

(REVIEW ARTICLE)



Gene regulatory network models for modules of molecular mechanism of the control of the photo-morphogenesis in plants

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Abstract

Plants are dynamic systems able to continuously adapt to changing environmental conditions, showing a remarkable phenotypic plasticity as from transition from germination to vegetative growth then to reproductive development. In this review, effect of light, molecular mechanisms photo-morphogenesis and gene regulatory networks were reviewed. This review provides insight into regulatory mechanisms for phytochrome-mediated light signaling pathway; and the roles of phytochromes and their downstream signaling components, molecular mechanisms light-perceiving photoreceptors and other positive and negative regulators of light signaling as well as interactions between these components during plant growth and development. Light is one of the most important factors regulating plant growth and development (photo-morphogenesis). Photomorphogenesis and skotomorphogenesis are two key events that control plant development, from seed germination to flowering and senescence. A group of wavelength-specific photoreceptors, E3 ubiquitin ligases, and various transcription factors work together to regulate these two critical processes. Phytochromes are the main photoreceptors in plants for perceiving red/far-red light and transducing the light signals to downstream factors that regulate the gene expression network for photomorphogenic development.

Keywords: Photomorphogenesis; Skotomorphogenesis; Molecular mechanism and phytochromes

1 Introduction

In developmental biology, photomorphogenesis is light-mediated development, where plant growth patterns respond to the light spectrum (*Li et al., 2011; Hans Mohar, 2012*). This is a completely separate process from photosynthesis where light is used as a source of energy. Phytochromes, cryptochromes, and phototropins are photochromic sensory receptors that restrict the photomorphogenic effect of light to the UV-A, UV-B, blue, red and far red portions of the electromagnetic spectrum (*Ulm et al., 2015; Parks and Brian, 2003; Tavridou et al., 2020*).

Among all the external stimuli affecting plant development, light has an important role in photosynthesis, chloroplast biogenesis, germination, seedling development, floral induction, photoperiodism (the switch from the vegetative to the flowering stage (*Hans Mohr, 2012*), and shade avoidance (*Dong et al., 2015*).

The effect of light on plant development can be clearly detected during seedling growth. Seedling growth in the dark (skotomorphogenesis) has a developmentally arrested etiolated phenotype with elongated hypocotyls (embryonic stems), small folded cotyledons (embryonic leaves), and undeveloped chloroplasts (figure 2) (*Reed et al., 1993*). In contrast, seedling growth in the light (photomorphogenesis) results in short hypocotyls, open cotyledons, and developed chloroplasts (Figure 2) (*Reed et al., 1993; Parks and Brian, 2003*)

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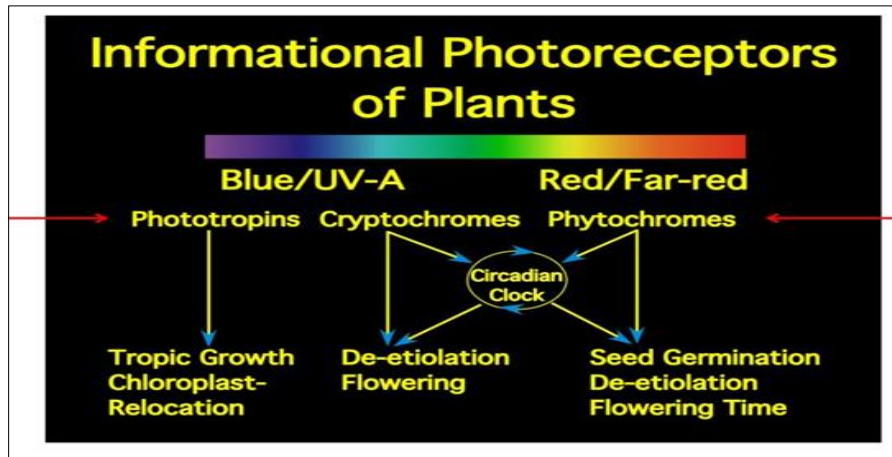
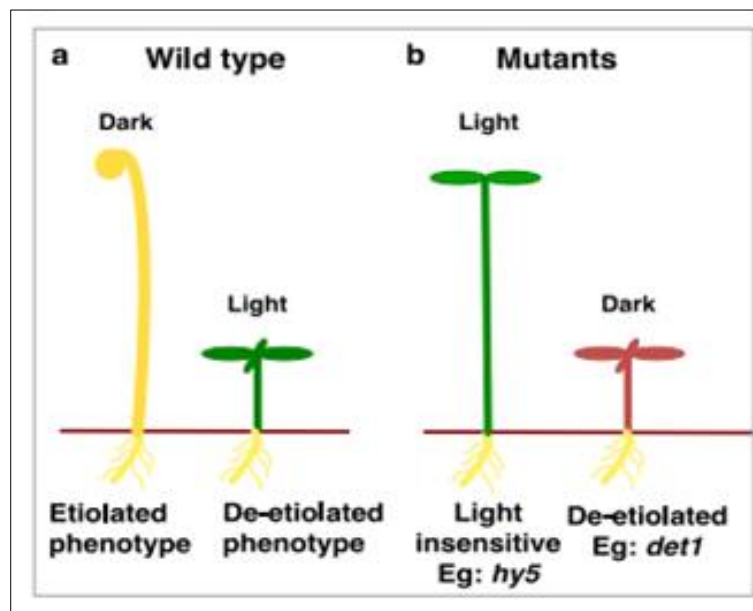


Figure 1 Informational photoreceptors of plants

Mutants have been identified in the model plant *Arabidopsis thaliana* that show the opposite phenotypes to those exhibited in wild type plants. These light signaling mutants are broadly divided into two classes, mutants showing light grown phenotypes in the dark and mutants showing dark grown phenotypes in the light (Figure 2b). These phenotypes are a consequence of defects in either positive or negative regulators of light signaling (Li *et al.*, 2011; Reed *et al.*, 1993).



(Source: Ceylon Journal of Science 45(1) 2016: 3-13)

Figure 2 Dark and light grown wild type seedling phenotypes (a) and light signaling mutants (b)

2 Molecular Mechanisms of Photo-Morphogenesis

2.1 Molecular Mechanisms Underlying Phytochrome Photoreceptors Controlled Morphogenesis

There are two forms of phytochromes: red light absorbing, Pr, and far-red light absorbing, Pfr. Pfr, which is the active form of phytochromes, can be reverted to Pr, which is the inactive form, slowly by inducing darkness or more rapidly by irradiation by far-red light (Li *et al.*, 2011; Burgie *et al.*, 2014). The Pfr promotes and regulates photomorphogenesis in response to FR light, whereas Pr regulates de-etiolation in response to R light (Li *et al.*, 2011; Burgie *et al.*, 2014; Junko, 2021).

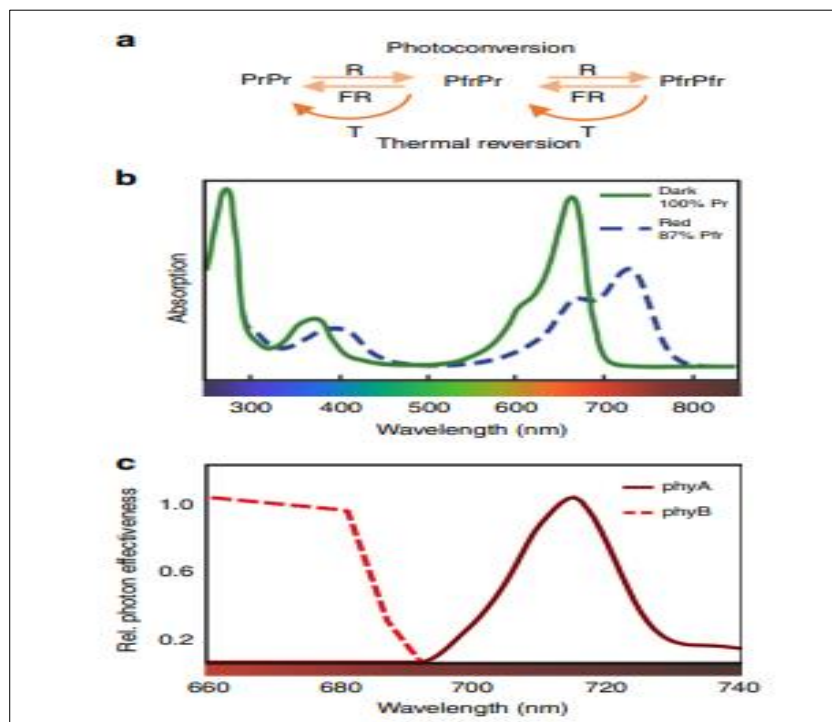
Phytochromes act as dimers, resulting in three possible phytochrome species: Pr-Pr, Pfr-Pr, and Pfr-Pfr₃ (Figure 3a). Pr and Pfr have different absorption maxima, but due to overlapping spectra both conformers are always present in the light while only prolonged darkness returns all phytochrome to Pr (Figure 3b) (*photobiology.info*. Retrieved 2018). Given

that phytochrome responses depend on the proportion of Pfr conformers, signaling is influenced by a combination of light quantity, color, and temperature (*photobiology.info. Retrieved 2018, Eberhard Schc\$fer and Ferenc Nagy, 2006, Eckardt and Nancy A., 2001*).

The chromophore for phytochrome is photochromic, i.e., it undergoes a change in conformation that makes a stable change in its light absorption properties (*Burgie et al., 2014*).

Phytochromes are synthesized in the inactive form, for which the absorption maximum is 660 nm. The red absorbing form, Pr, on absorption of a photon, converts to a form with an absorption maximum of 730 nm, Pfr (far red) (*Burgie et al., 2014; Li et al., 2011*). The Pfr form is the active form, but it can be converted back to Pr (and inactivated) by the absorption of a far-red photon (Figures 3 and 4) (*Dong et al., 2015; Burgie et al., 2014*).

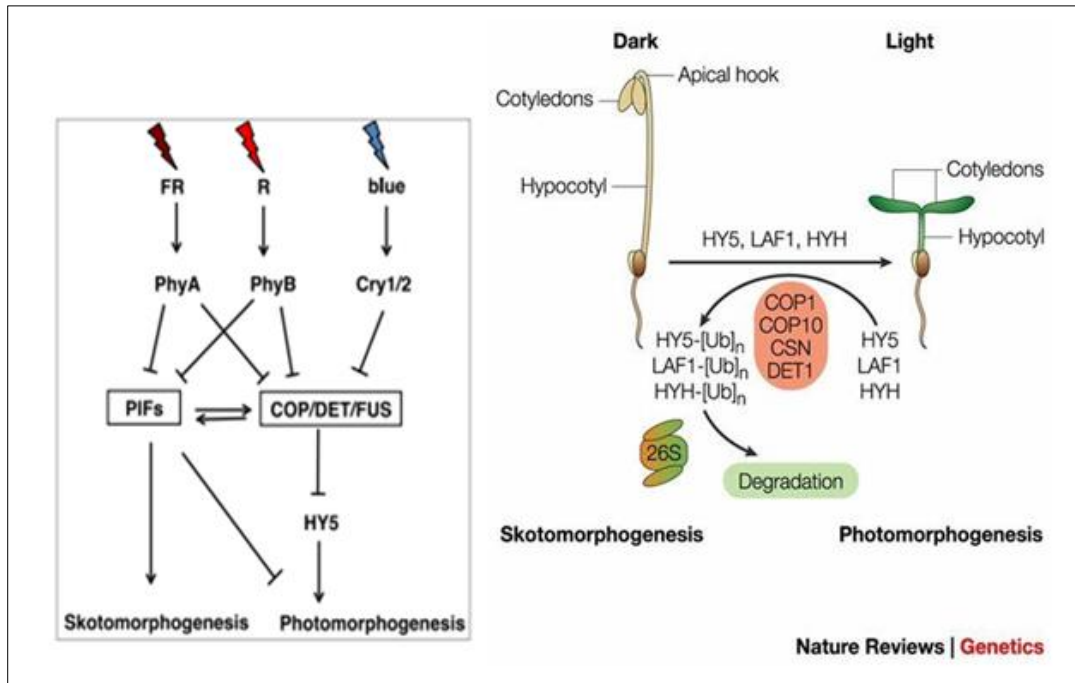
Most plants have multiple phytochromes encoded by different genes. The different forms of phytochrome control different responses but there is also redundancy so that in the absence of one phytochrome, another may take on the missing functions (*Li et al., 2011; Dong et al., 2015; Burgie et al., 2014*). There are five genes that encode phytochromes in the *Arabidopsis thaliana* genetic model, *PHYA-PHYE* (*Taiz et al., 2015*). *PHYA* is involved in the regulation of photomorphogenesis in response to far-red light (*Taiz et al., 2015; Li et al., 2011*). *PHYB* is involved in regulating photoreversible seed germination in response to red light. *PHYC* mediates the response between *PHYA* and *PHYB*. *PHYD* and *PHYE* mediate elongation of the internode and control the time in which the plant flowers (*Taiz et al., 2015*).



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Figure 3 Interconversion and control of the Pr and Pfr forms of phytochrome and absorption spectra for the 2 forms of phytochrome

Interconversion and control of the Pr and Pfr forms of phytochrome and absorption spectra for the 2 forms of phytochrome shown in figure 3. Adapted from *Biochemistry and Molecular Biology of Plants*, (c) American Society of Plant Biologists, with permission.



Source: Nature Reviews | Genetics

Figure 4 Molecular Mechanism of Light perception and signalling pathways in Photo-morphogenesis

A) Factors controlling phytochrome activity. Phytochromes exist in two conformations, Pr and Pfr, the latter being the active form. They exist as dimers so three species can be found. Each monomer can be activated by red light (R) and inactivated by far-red light (FR) or by thermal reversion, a process that depends on temperature (T). At least in the case of phyB, Pfr in heterodimers reverts much faster than that in homodimers, allowing phyB to perceive temperature both during the day and during the night. B) Plant phytochrome absorption spectra of the Pr and Pfr conformations. In dark-adapted seedlings phytochromes are in the Pr form. Upon a saturating R pulse, due to overlapping absorption spectra of Pr and Pfr, only 87% of Pfr is achieved. C) Action spectra for phyA and phyB in the control of hypocotyl elongation. Data from (Klose *et al.*, 2017, Li *et al.*, 2011, Tavridou *et al.*, 2020).

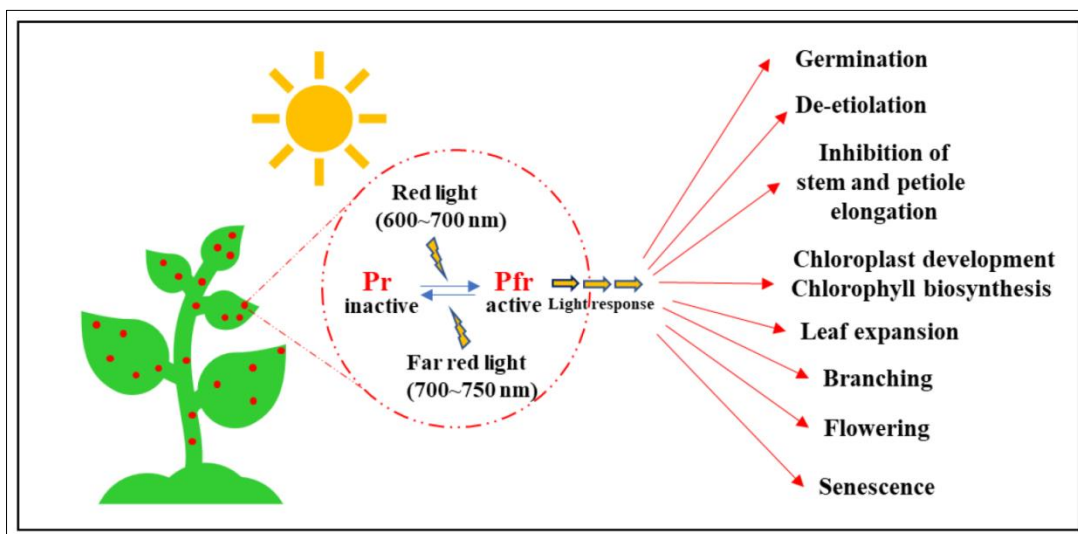


Figure 5 Regulation of Photomorphogenic Development by Plant Phytochromes

A schematic diagram depicting the involvement of plant phytochromes in different stages of photomorphogenesis. The red dots represent phytochromes that are present ubiquitously in plants. Inactive phytochrome (red light-absorbing Pr form) can be converted to active phytochrome (far-red light-absorbing Pfr form) by absorbing red light. The Pfr form can be converted back to the Pr form upon absorbing far-red light or in the dark (known as dark reversion, or more

recently, thermal reversion). The active Pfr form regulates various photomorphogenic development through other downstream components of the phytochrome-mediated light signaling pathway (Klose *et al.*, 2017, Li *et al.*, 2011, Tavridou *et al.*, 2020).

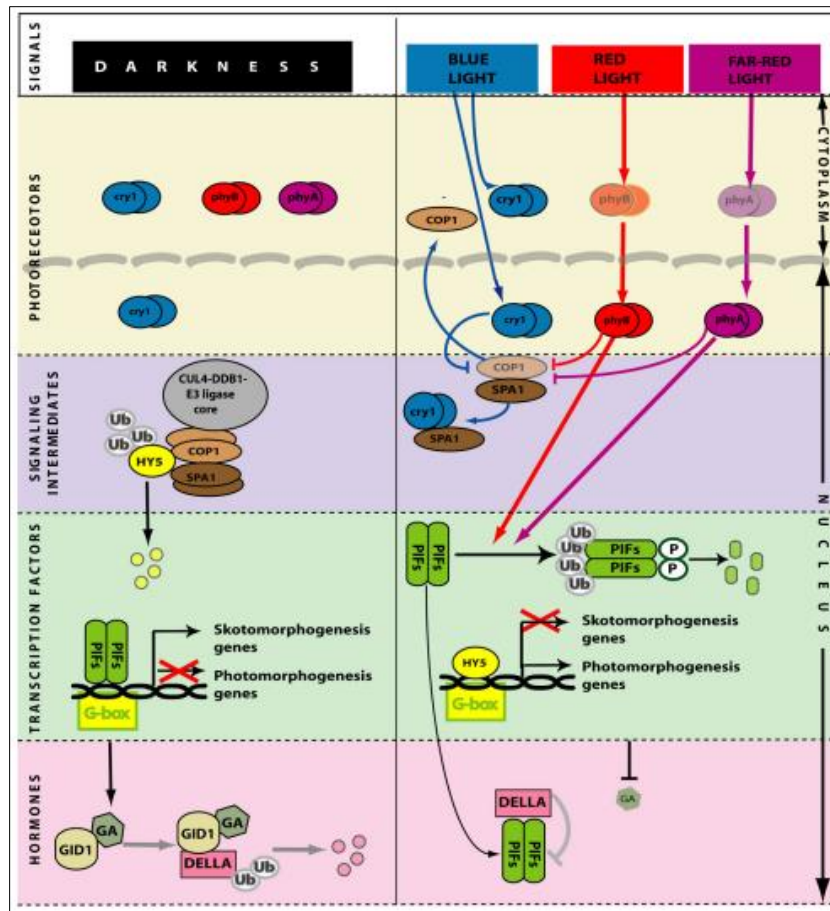


Figure 6 Simplified model of light perception and signaling during de-etiolation

In darkness (left) the photoreceptors are inactive. PIF transcription factors promote skotomorphogenesis. HY5 and other transcription factors that promote photomorphogenesis are ubiquitinated by CUL4-DDB1-COP1-SPA1 E3 ligase complex and degraded in the 26S proteasome. High levels of gibberellins induce degradation of DELLA. Light (right) activates the photoreceptors. In the nucleus, phytochromes (that migrate from the cytoplasm in their active form) and cryptochromes interact with COP1, reducing its activity and allowing the abundance of HY5 to increase. In the nucleus, phytochromes also reduce the activity of PIFs. Gibberellin levels are reduced, DELLA accumulate and bind PIFs further reducing their activity (Tavridou *et al.*, 2020).

2.2 Phytochrome Functions as a Protein Kinase in Plant Light Signalling

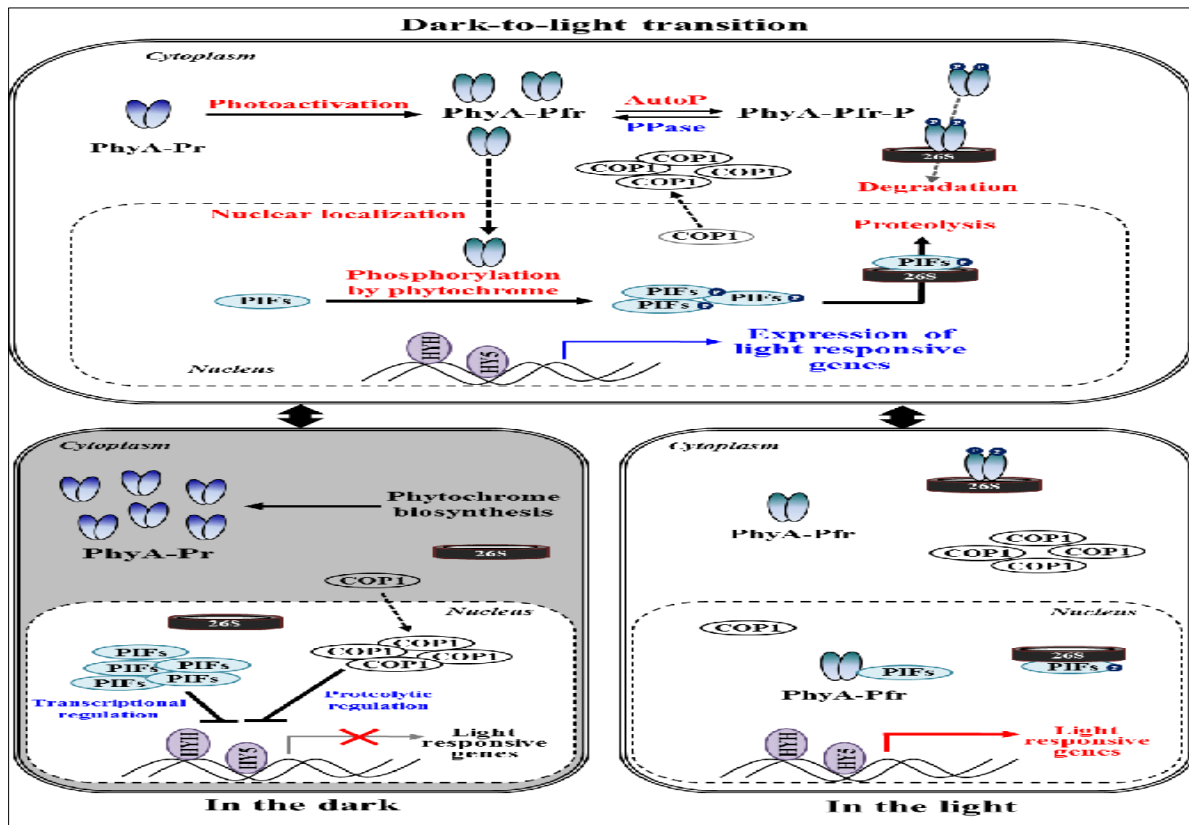


Figure 7 A proposed model for molecular mechanism of phyA (Tavridou, et al., 2020)

2.3 Blue light

Plants contain multiple blue light photoreceptors which have different functions. Cryptochromes were the first blue light receptors to be isolated and characterized from any organism, and are responsible for the blue light reactions in photomorphogenesis (Taiz, L. et al., 2015). The proteins use a flavin as a chromophore. The cryptochromes have evolved from microbial DNA-photolyase, an enzyme that carries out light-dependent repair of UV damaged DNA (Yu et al., 2010).

There are two different forms of cryptochromes that have been identified in plants, CRY1 and CRY2, which regulate the inhibition of hypocotyl elongation in response to blue light (Yu et al., 2010). Cryptochromes control stem elongation, leaf expansion, circadian rhythms and flowering time. In addition to blue light, cryptochromes also perceive long wavelength 350–400 nm UV irradiation (UV-A) (Yu et al., 2010).

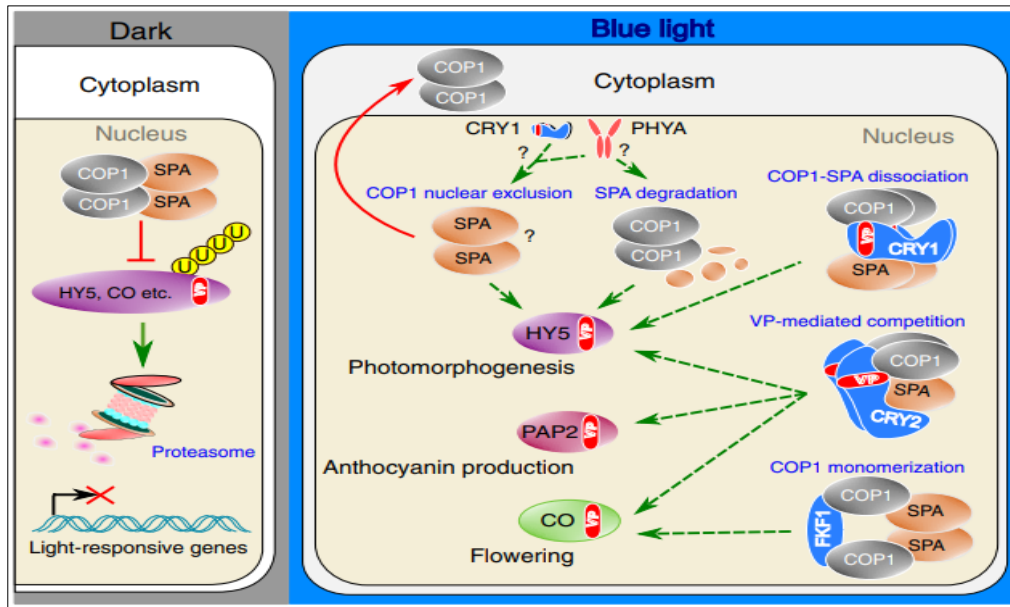


Figure 8 Molecular mechanisms of blue light-induced suppression of COP1/SPA E3 ligase activity in plants

(Left panel) In darkness the active COP1/SPA complex negatively regulates photomorphogenesis-promoting transcription factors by ubiquitination. The ubiquitinated proteins are subsequently degraded via the proteasome. As a result, transcription of light-responsive genes is prevented in darkness. (Right panel) Blue light suppresses COP1/SPA function via several mechanisms: nucleocytoplasmic partitioning of COP1, degradation of SPA proteins, COP1-SPA dissociation, cryptochrome mediated competitive eviction of COP1-targets from the COP1 complex via the VP motifs in the CCT domain of cryptochromes and FKF1-mediated prevention of COP1 dimerization. These mechanisms subsequently lead to the stabilization of HY5, PAP2, CO and so on, thereby promoting photomorphogenesis, anthocyanin accumulation and flowering (Yu *et al.*, 2010; Klose *et al.*, 2017).

2.4 UV light

Plants show various responses to UV light. UVR8 has been shown to be a UV-B receptor (Ulm *et al.*, 20 2015; Jenkins and Gareth I. 2017). The UV-B photoreceptor, UV Resistance Locus8 (UVR8) detects UV-B rays and elicits photomorphogenic responses (Ulm *et al.*, 20 2015; Jenkins, Gareth I., 2017). These responses are important for initiating hypocotyl elongation, leaf expansion, biosynthesis of flavonoids and many other important processes that affect the root-shoot system (Jenkins, Gareth I. (2017). Upon perception of inductive wavelengths, activated phytochromes together with blue (phototropins, cryptochromes, and Zeitlupes) and UV light receptors (UVR8) control plant physiology and development (Ulm *et al.*, 20 2015; Li *et al.*, 2011, Taiz *et al.*, 2015).

2.5 Molecular Mechanisms of UVR8-Mediated Action Spectra on Photomorphogenesis

Upon UV-B irradiation, a UVR8 dimer dissociates and accumulates in the nucleus and photomorphogenesis begins following two pathways (Junko, 2021; Jenkins, Gareth I., 2017; Tavridou *et al.*, 2020): one in which the UVR8 monomer binds to transcription factor(s) of gene(s) supporting hypocotyl growth to stop gene expression resulting in hypocotyl growth inhibition and the other pathway in which the UVR8 monomer binds both with CONSTITUTIVELY PHOTOMORPHOGENIC1- SUPPRESSOR OF PHYA (COP1-SPA) to release HY5 (referred to as “stabilized”) and WRKY DNA-BINDING PROTEIN 36 (WRKY36) on the ELONGATED HYPOCOTYL 5 (HY5) gene to release HY5 transcription, and both HY5 and another UV-B-activated UV-B sensor (denoted the Hyp sensor) through a self-interacting factor (HIF) associates with the HY5 promoter to initiate HY5 transcription, leading to anthocyanin synthesis, (figure 9) (Jenkins, Gareth I., 2017, Binkert *et al.*, 2014). These two pathways can be distinguished by action spectra in the UV-B region, with a single peak at 280 nm and two peaks (or a broad peak near 280– 300 nm) for the former and the latter, respectively (Junko, 2021; Jenkins, Gareth I., 2017; Tavridou *et al.*, 2020).

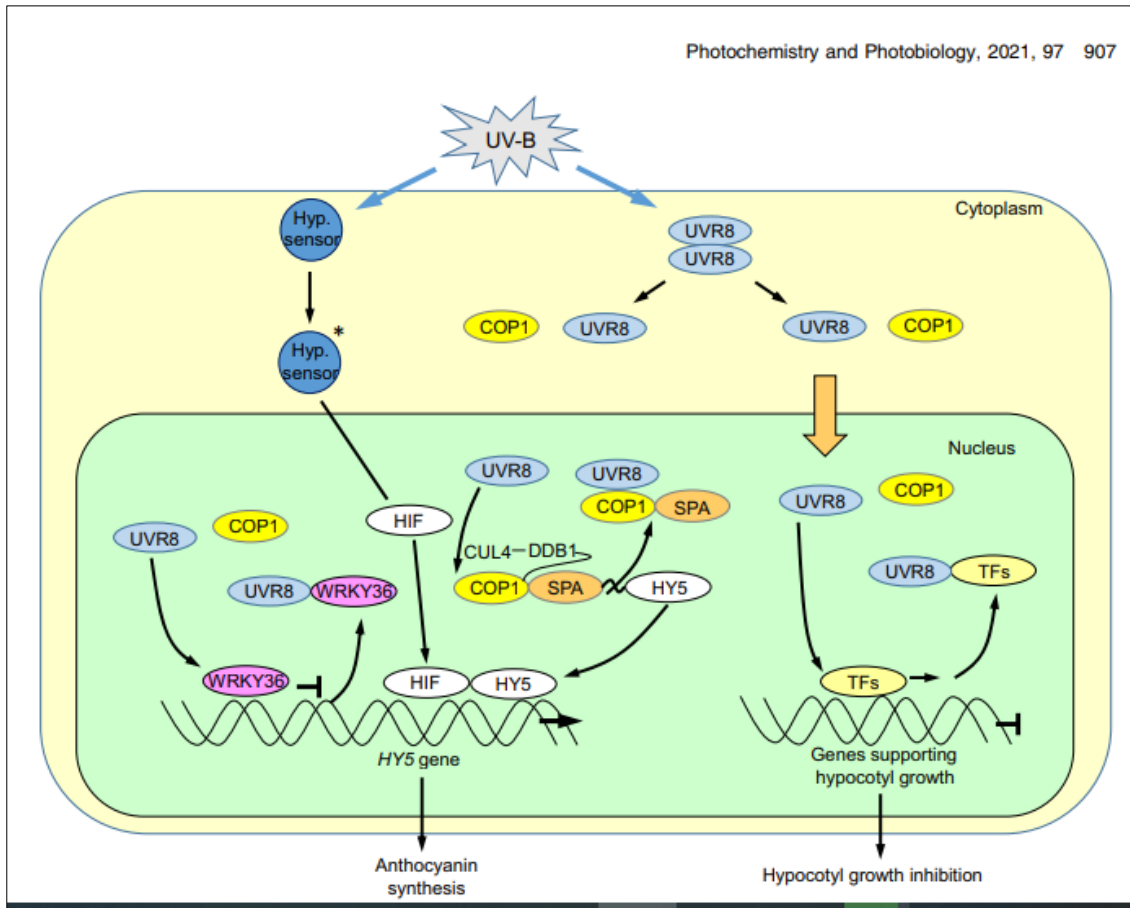


Figure 9 A hypothetical model for UVR8-mediated photomorphogenesis based on action spectra

The scheme for UVR8-mediated photomorphogenesis was completed by adding the pathway from the UVR8 monomer to hypocotyl growth inhibition to Figure 9. Upon UV-B irradiation, the UVR8 dimer dissociates and accumulates in nucleus, and photomorphogenesis starts by two pathways; in one, UVR8 binds to transcription factor(s) (TF(s)) of genes supporting hypocotyl growth, such as BES1-BIM1, MYB73/77 and WRKY36, and arrests gene expression, resulting in hypocotyl growth inhibition (Junko, 2021; Jenkins, Gareth I., 2017; Tavidou *et al.*, 2020). In the other, it binds to WRKY36 on the HY5 gene to release the suppression of HY5 transcription. Then, stabilized HY5 and the UV-B-activated Hyp sensor (Hyp*), possibly through its own interacting factor (HIF), also simultaneously associate with the HY5 promoter and initiate HY5 transcription leading to anthocyanin synthesis. These two pathways can be distinguished by their action spectra in the UV-B region: a single peak at 280 nm and two (or one broad) peaks for the former and latter, respectively (Binkert *et al.*, 2014; Junko, 2021).

2.6 Molecular Mechanisms of hormonal regulation of Photomorphogenesis

2.6.1 ABA inhibits hypocotyl elongation acting on gibberellins, DELLA proteins and auxin

Hypocotyl elongation of *Arabidopsis* seedlings is influenced by light and numerous growth factors. Abscisic acid (ABA) plays a major role in these processes, but the molecular mechanism remains unclear (Lorrai *et al.*, 2019).

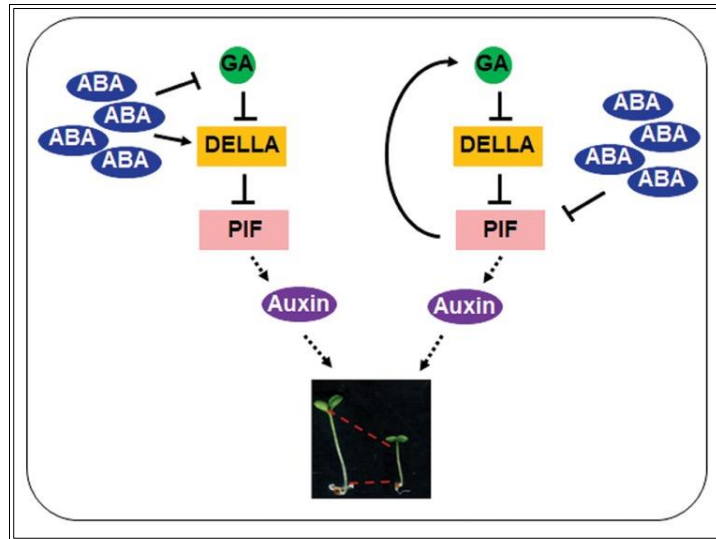


Figure 10 Schematic model of ABA function in the inhibition of hypocotyl elongation

Schematic model of ABA function in the inhibition of hypocotyl elongation in a DELLA-dependent or independent pathway; ABA represses GA biosynthesis, thus DELLA proteins are stabilized, and inhibit the activity of PIFs, ultimately repressing auxin biosynthesis (left) in (figure 10). Alternatively, ABA inhibits PIF proteins, which no longer induce both GA and auxin biosynthesis (right figure 10) Image credit: (Lorrai *et al.*, 2019)

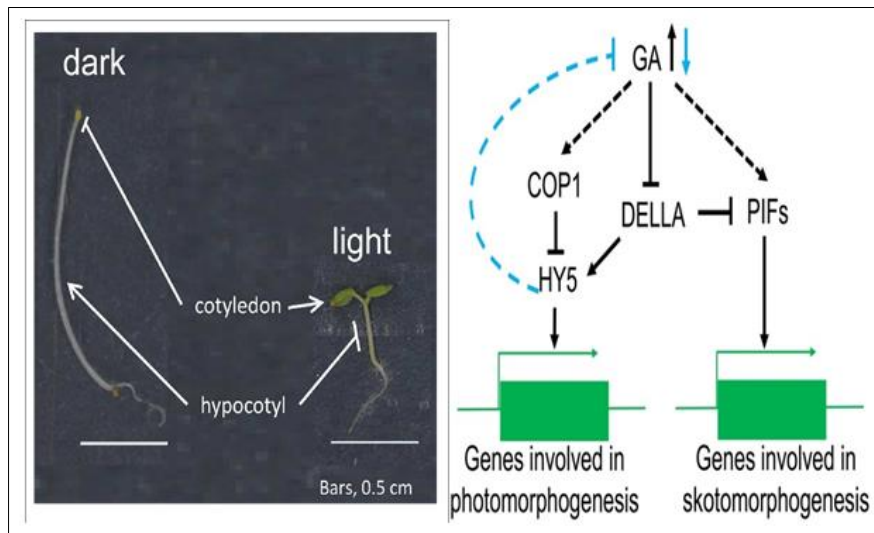


Figure 11 Photomorphogenesis as morphological and GA process in seedlings

The left photos show the change in form of an *Arabidopsis thaliana* seedling grown in darkness and white light in (figure 11). The right hand illustration shows the cellular process involving GA in seedlings in controlling responsive gene expression in dark and light. Adapted from Biochemistry and Molecular Biology of Plants, (c) American Society of Plant Biologists, with permission.

3 Conclusion and Perspectives

This review provides insight into regulatory mechanisms for phytochrome-mediated light signaling pathway; and the roles of phytochromes and their downstream signaling components, molecular mechanisms light-perceiving photoreceptors and other positive and negative regulators of light signaling as well as interactions between these components during plant growth and development. Genetic and molecular evidence for the basis of light signaling mechanisms are discussed as well as the importance of light signaling in plant development. The signaling network for phytochrome-mediated photomorphogenic development is divided into four parts. The first part is the light absorption

and conformational changes, the second part is the interaction of phytochromes with various downstream components and signaling initiation, the third part is the regulation of signaling via ubiquitin/26S proteasome-mediated proteolysis and signal integration, and the final part is the regulatory gene expression of light-responsive genes (CO). Extensive research over several decades in plant light signaling mediated by photoreceptors has identified the molecular mechanisms for how phytochromes regulate photomorphogenic development, which includes degradation of phytochrome-interacting factors (PIFs) and inactivation of COP1-SPA complexes with the accumulation of master transcription factors for photomorphogenesis, such as HY5. Thus, the function of phytochromes could be the transcriptional regulation of genes involved in photomorphogenesis via negative (PIFs, COP1/SPA complexes, etc.) or positive (HY5, HFR1, etc.) transcription factors. Moreover, phytochromes are also involved in other physiological processes including stress responses, defense, stomatal opening, and the relative oxygen species (ROS) pathway. In addition, phytochromes interact with other photoreceptors to regulate these processes, including cryptochromes and phototropins. Applying action spectra analysis to determine the molecular mechanism of red, far red; and UVR8-mediated photomorphogenesis, a molecular mechanism for UV-B responses in terrestrial plants, is discussed, although the molecular identity of the Hyp sensor remains unclear.

The gene regulatory network in the photomorphogenic control of photomorphogenesis in model plants was reviewed. This review highlights:-

- Molecular mechanism of light perception and signaling pathways in Photomorphogenesis.
- Molecular mechanisms underlying phytochrome role in controlling photo-morphogenesis.
- Molecular mechanisms of blue light-induced suppression of COP1/SPA E3 ligase activity.
- Molecular mechanisms of UVR8-mediated action spectra on photomorphogenesis and hormonal process in controlling seedlings.

Compliance of ethical standard

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Disclosure of conflict of interest

The author has no conflict of interest.

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