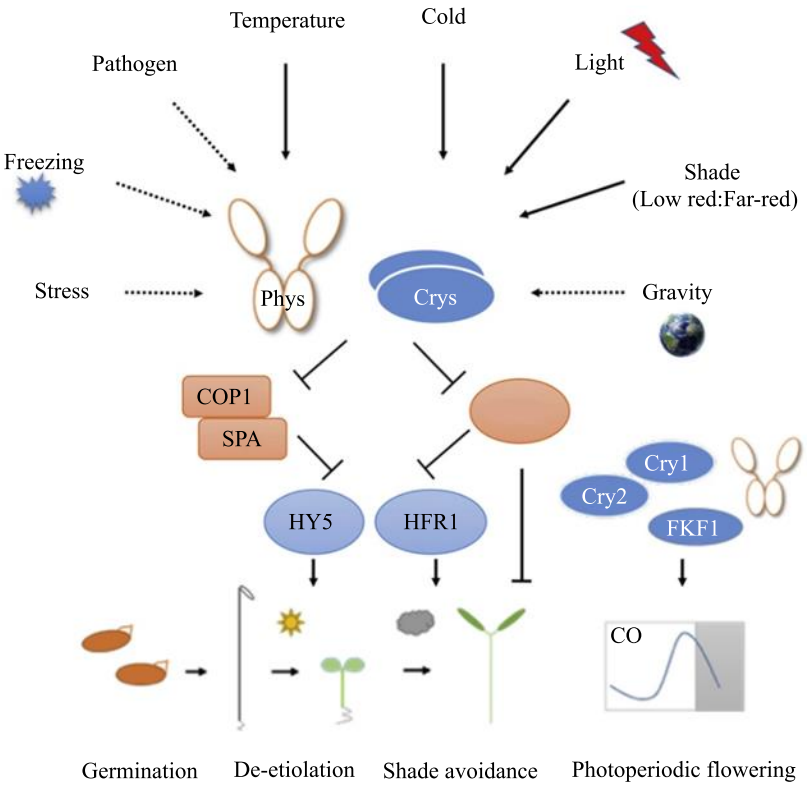


Figure 3. Convergence on photoreceptors of various environmental signals.

INTERACTING FACTORS), HY5, and HFR1. By inactivating the negative light regulators COP1-SPA and PIF, photoreceptors can initiate various changes in gene expression in response to the signal. Additionally, transcription factors like HY5 and HFR1, which impact many genes in the Arabidopsis genome, are produced by photoreceptors. These photoreceptor-mediated regulations ultimately lead to optimization of plant growth and health, increasing crop and biomass yields in agriculture.

Activated phytochrome causes a number of changes, mainly due to the unstable/stable state mentioned above. However, apart from indirect control through transcriptional regulation, the direct effect of phytochromes on transcription is unclear. Some studies have reported the association of phytochrome with light promoters and thermoregulatory genes, but the importance of these interactions remains unclear [3]. It has also been noted that the gene expression ratio between dark pifQ (pif1pif3-pif4pif5) mutants and wild-type seedlings grown in red light is only 0.78 [80, 81]. This suggests that additional transcription factors or non-transcriptional factors are involved in the phytochrome-mediated signaling pathway (Figure 3).

In parallel, many reports indicate that phytochromes are regulated at the post-transcriptional level during deetiolation. Approximately 7% of the annotated Arabidopsis genome exhibits alternative splicing in a signal- and phytochrome-dependent manner [82]. In particular, the phytochrome-associated splicing factor SFPS has been identified to function in signal-mediated splicing events [83]. Additionally, phytochrome regulates the translation of mRNA of the chlorophyll biosynthetic gene PORA [84]. A proteomics study also found that phytochrome influences the activity of transducers in etiolated Arabidopsis seedlings, suggesting a role for photoreceptors in translation control [85]. Another interesting study discovered alternative promoter selection for phytochromes, leading to the production of different protein isoforms with distinct subcellular localizations [86]. The relationship between alternative promoters and specificity in phytochrome signaling warrants further investigation.

During early light exposure, phytochrome promotes the expansion of cotyledon cells while inhibiting the expansion of hypocotyl cells, illustrating tissue-specific roles of phytochromes in different plant tissues [87, 88]. This suggests that light exerts tissue-specific effects, resulting in distinct physiological responses across different plant tissues [88]. A recent study detailing the tissue-specific function of phytochrome B in the gravitropic response in Arabidopsis provided additional evidence supporting this notion [89].

Shade Avoidance Response

One of the difficulties faced by plants in agriculture and nature is the limitation of light from neighboring plants. Dense trees reduce photosynthesis and weaken plants due to low red/far-red light ratio and low blue/green. To survive in the shade, photoreceptors in plants produce a protection against shade called the shade avoidance response (SAR), which inhibits rapid stem (hypocotyl) elongation, leaf abscission, and flower formation (Figure 3).

Phytochrome B (phyB) plays an important role in maintaining shade. Because shade conditions reduce phyB activity in plants, phyB-mediated illumination is also inhibited in shade conditions. phyB mutants consistently have hypocotyl elongation responses, delayed cotyledon and leaf growth, and a protective defense against premature flowering [90]. PIF plays an important role in the phyB-mediated shadow inactivation response. Among all PIFs, PIF4, PIF5, and PIF7 in particular have been found to be important for the biosynthesis of the plant growth hormone auxin and allow cell elongation rate in response to pain shade conditions [91, 92]. There is also an inhibitory pathway for color tolerance mediated by phyB-PIF. Phytochrome A has an antagonistic effect with phyB under strong red light [93]. Furthermore, the atypical bHLH protein HFR1 inhibits PIF activity to prevent excessive shadowing [94]. Because the amount of blue and UV-B light in the shadow is reduced, other photoreceptors, like UVR8 and cryptochromes, also contribute to shadow avoidance. Remarkably, PIF4 and PIF5 are also implicated in the color response mediated by cryptochrome [95].

Flowering Time

One of the difficulties faced by plants in agriculture and nature is the limitation of light from neighboring plants. Dense trees reduce photosynthesis and weaken plants due to low red/far-red light ratio and low blue/green. To survive in the shade, photoreceptors in plants produce a protection against shade called the shade avoidance response (SAR), which inhibits rapid stem (hypocotyl) elongation, leaf abscission, and flower formation (Figure 3).

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Correctly determining the flowering time is important for planting during the transition period. For perennials and biennials that experience at least one winter during their life cycle, it is important to anticipate winter blooms in the spring. Although they are annual plants, the transition from plant to growth stage is important for their successful growth. Other photoreceptors, such as UVR8 and cryptochromes, also aid in shadow avoidance since the amount of blue and UV-B light in the shadow is decreased. Surprisingly, PIF4 and PIF5 are also connected to the cryptochrome-mediated color response. FKF1, phytochrome A, and cryptochrome (Figure 2) [96]. How do plants measure "day length"? Scientists have developed a concept called the "external coincidence model" using various molecular and genetic methods. The main idea of this model is that the adaptive signal and the external photoperiodic signal must be synchronized to trigger flowering.

FT (Flowering locus T) is a florigen that affects plant flowering [97]. CO (CONSTANS) is the power factor of FT and is an important part of the external correlation structure [98]. CO expression varies in the diurnal cycle (Figure 2). Photoreceptors must be triggered in the afternoon, when CO is most potent, in order to stabilize CO proteins and induce photoperiodic blooming. Therefore, changes in CO expression follow intrinsic factors, whereas photoreceptor activation in the afternoon follows extrinsic factors. In the long day cycle (16 hours: 8 hours, light: dark), photoreceptors can be activated by light in the afternoon. However, on short days (8 hours: 16 hours, light: dark), there is no external light in the afternoon because early sunset makes the CO protein high enough.

Activated by blue light, cryptochrome 2 directly interacts with and inactivates the COP1/SPA E3 ligase complex. COP1/SPA was unable to remove Cry2's target CO protein, resulting in CO levels rising [99]. Additionally, phyA promotes flowering by stabilizing carbon dioxide in response to far-red light. Unlike phyA, phyB inhibits flowering induction because it destabilizes CO. However, a new regulator of photoperiod flowering in phyB signaling has recently been proposed. Through the actions of FKF1 and cryptochrome, far-red light and blue light, respectively, stimulate flowering in flowering induction. Cryptochrome 2 directly interacts with and deactivates the COP1/SPA E3 ligase complex when blue light is activated. COP1/SPA is unable to remove Cry2's target CO protein, resulting in CO levels rising [100]. Additionally, PHYTOCHROME-dependent late flowering (PHL) has been identified as a pathway for phyB and CO, but it is unclear how PHL promotes flowering in the phyB-PHL-CO complex. Phytochrome B also exhibits tissue-specific activity in flower cells. Studies have

shown that phyB expression in mesophyll cells can delay flowering by suppressing FT expression in vascular bundles [101].

The F-box protein FKF1, another blue light receptor, is crucial for the photoperiodic induction of flowering [68]. FKF1 forms a pathway with GI (GIGANTEA), a floral protein with co-chaperone function [102, 103]. Both FKF1 and GI are expressed in the circadian clock. When FKF1 and GI are highest during the long afternoon, blue light-activated FKF1 can interact with GI, leading to degradation of ubiquitin-mediated CDF (CO repressor), which attenuates CO repression [63]. The FKF1 mechanism of action is also an example of an external relationship model in which the circadian clock controls FKF1-GI gene expression and external light activates FKF1 on long days, CO and FT can be expressed, thereby triggering flowering.

Plant Physiology is Regulated by Photoreceptors in Response to Various Environmental Stimuli. Multifunctional Plant Photoreceptor: Thermosensing

Recent advances have revealed an unexpected role for photoreceptors in plant physiology. Interestingly, phytochrome B (phyB), in addition to being sensitive to red/infrared light, is also thought to be a thermal sensor that can detect ambient temperature [2, 3]. How does this operate? Ion channels form the basis of thermal sensors in insect and mammalian systems. For instance, in mammals, ion channels from the transient receptor potential (TRP) family serve as sensors for heat and cold, initiating ion flow for downstream signaling [104]. However, the detailed molecular mechanism of temperature regulation by TRP channels is not fully understood. The thermodynamic process of protein changes at different temperatures can be likened to RNA secondary structure changes serving as a thermal sensor in bacteria [105].

Unlike animal systems, specific ion channels serving as thermal sensors in plants have not yet been identified. However, phytochrome B (Pfr), triggered by light, is known to be thermodynamically unstable (in the high-energy state) and progressively reverts to its stable inactive form (Pr) in the absence of light—a process known as the "relaxation" pathway ("hot state") [106]. Researchers have found that at high temperatures, the active Pfr form of phyB converts to the inactive Pr form more rapidly than at low temperatures, leading to a decrease in active phyB content. The ambient temperature sensed by phyB translates into the Pfr/Pr ratio of phyB, influencing changes in gene expression. Indeed, recent studies have demonstrated that the regulation of temperature-responsive genes is also under the control of phyB through chromatin binding [2, 3]. Phytochromes in Arabidopsis can directly sense at least two different environmental factors (light and temperature). Given that sunlight exposure often correlates with temperature changes, it is not surprising that photoreceptors also function as thermal sensors.

It would be intriguing to explore whether other photoreceptors, including cryptochromes, are involved in temperature detection. Considering that cryptochromes also undergo thermal relaxation [52], there may be variations in the deactivation of cryptochromes at different temperatures. While cryptochrome itself may not function as a temperature sensor, recent research has indicated that cryptochrome 1 (cry1) mediates heat stress responses in hypocotyl elongation by directly interacting with the bHLH transcription factor PIF4 [107].

Photoreceptor Regulation of Heat and Cold Stress

Many studies have shown that photoreceptors play a direct role in the response to stress, heat, and other physiological responses to abiotic challenges in plants. Temperatures below or above the optimal range can cause serious tissue damage and are often fatal. Sessile plants must respond to extreme stress by anticipating freezing or heat stress. Early research on the molecular mechanism of phytochrome's role in cold response revealed light-dependent resistance to freezing. At low red/far-red light ratios, phytochrome activity is reduced, enhancing plants' stress tolerance [108]. This is

achieved by inducing key elements like CBF1, CBF2, and CBF3, which are crucial for plant acclimation to cold and improved frost resistance [109]. Therefore, lower phytochrome activity appears to help plants anticipate cold temperatures, a strategic adaptation considering that the lowest temperatures are typically experienced before dawn when phytochrome activity is naturally lower during the night.

Numerous studies have further elucidated the connection between phytochromes and frost tolerance. It has been demonstrated that phytochromes also regulate the signaling of plant stress hormones such as ABA and JA [110]. Additionally, PIF4 and PIF7 have been shown to directly regulate the synthesis of CBF genes by binding to their promoters, thereby upregulating the expression of antifreeze proteins [111].

Furthermore, studies have highlighted a synergistic relationship between phyB signaling and short-term heat stress, particularly in Arabidopsis where temperatures above 28°C inhibit phyB activity [112]. Downstream transcription factors, including PIF4, PIF5, and HY5, are involved in mediating this response. Additionally, there is evidence suggesting that transient changes in phytochrome activity may occur in response to heat stress, impacting gene expression [113]. Moreover, rice mutants lacking phyA and phyB exhibit mutations in various heat shock proteins, which are essential for proper development of anthers and pollen, underscoring phytochrome's role in regulating heat shock protein abundance [114]. Overall, phytochromes play a significant role in temperature regulation and adaptation in plants, integrating light and temperature signals to optimize plant growth and stress response.

Photoreceptor Regulation of Gravitropism

Sensing gravity is another important function of plant photoreceptors. Plants detect gravity by using the motion of amyloplasts, starchy subcellular organelles found in the tissues of their roots and shoots. Although phytochromes cannot detect gravity signals, they play an important role in signal-induced inhibition of negative gravitropism of shoots and gravitropic curvature of roots. In seedlings germinating in the dark, perceived gravity cues help the hypocotyl extend upward toward the soil surface against gravity; this is a process called negative gravitropism. When the seedling reaches the surface, light becomes the first signal for the plant to grow and destroys the flower's negative gravity response through the action of photoreceptors [115]. Phytochrome causes endodermal amyloplasts to change into plastids at the molecular level by deactivating PIF function [115]. Phytochrome can remove damaged bone from gravity-sensing organelles and amyloplasts in the differentiated hypocotyl endoderm cell layer [115].

Phytochrome B was found in this particular reaction Interestingly, in a specific tissue activity. The researchers found that only epidermally expressed phyB was able to inhibit floral negative gravitropism, but endoderm-expressed phytochrome B was not. The effect is non-cell autonomous. This is a very interesting phenomenon; However, the details of the mechanism by which epidermal phytochrome affects endodermal PIF and its downstream signaling are unclear.

Phytochromes are also required for root gravitropism. In response to changing gravity cues, roots change the direction of their growth. Arabidopsis phyAphyB mutants are less responsive to changes in gravitational cues [116]. The PhyAphyB mutant also exhibits shorter root length compared to the wild type; This suggests that photoreceptor activity plays an important role in root growth and gravitropic responses.

Numerous species, including European robins and migratory birds, have been shown to contain cryptochromes, which may serve as magnetoreceptors. In Arabidopsis thaliana, cryptochrome 1 has been shown to be biophysically detected and increased in a weak external magnetic field [118]. It is unclear whether plant cryptochromes are true magnetoreceptors and what the physiological effects of plant magnetoreceptors are. Cryptochromes appear to play a minor role in the gravitropic response.

As discussed earlier in this chapter, phototropism differs from geotropism, probably because the phototropic response is more important than the geotropic response to light. Phototropin is the main photoreceptor responsible for phototropism, and phytochrome indirectly helps the phototropic reaction by inhibiting the gravitropic reaction of light [115–119]. Thus, the cooperation between two photoreceptors can create a good balance between phototropism and geotropism.

Not surprisingly, recent studies have also shown that photoreceptors play a role in biotic stress responses in plants, for example in responses to pathogens. In general, mutants with reduced photosensitivity (e.g. phyB) result in decreased energy. Therefore, the high susceptibility to pathogens found in the mutants is thought to be an indirect effect of unhealthy plants. In contrast, recent genetic studies have revealed that photoreceptors and their signaling are directly regulated in plant response to disease, particularly by the anti-hormone jasmonic acid (JA) [120]. The reader may refer to a recent review [6, 121] which discusses this issue in detail.[122]

CONCLUSION

The light shines; Cryptochromes, Phototrpin, ZTL, and UVR8 photoreceptors function to control plant growth and response, and this stemless plant has the most complex photoreceptor system of any organism. New functions of plant photoreceptors have been identified by recent developments in photoreceptor research. Phytochromes, given ambient dynamic signals, can respond directly to at least two light sources, as this review discusses. It's important to note that photoreceptors either directly or indirectly mediate plant responses to numerous non-photo environmental inputs. Importantly, there are similar differences in plant responses to shade (low-red:far-red ratio), temperature, and stress; This makes the quality or direction of these responses meaningful. It is therefore not surprising that red/infrared light receptor phytochromes can be multisensors. Many important light sources are shared by different photoreceptors; this shows that photoreceptors work together as more than one receptor.

Although most of the following signals are generally expressed by photoreceptors, plants are still capable of producing vague and specific responses to different external signals. This is achieved by combining the spatiotemporal control of photoreceptors and their signaling molecules with the biochemical and spectral properties of photoreceptors and specific problems. Although not yet confirmed, it is still possible that plant photoreceptors use unknown cell signals (e.g., peptide hormones) and second messengers (e.g., Ca 2+ ion flux) to activate signaling cascades, as previously suggeste.

Plant photoreceptors control the interactions of plants with the environment. It would be very interesting to investigate whether photoreceptors are involved in other adverse effects of light and the molecular mechanisms of how this occurs. The emerging role of plant photoreceptors opens the door to new areas of plant photobiology.

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