

Plant Photo-morphogenesis and Virus Resistance: An important Molecular link

Dharmappa D Chavan* and Halima Khatoon

Advanced Centre of Plant Virology, Division of Plant Pathology, ICAR-Indian Agricultural Research Institute, New Delhi, India

***Corresponding Author:** Dharmappa D Chavan, Advanced Centre of Plant Virology, Division of Plant Pathology, ICAR-Indian Agricultural Research Institute, New Delhi, India.

Received: August 01, 2023; **Published:** August 07, 2023

DOI: 10.55162/MCAES.05.123

Abstract

Both the propagation of plants (Wang et al., 2019) and the transmission of viruses (Paudel and Sanfacon, 2018) are dependent on the presence of light in their environments. When it comes to plants, light is the primary environmental factor that contributes to photosynthesis (Liu et al., 2019) and photomorphogenesis (Montgomery, 2016). According to Paik and Huq (2019), the term “photomorphogenesis” describes a sequence of morphological changes that occur in the development of plants when dark-grown seedlings are exposed to light. A well-known component of light-mediated plant development, the E3 ubiquitin ligase COP1 (Constitutive Photomorphogenesis 1) functions as a repressor of photomorphogenesis. COP1 is also known as Constitutive Photomorphogenesis 1. In this study, we demonstrate that the protein COP1 positively modulates the defence mechanism against the turnip crinkle virus (TCV) and avrRPM1 bacteria by contributing to the stability of the resistance (R) protein HRT and RPM1, respectively. In the context of a *cop1* mutant background, both HRT and RPM1 levels, and hence pathogen resistance, are drastically decreased. It is noteworthy that the levels of at least two double-stranded RNA binding (DRB) proteins, DRB1 and DRB4, are reduced in the backdrop of the *cop1* mutant, which suggests that COP1 decreases HRT stability via its effect on the DRB proteins. In point of fact, the degradation of HRT was brought about by a mutation in either *drb1* or *drb4*. In contrast to COP1, a multi subunit E3 ligase that was encoded by anaphase-promoting complex (APC) 10 had no effect on DRB1 levels but did negatively affect DRB4 and TCV resistance. Our hypothesis is that the positive control of HRT that is mediated by COP1 is dependent on equilibrium between COP1 and the negative regulators that target DRB1 and DRB4.

Introduction

Plants are unable to actively seek out favourable or avoid unfavourable environmental conditions due to their sessile nature. In order to maximise growth and reproduction in response to their surrounding conditions, plants have evolved a high degree of developmental plasticity. One of the most important environmental signals for plant growth and development is light. Light is essential for photosynthesis, but it also helps plants determine their spatial orientation, which affects a wide range of processes from germination to de-etiolation to gravitropism to phototropism to chloroplast movement to shade avoidance to circadian rhythms to flowering. Plants can detect almost all facets of light such as direction, duration, quantity, and wavelength by using three major classes of photoreceptors: the red (R)/far-red (FR) light (600-750 nm) absorbing phytochromes (phys), the blue (B)/UV-A (320-500 nm) absorbing cryptochromes (crys) and phototropins (phots), and the UV-B (282-320 nm) sensing UV-B receptors (Kendrick and Kronenberg, 1994; Briggs and Olney, 2001; Briggs et al., 2001). These photoreceptors are responsible for detecting light, processing that information, and then relaying it to the nucleus, where it can activate or repress the expression of specific photoresponsive genes. Among the most dramatic events mediated by these photoreceptors are the phenotypic alterations associated with seedling photomorphogenic development. During skotomorphogenesis (etiolation), the proplastids transform into etioplasts, resulting in the tall hypocotyls, closed cotyledons,

and apical hooks that are characteristic of seedlings grown in the dark. Short hypocotyls, open and expanded cotyledons, and the transformation of proplastids into mature chloroplasts (thus the term “de-etiolation” of the etioplasts) are all hallmarks of light-grown seedlings undergoing photomorphogenesis (de-etiolation), as shown in Figure 1 of McNellis and Deng (1995).

All energy not derived from nuclear fission ultimately comes from the sun. The sun’s nuclear fusion reaction turns protons into helium nuclei at a rate of almost 1017 kg of TNT per second, resulting in solar energy. Annually, the Earth’s atmosphere, seas, and land-masses receive about 5.62 1024 joules of solar energy (Figure 2), with photosynthesis capturing about 3.16 1021 joules.

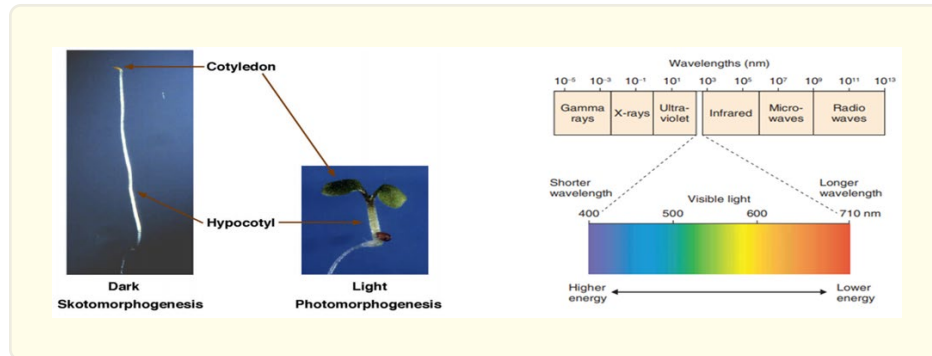
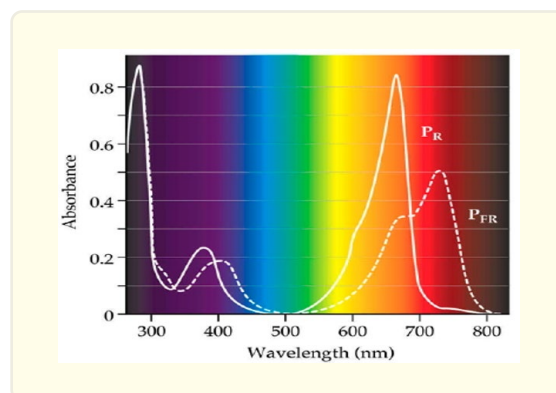
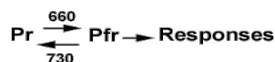


Figure1, Arabidopsis seedlings raised in the dark have a different phenotype than those produced in the light. These dark-grown seedlings have extended hypocotyls, closed cotyledons, and apical hooks because they have undergone a skotomorphogenic development programme (etiolation). Photomorphogenesis causes seedlings raised in bright light to develop elongated, open, and green cotyledons and short hypocotyls. As seen in Figure 2, the visible spectrum is depicted as an extended region of the electromagnetic spectrum between 400 and 710 nm. The human visual system can process light with a wavelength of 380 nm in the blue and 760 nm in the red.

Phytochrome

Red light (R; around 660 nm) stimulates the germination of light-sensitive lettuce seeds. See Figure 6.24 for what happens to germination rates when red light is followed by far-red light (FR; 730 nm). Conversely, red light can counteract the effects of far-red light. Because of its photoreversible (R/FR) nature, phytochrome was first identified and purified using spectrophotometry. The genes responsible for producing phytochrome have been isolated. Phytochrome controls a wide variety of plant processes, including germination in light-sensitive seeds, de-etiolation and enhanced chlorophyll synthesis (see Figure 8.1), stem elongation, leaf expansion, shade avoidance, photoperiodism, and flowering.

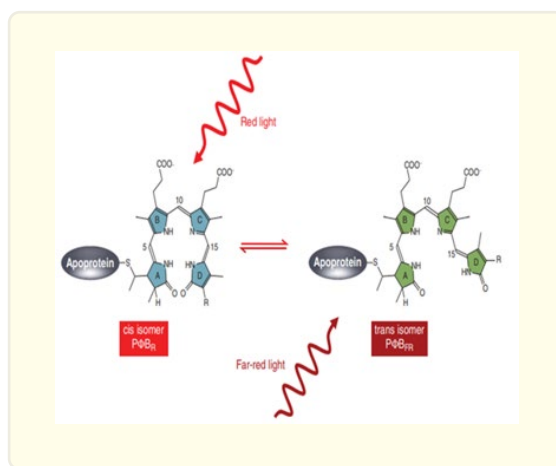




The Phytochrome Gene Family and The Chromophore

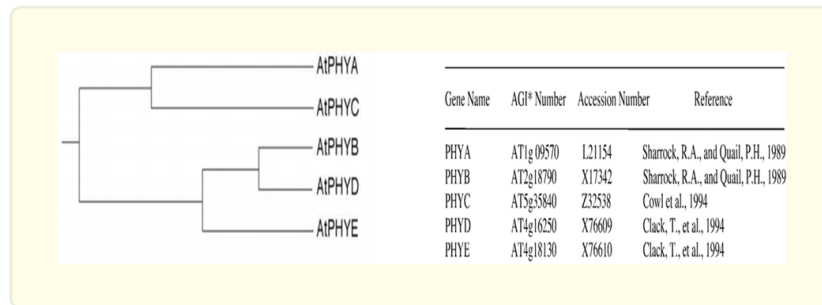
Two Reversible Forms of Phytochromes

Due to the absence of photosynthetic pigments in dark-grown seedlings, it was discovered that phytochrome is abundant in these plants (Butler et al., 1959, 1964), making its purification very straightforward. The existence of two photoreversible versions of phytochromes *in vivo* was expected on the basis of numerous physiological facts. This theory was supported by the purification of phytochrome, which demonstrated that the Pr form of the pigment is present in plants that were growing in the dark. The Pr form is transformed to the Pfr form, the physiologically active form, upon exposure to red light. Absorption of far-red light causes a reversion from the Pfr to the Pr form. The absorption maxima of the two forms of phytochrome vary as a result of photoconversion; purified Pr form phytochrome is blue and absorbs most strongly at 666 nm, whereas Pfr form phytochrome is olive-green and absorbs most strongly at 730 nm.



Classification of Phytochromes and the Gene Family

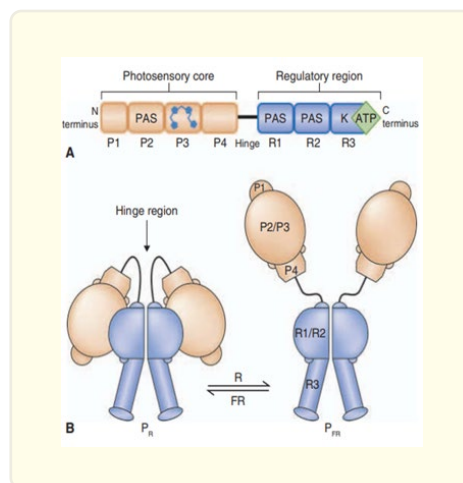
Soluble homodimers of Apo proteins with linear tetrapyrrole chromophores were identified in the purified phytochrome from etiolated seedlings. About 120 kDa is the estimated molecular weight of the phytochrome apoprotein. All phytochromes share a highly conserved region where the chromophore is connected via a thioether bond to an invariant cysteine. Spectrophotometric investigations conducted in the 1980s established the existence of two groups of phytochromes, types I (light labile) and II (light stable). When exposed to red or white light, the light-labile pool degrades rather quickly. Five different genes in the phytochrome gene family (phyA-phyE) have been identified in *Arabidopsis* (Sharrock and Quail, 1989). Type I phytochrome phyA is distinguished from type II phytochromes phyB-phyE. Polypeptides PHYB and PHYD are roughly 80% similar; they are more closely related to PHYE than to PHYA or PHYC (both of which are around 50% similar). The most recently developed phytochromes are the PHYB, PHYD, and PHYE polypeptides (Figure 3A; Table 2). In contrast to lower plants, which lack homologs of PHYA, PHYB, and other PHY genes (Clack et al., 1994; Sharrock and Quail, 1989; Mathews and Sharrock, 1997), higher plants possess these genes.



PHYB and PHYD share 80% amino acid sequence commonality, as shown by their close proximity on the phylogenetic distance tree of the five phytochrome species from *Arabidopsis thaliana*. They have a higher degree of similarity with PHYE (55% identity) than with any other phytochrome. (Clack et al., 1994, adapted).

General Structure of Phytochromes

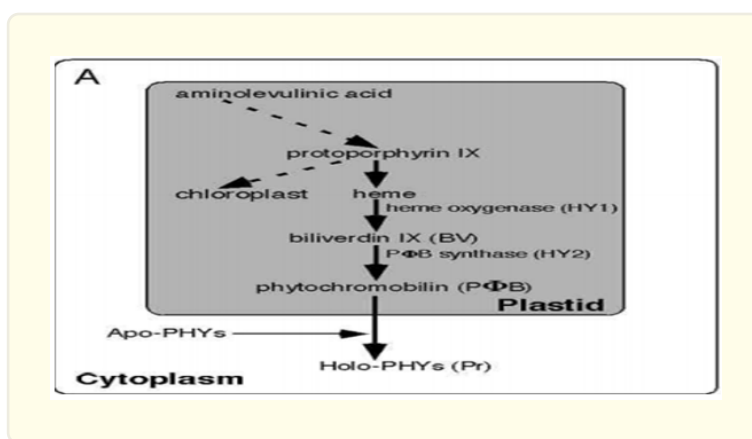
According to biochemically purified phyA holoproteins from multiple plant species, the phytochrome molecule is composed of two structural domains: a photosensory, globular N-terminal chromophore-binding domain that is sufficient for light absorption and photoreversibility (70 kDa), and a regulatory, conformationally more extended C-terminal domain that is important for dimerization and downstream signalling (55 kDa). A movable hinge connects these two sections. The regulatory core sequence (Quail box), the dimerization motif, and the histidine kinase-related domain (HKRD) are all conserved subdomains/motifs found in the C-terminal domain. In Figure 3B, we can see that the Quail box overlaps with a pair of Per-Arnt-Sim (PAS) motifs. In addition to serving as protein-protein interaction platforms, PAS domains can also be used as response modules in reaction to tiny ligands or changes in environmental factors such as light intensity, oxygen concentration, or redox potential (Quail, 1997; Neff et al., 2000). Biological activity is lost, but not photoreversibility, when single amino acid changes are made in the PRD domain of phyA or phyB (Quail et al., 1995; Quail, 1997).



Phytochrome domain structure and possible conformations (Figure 3). (A) Domain arrangement, highlighting the photosensory domain's P1-P4 sections, the PAS motif repeated throughout the molecule's regulatory region, and the C-terminal histidine kinase module. The chromophore is seen bound to peptide 3 (P3). Phytochrome dimerization, protein receptor (PR) and phosphatase (PFR) conformations B.

Chromophore Biosynthesis

A chromophore must be covalently attached to each monomer of the phytochrome apoprotein for the holoprotein to operate properly. First, degradation methods were used to determine that the phytochrome chromophore, called phytochromobilin (PFB), is a linear tetrapyrrole. Proton nuclear magnetic resonance spectroscopy was used to examine phytochrome peptides extracted from sequential pepsin-thermolysin digestion of oat phytochrome in the Pr form to learn more about the chromophore's ligation site. It was discovered that PFB binds to a cysteine residue in the N-terminal half of PHYA's apoprotein by way of its A-ring (Lagarias and Rapoport, 1980). It's worth noting that the chromophore assembly and photochromic characteristics of phytochromes may vary depending on which pyrrole ring is chosen for the linear tetrapyrrole. According to recent research, the A-ring serves primarily as an anchor for ligation to PHYB. To achieve photoreversible spectrum shifts and appropriate positioning of the chromophore in the chromophore pocket of PHYB, the side chains of the B- and C-rings are essential. The D-ring side chain is essential for the adduct's reversible spectrum alteration (Hanazawa et al., 2001). An enzymatic cascade in the plastid, initiated by 5-aminolevulinic acid, directs PFB production. Chlorophyll and heme synthesis begin with the same first steps as the PFB process. The obligated process involves biliverdin IX (BV) formation via oxidative cleavage of a subset of the heme pool by a ferredoxin-dependent heme oxygenase (HO). The bilin reductase PFB synthase, which requires ferredoxin, then converts BV into 3Z-PFB. Functional precursors of the phytochrome chromophore include both 3Z-PFB and its isomerized counterpart 3E-PFB. After apo-phys is synthesised, PFB is imported into the cytoplasm and binds to it (Terry et al., 1997, Figure 4A,B). When the linear tetrapyrrole is exposed to red light, the C-15 double bond between the C and D rings undergoes an isomerization from "Z" to "E," creating the far-red light-absorbing form Pfr. The structural integrity of the protein is altered during the metamorphosis from Pr to Pfr. Dark reversion, which does not require light, is a significantly slower route to converting Pfr to Pr than absorbing far-red light does (Quail, 1997; Fankhauser, 2001; Figure 4).



Actions and Interactions of Phytochrome Family Members

Phytochrome comes in a wide variety of forms, each with its own light sensitivity and set of regulated reactions. The high irradiance reaction (HIR) and the low fluence response are two examples of phytochrome-mediated reactions. The number of photons that strike a certain region (the "fluence") is measured in moles per square metre. The rate of fluence, expressed in terms of moles per square metre per second, is known as the irradiance. In contrast to HIR, low fluence responses can be triggered either by prolonged exposure to light or by brief exposure to high irradiance. The low fluence red/far-red reversible reaction (LFR) and the very low fluence response (VLFR) are two subtypes of the low fluence response. Figure 5 provides a concise overview of the fluence-response connections of VLFR, LFR, and HIR, as well as instances of photomorphogenic events associated with each category. Several plant species have had mutations discovered in phytochrome genes, and this has led to the identification of specific fluence responses linked with individual members of the phytochrome gene family. For instance, in white light, PHYB-deficient mutants like the lh mutant of cucumber

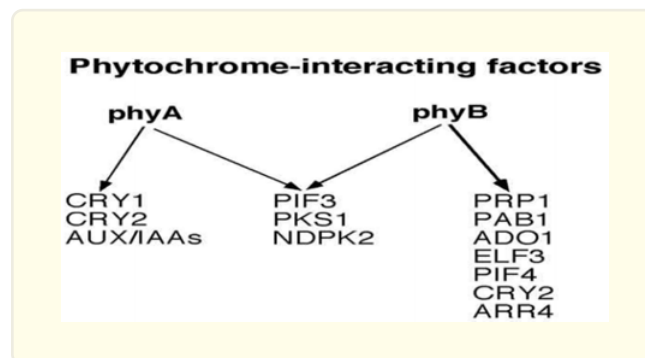
(Figure 8.12) and the *hy3* mutant of *Arabidopsis* grow taller than wild-type plants. This phenotype is compatible with phytochrome's ecological involvement in proximity-sensing and competition for light in plant communities, which resembles the effect of shading. Tomatoes cultivated in white light cause the aurea mutant, which lacks PHYA, to develop yellow-green leaves.

Comparison of the very-low-fluence (VLFR), low-fluence (LFR), and high-irradiance responses (HIR)				
Type of Response	Photoreversibility	Reciprocity	Peaks of action spectra ^a	Photoreceptor
VLFR	No	Yes	Red, Blue	phyA, phyE ^a
LFR	Yes	Yes	Red, far red	phyB, phyD, phyE
HIR	No	No	Dark-grown: far red, blue, UV-A Light-grown: red	Dark-grown: phyA, cryptochrome Light-grown: phyB

Phytochrome-Interacting Signaling Partners

Phytochrome-interacting Partners (PIFs)

Many signal transduction cascades cannot function without protein-protein interactions. To communicate information about the light environment within the cell, phytochrome is expected to interact with some partner protein(s). Research is presently focused on determining the molecular components responsible for intracellular photosignal transduction. Phytochrome-interacting factors (PIFs) have been discovered by both broad phytochrome-interaction screenings and more narrowly focused protein-protein interaction studies. PIF3 (Ni et al., 1998), PKS1 (Fankhauser et al., 1999), NDPK2 (Choi et al; 1999), cryptochromes (CRY1 and CRY2), and the AUX/IAA proteins (Ahmad et al., 1998; Colón-Carmona et al., 2000; Mas et al., 2000; Reed, 2001; Figure....). Some of these components' physiological involvement in phytochrome signalling have been confirmed by recent molecular genetic research. PIF3 is a basic helix-loop-helix (bHLH) protein that is found in the nucleus. Strongly reduced responsiveness to light signals received by phyB, and moderate reductions in responsiveness to signals perceived by phyA, were observed in transgenic *Arabidopsis* seedlings with antisense-imposed reductions in PIF3 levels. These results are consistent with PIF3 binding to both phyA and phyB photoreceptors, suggesting that it is functionally involved in both phyA and phyB signalling pathways in the plant cell. Increased sensitivity to red light has also been shown in a *pi f 3* mutant that has had its T-DNA tagged (named *p o c 1*) (Halliday et al., 1999). Mutants with a T-DNA insertion in the promoter of the P I F 3 gene have an increased reaction to red light, which is most likely a gain-of-function phenotype. This mutant's sensitivity to the phyB mutation demonstrates that PIF3 is a genuine component of the phyB signalling pathway. PKS1 is a basic, soluble, cytoplasmic protein that has been shown to be a substrate for light-regulated phytochrome serine/threonine kinase activity. This finding suggests that protein phosphorylation is involved in phytochrome signalling and that PKS1 overexpression may act as an inhibitor of phyB signalling by decreasing the sensitivity of plants to red light (Fankhauser et al., 1999). Although hypocotyl elongation is not obviously impacted by NDPK2 (nucleoside diphosphate kinase 2), it appears to be a positive regulator of both phyA and phyB signals. Decreased cotyledon greening and hypocotyl/cotyledon hook opening during de-etiolation are observed in its loss of function alleles (Choi et al; 1999).

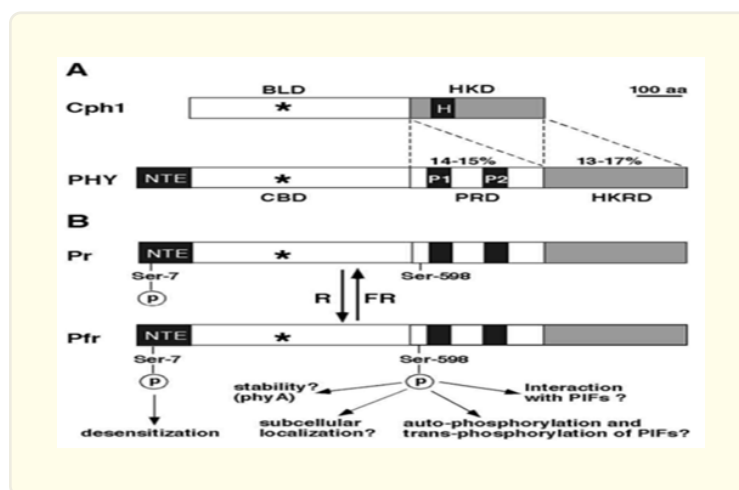


Higher Plants Phytochromes

The resemblance between the C-termini of phytochromes and BphPs was identified after the discovery of BphPs (Schneider-Poetsch, 1992, Figure 5A), prompting a more thorough sequencing investigation of phytochromes in higher plants. In contrast to animal phytochromes, which only contain the CBD and HKRD, plant phytochromes also feature a serine-rich N-terminal extension domain (NTE) and a PAS repeat domain (PRD) in between these two regions. In addition, not all phytochromes have the same essential residues that are required for activation in the vast majority of bacterial sensor kinases. The activity of His kinase is also unaffected by mutations in the few remaining essential residues. The phytochromes in plants do not appear to be functional His kinases, as suggested by previous research (Vierstra and Davis, 2000). The lab of Clark Lagarias set out to answer this question by creating a recombinant technology to generate and purify phytochromes in yeast. PCB was used for in vitro assembly of purified phyA from oats expressed in *S. cerevisiae* and ph -ytochrome from the green alga *Mesotaenium caldariorum* expressed in *P. pastoris*. These phytochromes respond to changes in light and chromophore concentration by exhibiting characteristic spectroscopic characteristics and protein kinase activity. Furthermore, isolated oat phyA phosphorylates histone H1 and the Cph1 substrate Rcp1. In contrast to cyanobacteria, which auto-phosphorylate on His/Asp, these organisms auto-phosphorylate on Ser/Thr. Based on the results of these experiments, it is clear that the kinase activity of plant phytochromes is not an artefact caused by the co-purification of another protein kinase (Yeh and Lagarias, 1998).

Bacterial Phytochromes

Bacteria use a “two-component” system consisting of a sensor protein and a response regulator protein to constantly regulate their physiology and behaviour in order to respond and adapt to their external environment. When the sensor protein picks up on a shift in its external environment, it relays that information to the response regulator protein, which then adjusts the activity of certain genes or triggers other cellular processes in response to the stimulus. These two halves talk to one another through cycling through phosphorylation and dephosphorylation. It is generally known that these sensor proteins perform the role of histidine kinases, autophosphorylate themselves, and transfer the phosphate group to a regulator molecule, setting in motion a series of events that affect gene expression. In order to maximise photosynthesis in different lighting situations, early physiological studies showed that cyanobacteria have photoreversible effects similar to those of plant phytochromes (Vierstra and Davis, 2000).

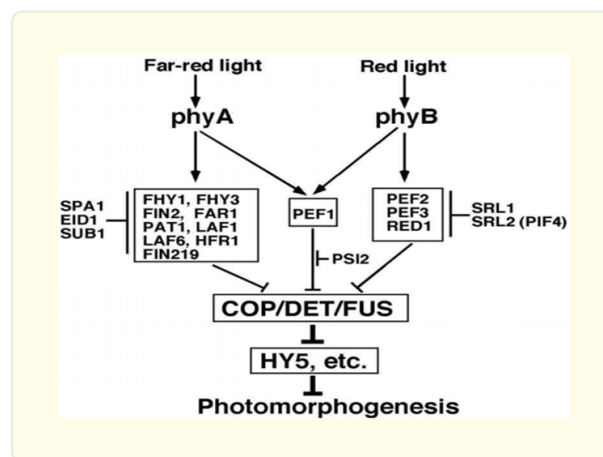


The phytochromes in *Arabidopsis* are kinases that respond to light. (A) Domain conservation between the phytochrome Cph1 from cyanobacteria and the phytochromes from *Arabidopsis*. The chromophore-binding cysteine residue (*) is conserved across species. Histidine kinase domain; phosphatidylinositol 3-kinase related domain; histidine kinase domain-related domain. The histidine (H) symbol calls attention to the conserved histidine in Cph1’s HKD domain. The percentage of shared amino acids between Cph1’s HKD

and the PRD and HKRD of Arabidopsis phytochromes is shown. Phytochromes in Arabidopsis also feature unique N-terminal extensions (NTE). Arabidopsis phytochrome kinase activity (B) possible functions. The phytochrome molecules themselves may undergo auto-phosphorylation or trans-phosphorylation through light-regulated kinase activity, or both. Subcellular location, interaction with PIFs, and the actions of other signalling intermediates may all be influenced by phosphorylation processes, including the stability of photoreceptors like phyA. Oat phyA (derived from Neff et al., 2000) amino acid sequence.

Signaling Components Shared by Both phyA and phyB

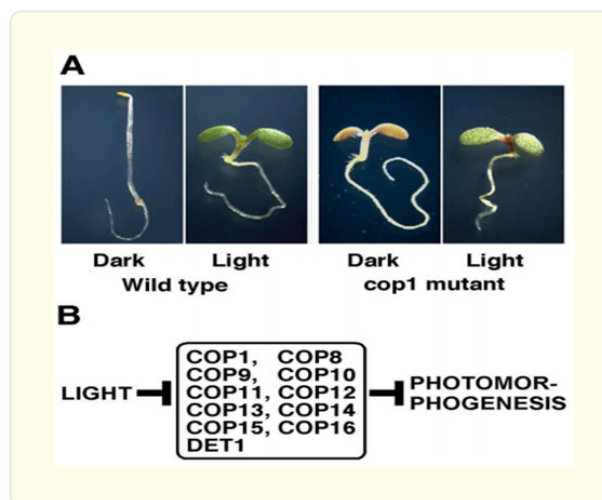
The *pef1* and *psi2* mutants have overlapping effects on the *phyA* and *phyB* signalling pathways; the *pef1* mutants have attenuated red and far-red responses, while the *psi2* mutant is hypersensitive to red and far-red light and has necrotic lesions in light-grown plants (Ahmad and Cashmore 1996; Genoud et al., 1998). Understanding how these two processes converge to regulate photomorphogenesis should be substantially improved after these genes have been cloned and their functions have been characterised.



Phytochrome Signaling and The Downstream Cop/Det/Fus Proteins

Different photoreceptors can trigger comparable signalling processes, suggesting that these pathways converge to regulate key genes during development via a shared collection of late signalling intermediates. Indeed, eleven pleiotropic COP/DET/FUS loci have been identified through genetic screens, and their gene products act as negative regulators of photomorphogenesis and function downstream of multiple photoreceptors, including *phyA* and *phyB* (Wei and Deng, 1996, Figure 8). COP1 is a RING-finger protein with WD-40 repeats (Deng et al., 1992), and it is one of the COP/DET/FUS proteins. Using a GUS-COP1 fusion protein, researchers were able to determine that COP1 operates within the nucleus to suppress photomorphogenic growth in the dark, and that COP1 inactivation by light is accompanied by a decrease in COP1 abundance in the nucleus (von Arnim and Deng, 1994). HY5, a bZIP transcription factor that promotes photomorphogenic growth, is a direct target of COP1's in the dark, where it is degraded by a 26S proteasome-mediated mechanism (Figure 9). Oyama et al. (1997), Ang et al. (1998), and Osterlund et al. (2000) all suggest that COP1 is a potential ubiquitin ligase. Castle and Meinke (1994), Peng et al. (2001a, 2001b), Karniol (1999), Kwok (1998, 1999), Serino (1999), Wei (1994), and Wei (1994) (Table 2) report that in addition to COP9, eight other COP/DET/FUS proteins constitute subunits (CSN1-CSN8) of a protein complex called the COP9 signalosome. The COP9 signalosome has been hypothesised to be involved in controlled proteolysis due to its subunit-by-subunit similarity to the lid subcomplex of the 26S proteasome and its observed interaction with this protein complex (Kwok et al., 1999; Peng et al., 2001c; Schwechheimer and Deng, 2000). More recent research has shown that the COP9 signalosome physically interacts with the SCFTIR1 E3 ubiquitin ligase and is necessary for efficient degradation of a putative substrate of SCFTIR1 (Schwechheimer et al., 2001), lending credence to this idea. It is likely that the COP/DET/FUS proteins restrict the actions of several transcription factors or transcriptional regulators, as evidenced by the pleiotropic character of the *c o p / d e t / f u s* mutant pheno-

type. This idea is supported by the discovery of additional transcriptional factors that interact with COP1 in addition to HY5 (Osterlund et al., 1999; Holm et al., 2001). Inactivation of these COP/DET/FUS proteins is often thought to be necessary for light-induced photomorphogenic growth. However, how the light-activated photoreceptors (such as phytochromes) regulate the activities of the COP/DET/FUS proteins that are involved in the physiological responses is poorly understood. Light-responsive regimes (FR and R for phyA and phyB, respectively) are known to trigger the nuclear depletion of COP1 (Osterlund and Deng, 1998). This is at least one mechanism by which phytochrome signalling regulates the downregulation of COP/DET/FUS protein activities. Mutations in phyA-specific signalling components (such as phyA, fhy3, fhy1, far1, and fin219) were found to affect the kinetics of FRc-mediated nuclear depletion of GUS-COP1, suggesting that these components regulate the nucleo-cytoplasmic partitioning of COP1 upstream of FRc. These mutants' levels of photomorphogenic development are altered as a result of changes in the concentration of the bZIP transcription factor HY5 (Wang and Deng, 2001). Nonetheless, it's worth noting that there's evidence that these loci involve signalling pathways outside of those involving COP1 (Wang and Deng, 2001).

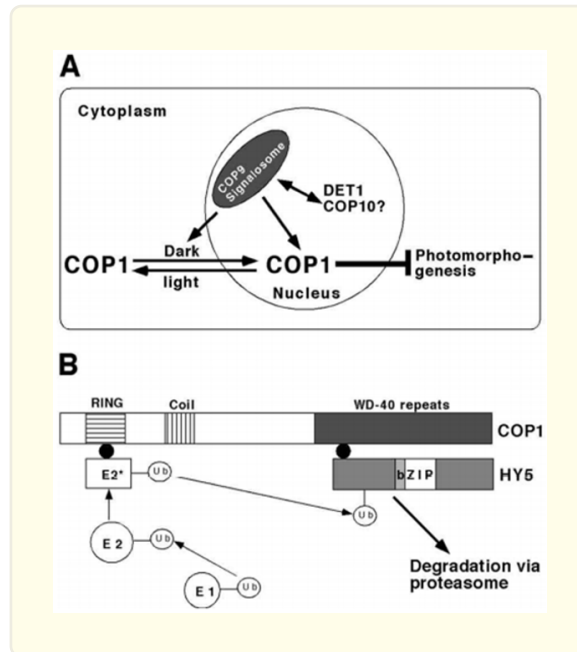


See in Figure 8 the possible functions of the COP/DET/FUS proteins during photomorphogenesis and the phenotype of *cop1* (constitutive photomorphogenic) mutants. (A) *Cop1* mutant seedlings cultivated in the dark have similar phenotypes to those of wild-type seedlings reared in the light. To suppress photomorphogenesis, (B) eleven pleiotropic COP/DET/FUS loci are involved. Multiple photoreceptors work together to transduce light signals that inactivate COP/DET/FUS proteins and activate photomorphogenic growth.

An Emerging Integrated Picture of Phytochrome Signaling

Two major findings in the field of phytochrome research have significantly shifted our perspective on how these molecules communicate with one another. To begin, it has been shown that phytochromes (both phyA and phyB) are capable of translocating from the cytoplasm into the nucleus upon photoconversion of Pr to Pfr (Kircher et al., 1999; Nagyet al., 2000). Second, PIF3, a bHLH protein coupled to a light-responsive element (G box) (Ni et al., 1999; Martinez-Garca et al., 2000), has been shown to interact with the Pfr form of phytochromes. These results support a new paradigm for phytochrome signalling in which phytochromes operate as photoreceptors, enter the nucleus, and influence gene transcription through interactions with transcriptional regulators. Plants may be able to continually monitor their light surroundings and respond to changes in light availability by corresponding changes in light-regulated gene expression if light signals are directly targeted to a promoter-element binding transcription factor. Nonetheless, it is worth noting that the biochemical basis for the regulation of gene expression brought about by the interaction of phytochrome with PIF3 is not yet established. Phytochrome can biochemically or allosterically alter the intrinsic transcriptional regulatory activity of PIF3 by binding to its G-box (Quail, 2000). Alternatively, phytochrome can regulate transcription directly by acting as a transcriptional coactivator or

corepressor in the recruitment or modulation of the pre-initiation complex. Since phytochrome is a light-regulated kinase and phosphorylation has been shown to regulate the activity of a number of transcription factors (Hardtke et al., 2000), it will be interesting to determine whether PIF3 is a substrate of phytochrome kinase activity and how it may modulate the function of PIF3.



In darkness, COP1 is enriched in the nucleus to suppress photo morphogenic development.

Light signals trigger the nuclear depletion of COP1, thus abrogating the repressive effect of COP1.

A putative role of COP1 as an E3 ubiquitin ligase. COP1 mediates the ubiquitination of HY5 and its subsequent degradation via the proteasome by recruiting an E2 and HY5 through distinct interacting domains (Osterlund et al., 2000).

Virus Resistance and Photomorphogenesis

- Light intensity can modulate the outcome of plant-virus interactions since both photosynthesis and many viral infection events occur in the chloroplast (Li et al., 2016; Zhao et al., 2016; Bhattacharyya and Chakraborty, 2018).
- Recent research suggests that plant-virus interactions are potentially regulated by several photoreceptors and photomorphogenesis regulators, including PHYA and PHYB, CRY2, PHOT2, COP1, the NAM, ATAF, the Aux/IAA protein phytochrome-associated protein 1 (PAP1), and the homeodomain-leucine zipper (HD-Zip) TF HAT1.
- For example, high light intensity promotes the infection of clover by *Subterranean clover red leaf virus* (SCRLV) (Helms et al., 1987).
- *Arabidopsis* plants exhibit light-dependent hypersensitive response (HR) and resistance signaling against *Turnip crinkle virus* (TCV) (Chandra-Shekara et al., 2006).
- Both light deficiency and photosystem impairment can increase the susceptibility of *Nicotiana benthamiana* to *Turnip mosaic virus* (TuMV) infection (Manfre et al., 2011)
- The plant growth promoting brassinosteroid (BR) hormones play critical roles in integrating the regulatory pathways of plant photomorphogenesis and viral defense.

Transcription factors

“Transcription factors are regulatory class of proteins responsible for turning on and off the gene expression”.

- Arabidopsis thaliana homeobox 1 (AtHB1) acts downstream of PIF1 (PHYTOCHROME- INTERACTING FACTOR 1) to promote hypocotyl elongation (Capella et al. 2015).
- HAT1 TF belongs to Homeodomain Leucine zipper family.
- It regulate the gene expression in Dominant Negative manner.
- To investigate TF HAT1 in Antiviral defence, they compared HAT1 and its mutants.

Role of light in other Organism

Kingdom	Genus	Process / Function
Plants	Multiple	Photomorphogenesis De-etiolation
Fungi	<i>Hyaloperanospora arabidopsis</i>	Spore germination Mycelial development and Sporulation
	<i>Botrytis cinerea</i>	Mycelial growth
Monera	<i>Freymyella</i>	Complementary chromatic adaptation
Protista	<i>Euglena</i>	Regulation of chloroplast development

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Volume 5 Issue 1 August 2023

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