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Light signaling pathways regulating early plant development: an evo-devo approach

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Among several factors regulating early plant development, light plays a crucial role. In seed plants just after germination, the presence or absence of light determines the morphology of the developing seedling. The presence of light initiates photomorphogenesis in which plants undergo several developmental changes like inhibition of hypocotyl elongation, apical hook opening, cotyledon expansion and greening. Most of the photoreceptors and light-signaling transducers regulating these processes have been identified and well-studied, especially in *Arabidopsis thaliana*. Here we provide insights into some recent developments in the molecular regulation of seedling de-etiolation and chloroplast biogenesis. In the past few years several reports have enhanced our understanding of light-regulated development in algae and the bryophytes. In this review we highlight the key light-regulated mechanisms governing development in the simple unicellular algae *Chlamydomonas reinhardtii*. Further, we consolidate the current information about the role of light in regulating growth and development in the liverwort *Marchantia polymorpha* and the moss *Physcomitrium patens*. We finally discuss the conservation of the light signalling machinery in all these photosynthetic organisms.

KEYWORDS

algae, *Arabidopsis*, bryophytes, de-etiolation, early seedling development, light signaling

Introduction

Light plays an inevitable role in the lifecycle of all photosynthetic organisms including plants (Sullivan and Deng, 2003). In seed plants just after germination, seedlings exhibit a dramatic difference in morphology depending on whether it perceives light or not. Seedlings that emerge in the dark, buried under layers of soil, exhibit skotomorphogenic development. Skotomorphogenesis is characterized by elongated growth of the hypocotyl enabling the plant to reach out for light. In dicots like *Arabidopsis thaliana*, the two cotyledons enclose the shoot apical meristem (SAM) and form an apical hook. This hook

prevents damage to the SAM while the seedling tries to pierce its way through the abrasive soil particles. Once exposed to the light, seedlings orchestrate photomorphogenesis which is characterized by inhibition of hypocotyl elongation, opening of the cotyledons and formation of the chloroplasts resulting in greening. The molecular regulation of all these developmental changes in *Arabidopsis thaliana* is well studied and also discussed in some previous reviews (Gallego-Bartolomé et al., 2011; Abbas et al., 2013; Rehmani et al., 2023; Wang et al., 2023; Krahmer and Fankhauser, 2024). Therefore, in this review we primarily discuss some recent advancements in these fields. While the role of light in growth and development of *Arabidopsis thaliana* is well described, its role is less explored in primitive plants and their algal ancestors. During terrestrialization of plants, the quality and quantity of light varied significantly from water to land (Han et al., 2019; Lopez-Pozo et al., 2023). How the early land plants evolved from the aquatic algal ancestors to acclimatize to this sudden change in light quality and fluence is still not well explored. Here we attempt to comprehend the findings highlighting the role of light signaling in growth and development of the green algae *Chlamydomonas reinhardtii*, as well as in the non-vascular bryophytes *Marchantia polymorpha* and *Physcomitrium patens*.

Molecular regulators of the light signaling pathway

In land plants light is perceived by different classes of photoreceptors. UV-B is perceived by the UV RESISTANCE LOCUS 8 (UVR8) photoreceptor. There are several photoreceptors in plants that can detect blue light including the cryptochromes (CRYs), phototropins (PHOTs), ZEITLUPE (ZTL), FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1) and LOV KELCH PROTEIN 2 (LKP2). The phytochromes are responsible for perceiving the red and far red light. The Phytochromes exist in two photo-convertible forms the P_r form and the P_{fr} form. The P_r form of the phytochrome perceives red light and gets converted to the P_{fr} form. P_{fr} is the active form of phytochrome that localises to the nuclei and regulates downstream signalling. P_{fr} form of phytochrome upon perceiving the far red light gets converted back to the inactive P_r form (Kami et al., 2010; Casal, 2013). In *Arabidopsis* there are five different types of phytochromes. Phytochrome A (PhyA) is light labile while the Phytochrome B (PhyB), Phytochrome C (PhyC), Phytochrome D (PhyD) and Phytochrome E (PhyE) are light stable (Li et al., 2011). PhyA plays major role in far-red light mediated responses, while PhyB is the primary player in red light response pathways. The nuclear localised P_{fr} form of phytochromes interact with proteins called PHYTOCHROME INTERACTING FACTORS (PIFs) and inactivate them to regulate downstream signalling (Park et al., 2012; Legris et al., 2019). The cryptochromes are known to inhibit the dark accumulated E3 Ubiquitin ligase CONSTITUTIVE PHOTOMORPHOGENESIS 1 (COP1) to facilitate the photomorphogenesis in the seedlings (Ponnu and Hoecker, 2021). The photoactivated monomers of UVR8 interact

with the monomers of COP1 to induce UV-B photomorphogenesis (Tilbrook et al., 2013; Jenkins, 2014). Activation of the photoreceptors induce the downstream signalling cascade for gene regulation which involves key transcription factors like ELONGATED HYPOCOTYL 5 (HY5) and B-BOX (BBX) proteins (Gyula et al., 2003; Larner et al., 2018; Yadav et al., 2020b, a). In this review we primarily discuss the recent advances in the process of early seedling development.

Role of light signaling in regulation of hypocotyl elongation

The embryonic stem called hypocotyl connects the root to the cotyledons. It has a fixed number of cells at the end of the embryogenesis (Gendreau et al., 1997). Further elongation of the hypocotyl depends on the anisotropic expansion of cells, which depends on both environmental cues, such as light, and internal hormone signaling. Under dark, the germinated seedlings elongate their hypocotyl towards the soil surface. Hypocotyl elongation is driven by cell expansion by accumulating GIBBERELIC ACID (GA) in dark, which indirectly activates auxin via PHYTOCHROME INTERACTING FACTORS (PIFs). PIFs play a major role in hypocotyl elongation, as *pifq* mutants exhibit a photomorphogenic phenotype in dark with a shortened hypocotyl (Shin et al., 2009). PIFs physically interact with DELLA to promote their degradation to regulate the hypocotyl elongation (Li KunLun et al., 2015; Li et al., 2016; Griffiths et al., 2024). DE-ETIOLATED 1 (DET1) also increases the abundance of PIFs in dark by negatively regulating the DELLA (Dong et al., 2014). In the dark PIFs transcriptionally activate auxin biosynthesis and auxin-regulated genes like SMALL AUXIN UP-RNAs (SAUR)s including (SAUR19) (Figure 1) (Spartz et al., 2012; Sun et al., 2016). These SAURs inhibit PROTEIN PHOSPHATASE 2C.D (PP2C.D) and activate H^+ -ATPase which leads to the cell wall matrix acidification. This further activates EXPANSINs (EXPs) and XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE (XTH18,19) leading to hypocotyl cell elongation (Wolf et al., 2012). Auxin also induces the interaction between Transmembrane kinase (TMK) and H^+ -ATPase and promotes TMK-dependent phosphorylation of the H^+ -ATPase to promote cell elongation in the dark (Lin et al., 2021) (Figure 1). BR also positively regulates hypocotyl elongation by activating PIFs. In dark, COP1 is nuclear localised and plays a multifaceted roles by interacting and degrading the pathway components of different phytohormones. COP1 degrades the phosphorylated form of BES1 (BRASSINOSTEROID INSENSITIVE 1-EMS-SUPPRESSOR 1), increasing the active form of BZR1 (BRASSINAZOLE RESISTANCE 1) and BES1. BZR1/BES1 interact with PIFs to regulate cell elongation (Oh et al., 2012; Yang et al., 2017). COP1 promotes GA accumulation and GA increases PIF activity by causing GIBBERELLIN INSENSITIVE DWARF 1 (GID1) to degrade the GA inhibitor DELLA proteins (Blanco-Touriñán et al., 2020). In addition, COP1/DET1 negatively regulate HY5 protein, to promote hypocotyl elongation in the dark (Figure 1).

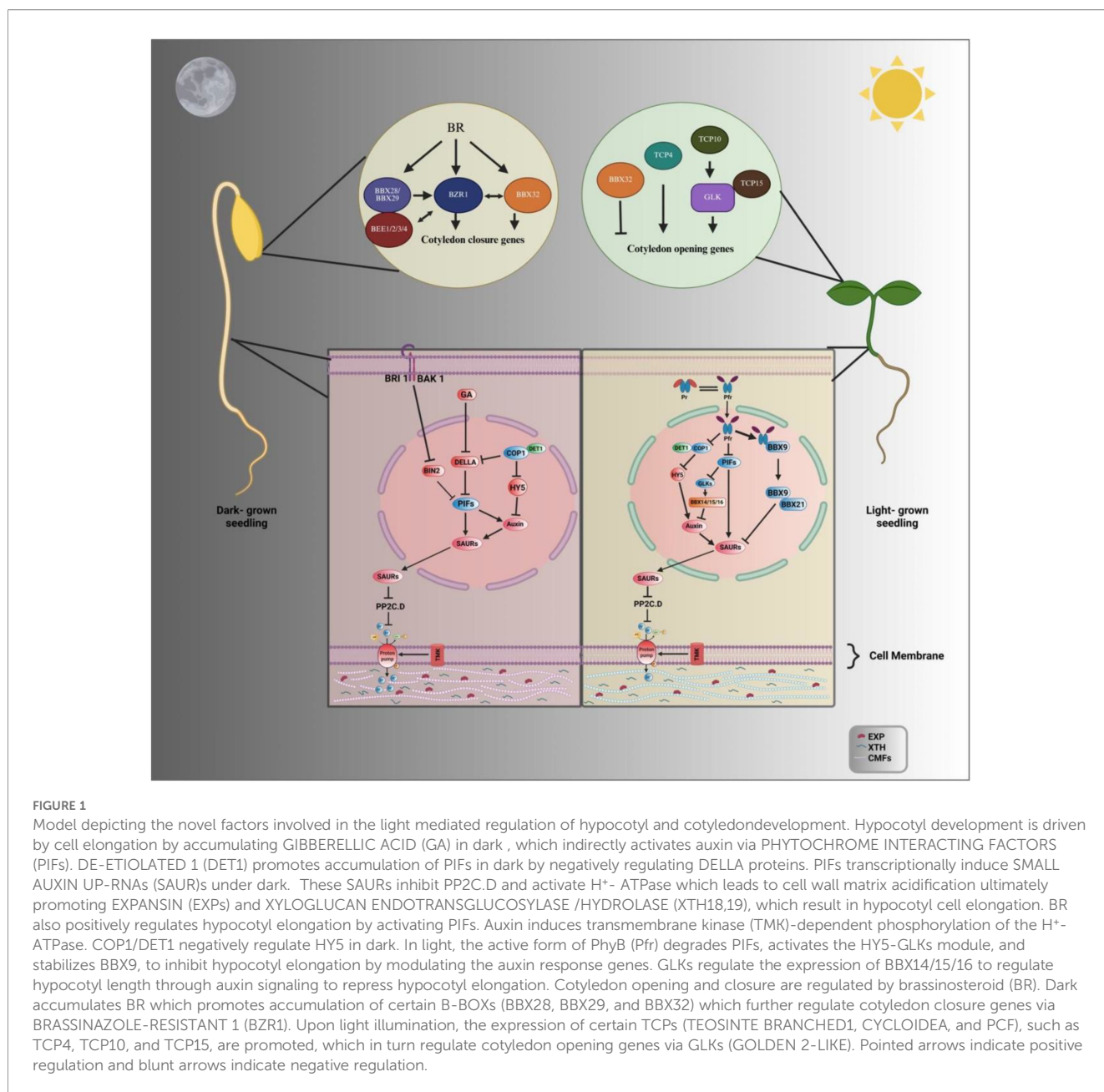


FIGURE 1

Model depicting the novel factors involved in the light mediated regulation of hypocotyl and cotyledon development. Hypocotyl development is driven by cell elongation by accumulating GIBBERELLIC ACID (GA) in dark, which indirectly activates auxin via PHYTOCHROME INTERACTING FACTORS (PIFs). DE-ETIOLATED 1 (DET1) promotes accumulation of PIFs in dark by negatively regulating DELLA proteins. PIFs transcriptionally induce SMALL AUXIN UP-RNAs (SAUR)s under dark. These SAURs inhibit PP2C.D and activate H^+ -ATPase which leads to cell wall matrix acidification ultimately promoting EXPANSIN (EXPs) and XYLOGLUCAN ENDOTRANSGLUCOSYLASE /HYDROLASE (XTH18,19), which result in hypocotyl cell elongation. BR also positively regulates hypocotyl elongation by activating PIFs. Auxin induces transmembrane kinase (TMK)-dependent phosphorylation of the H^+ -ATPase. COP1/DET1 negatively regulate HY5 in dark. In light, the active form of PhyB (Pfr) degrades PIFs, activates the HY5-GLKs module, and stabilizes BBX9, to inhibit hypocotyl elongation by modulating the auxin response genes. GLKs regulate the expression of BBX14/15/16 to regulate hypocotyl length through auxin signaling to repress hypocotyl elongation. Cotyledon opening and closure are regulated by brassinosteroid (BR). Dark accumulates BR which promotes accumulation of certain B-BOXs (BBX28, BBX29, and BBX32) which further regulate cotyledon closure genes via BRASSINAZOLE-RESISTANT 1 (BZR1). Upon light illumination, the expression of certain TCPs (TEOSINTE BRANCHED1, CYCLOIDEA, and PCF), such as TCP4, TCP10, and TCP15, are promoted, which in turn regulate cotyledon opening genes via GLKs (GOLDEN 2-LIKE). Pointed arrows indicate positive regulation and blunt arrows indicate negative regulation.

In light, phototropin1 (PHOT1) plays a rapid role in inhibiting cell elongation below the hypocotyl apex, mainly by inhibiting the activation of H^+ -ATPases in the elongating cells (Zhao et al., 2013). CRY1 inhibits elongation in the apical zone by interacting with and stabilizing AUX/IAA proteins to suppress auxin signaling (Bustamante et al., 2025). Exposure to light decreases the GA accumulation in the hypocotyl. Under light CRY1 physically interacting with GID1 which might attenuate GID1-DELLA interaction and promote the DELLA-mediated inhibition of PIFs (Zhong et al., 2021). In red light, phyB gets activated and degrades PIFs (Park et al., 2018). It also stabilizes HEMERA (HMR) to degrade PIF1/3 in photobodies (Galvão et al., 2012). Green light regulates hypocotyl elongation through brassinosteroid signaling, however its regulation needs further investigation (Hao et al., 2023). HY5 is a positive regulator of photomorphogenesis and *hy5*

mutants exhibit elongated hypocotyl (Oyama et al., 1997). HY5 competes with PIFs for binding to the promoters of auxin-producing genes like *YUC8* at E/G-box elements (Chen et al., 2013; Gangappa and Kumar, 2017). By decreasing the acetylation of HISTONE4 (H4), HY5 recruits HISTONE DE ACETYLASE 15 (HDA15) and other chromatin modifiers to suppress genes involved in auxin signaling and cell wall organization, while increased H3K27me3 levels suppress hypocotyl elongation (Zhao et al., 2019). Together with HY5, several BBXs also play a role in hypocotyl development, depending upon environmental cues. Cao et al., 2023, have summarized the role of BBXs in hypocotyl development. Here we primarily discuss the reports characterising the role of BBXs reported afterwards. BBX14/15/16 function redundantly to regulate hypocotyl elongation through the PIFs/HY5-GLK module, where HY5 and PIFs form a feedback regulatory

loop to antagonistically regulate hypocotyl elongation in the presence of light via auxin and BR-responsive genes (Nasim et al., 2024) (Figure 1). In red light phyB interacts with BBX9, and promotes its stabilisation. BBX9 interacts with PIFs and represses their transcriptional activities in the promoter of *SAUR* genes, e.g., *SAUR24/29* and *IAA29*. Interaction between BBX9 and BBX21, a previously identified cofactor of HY5, forms a positive regulatory loop to promote photomorphogenesis under light (Song et al., 2024)(Figure 1).

Light signal transduction during cotyledon opening and greening

De-etiolation is marked by the unfolding and expansion of cotyledon as well as the establishment of the photosynthetic apparatus. This transition is essential for seedling survival and photoautotrophic growth. Cotyledon opening is one of the most prominent morphological changes during de-etiolation. While the complete understanding of the mechanism involved in opening and expansion of the cotyledons is still missing, several reviews have nicely summarized this process (Yang et al., 2020; Wei et al., 2023; Reyes-Hernández, 2025). In the dark, after germination, cotyledons remain small and closed primarily due to the action of COP1 and PIFs which are major inhibitors of light signaling. *cop1* and *pifq* mutants exhibit open and expanded cotyledons in the dark suggesting that COP1 and the PIF proteins inhibit cotyledon opening in dark. Studies suggest, PIF1 and PIF3 play a major role in cotyledon closure as the *pif1pif3* double mutant displays partially open cotyledons in dark (Shin et al., 2009). Additionally, PIF3 also negatively regulates cotyledon opening under red and far-red light (Kim et al., 2003; Xin et al., 2018).

SAURs are known for their role in promoting cell expansion and are reported to be the direct target of PIFs (Spartz et al., 2014; Sun et al., 2016). SAUR17 is identified to be highly expressed in the cotyledons and the hook regions of etiolated seedlings and responsible for maintaining the apical hook and the closed cotyledons (Wang et al., 2020). *SAUR6*, *SAUR12*, *SAUR14*, *SAUR16*, and *SAUR50* are part of a subgroup of *SAUR* genes called *lirSAUR* (light-induced in cotyledons and/or repressed in hypocotyls *SAUR*), whose expression is oppositely affected by light in cotyledons and hypocotyls (Sun et al., 2016). *LirSAURs* mainly represented by *SAUR16* and *SAUR50*, on the contrary, act antagonistically to *SAUR17* and promote hook and cotyledon opening by inhibiting PP2C-D1. *SAUR17* has high affinity for PP2C-D1 which inhibits *SAUR50* from binding to PP2C-D1 thereby suppressing cell expansion and maintaining skotomorphogenesis under dark (Wang et al., 2020).

TEOSINTE BRANCHED1, CYCLOIDEA, and PCF (TCP) family of plant-specific transcription factors are known to be developmental regulators. CIN-like clade of *TCP* genes, including *TCP4*-like genes (*TCP3*, *TCP4*, and *TCP10*), were predominantly expressed in cotyledons and promotes cotyledon opening by directly regulating the expression of *SAUR16* and *SAUR50* (Figure 1). PIF3, which accumulates in the dark, functions to

antagonize *TCP4*'s binding to the promoter of *SAUR* genes (Dong et al., 2019). *TCP15*, a member of class I *TCP* proteins, is also known to participate in regulating cotyledon opening but through different mechanisms. *TCP15* requires *GLK1* for efficient cotyledon opening and induction of *SAUR* and *EXPANSIN* genes involved in cell expansion and chloroplast biogenesis (Alem et al., 2025). Class II TEOSINTE BRANCHED1, CYCLOIDEA, and PCF (*TCP*) *TCP10* are induced upon light perception which act together with *GOLDEN2-LIKE1* (*GLK1*) to promote cotyledon de-etiolation (Figure 1). *TCP15* also associates with the transcriptional loop between *TCP10* and *GLK1* through *GLK1*, which induces cell expansion (*SMALL AUXIN UP RNA*, *EXPANSIN*) and photosynthesis-associated nuclear genes (Alem et al., 2025).

Brassinosteroid (BR) is a steroidal hormone and acts antagonistic to light to regulate cotyledon opening (Wang et al., 2012). Central transcription factors, including HY5, PIFs, and BZR1, regulate downstream genes involved in cell expansion and organ movement. BZR1 induces auxin-related genes such as *LAX3*, *WAG2*, *PIN1*, and *ACS5* to suppress cotyledon opening (Figure 1) (Li and He, 2016). In contrast, HY5 inhibits the activity of BZR1 and prevents its binding to the promoters of the above mentioned genes, thereby promoting the photomorphogenesis. B-box proteins (BBXs) function as critical integrators of light and hormonal signaling in seedlings. Studies have shown that *BBX32* is expressed in cotyledons, induced by BR, and physically interacts with both BZR1 and PIF3 to suppress cotyledon opening in darkness. *BBX32* thus integrates light and BR pathways to regulate cotyledon opening during the dark-to-light transition (Figure 1) (Ravindran et al., 2021). In contrast, BZS1 (*BBX20*) enhances light signaling but represses BR signaling. It interacts with COP1 and undergoes COP1-mediated degradation. A gain-of-function allele, *BZS1-D*, partially suppresses the phenotype of the constitutively active *bzr1-1D* mutant, and BZS1 represses numerous BR-activated genes (Fan et al., 2012). Similarly, *BBX28* and *BBX29* positively regulate BR signaling in *Arabidopsis thaliana* (Figure 1). BR treatment stabilizes these proteins in a *BRI1* and *BIN2* dependent manner. The mutant seedlings *bbx28bbx29* display enhanced cotyledon opening in darkness when treated with brassinazole, whereas overexpression of *BBX28/29* can partially rescue BR-deficient phenotypes in *bri1-5* and *bin2-1* mutants (Cao et al., 2022). Recent studies have shown that jasmonate, which is a major defence hormone, promotes cotyledon opening in etiolated seedlings by inhibiting COP1 activity and stabilizing HY5 and *PAR1/PAR2* (Zheng et al., 2017).

Etiolated seedlings emerging from the soil strictly control chlorophyll biosynthesis and chloroplast development to harvest light energy and sustain growth, which is essential for the transition from heterotrophic to autotrophic growth. Greening of the cotyledons primarily involves the biosynthesis of chlorophyll in the chloroplasts. Chlorophyll biosynthesis is a multistep process, which starts with the conversion of glutamate to 5-aminolevulinic acid (5-ALA) via the activity of glutamyl-tRNA reductase, which eventually converts into protoporphyrin IX via the tetrapyrrole biosynthetic pathway (von Wettstein, 1991; Tanaka and Tanaka, 2007) These steps are similar to the biosynthesis of heme and

phytochromobilin. The first committed step towards chloroplast biosynthesis is when Mg-chelatase acts on protoporphyrin IX to form Mg-protoporphyrin IX which is further converted to protochlorophyllide (Pchlde) (Kobayashi and Masuda, 2016). In dark-grown seedling plastids exist as etioplasts, which accumulate protochlorophyllide. Upon light exposure, there is a transition of etioplast to chloroplast, which is catalyzed by protochlorophyllide oxidoreductase (POR) enzymes. The Pchlde pool must be stoichiometrically controlled, as upon light exposure excess protochlorophyllide can accumulate large amounts of reactive oxygen species (ROS), causing photooxidative damage or even cell death (Reinbothe et al., 1996; Wagner et al., 2004; Buhr et al., 2008).

Chlorophyll biosynthesis is tightly regulated at post-translational level and transcriptional level to avoid photooxidative stress (Matsumoto et al., 2004; Mochizuki et al., 2010; Kobayashi and Masuda, 2016; Zhang et al., 2022b). FLU (fluorescence) plays an important role during post translational regulation as it forms a protein complex with a subunit of the Mg-protoporphyrin IX monomethyl ester oxidative cyclase (CHL27), PORB, and PORC and is involved in the feedback control of glutamyl tRNA reductase (GluTR) by inhibiting 5-aminolevulinic acid (ALA) synthesis (Meskauskiene et al., 2001; op den Camp et al., 2003; Mochizuki et al., 2010; Kauss et al., 2012). Thus, dark-grown *fluorescence (flu)* mutants lead to rapid photobleaching due to excessive Pchlde accumulation. During transcriptional regulation, several transcription factors are involved that regulate the expression of photosynthesis-associated nuclear genes (*PhANGs*). PHYTOCHROME-INTERACTING FACTORS (PIFs) are known to be primarily involved in cotyledon greening by negatively regulating the expression of a number of tetrapyrrole biosynthetic genes including *CHLOROPHYLLIDE a OXYGENASE (CAO)*, *GLUTAMYL-tRNA REDUCTASE 1 (HEMA1)*, *GENOMES UNCOUPLED 4 (GUN4)*, and *GUN5* to repress chlorophyll biosynthesis. They also activate the transcription of ROS-responsive genes like *ASCORBATE PEROXIDASE 2 (APX2)* and *ZAT ZINC FINGER PROTEIN 10 (ZAT10)*, thereby enhancing ROS scavenging and preventing cell death during seedling de-etiolation (Monte et al., 2004; Stephenson et al., 2009). Dark grown *pif* mutants accumulate excessive Pchlde but low activity of POR enzymes causing photooxidative damage upon light exposure (Monte et al., 2004; Stephenson et al., 2009).

In light conditions, ELONGATED HYPOCOTYL5 (HY5), GOLDEN2-LIKE (GLK), GATA NITRATE-INDUCIBLE CARBON-METABOLISM-INVOLVED (GNC), CYTOKININ-RESPONSIVE GATA1 (CGA1)/GNC-LIKE (GNL), and MYB-related transcription factors (MYBS1/2) individually enhance *PhANG* expression, chlorophyll biosynthesis, and chloroplast development (Figure 2) (Lee et al., 2007; Waters et al., 2009; Wang et al., 2013; Hernández-Muñoz et al., 2024). BBX11 has been reported to regulate protochlorophyllide levels by acting downstream of PIF3 in the dark. Upon light exposure HY5 binds to the promoter of *BBX11* and activates it to promote photomorphogenesis (Job and Datta, 2021). Recently, BBX10 has also been reported for its role in cotyledon greening. In darkness it

inhibits the accumulation of protochlorophyllide which leads to reduced ROSs upon light irradiation ultimately promoting greening during de-etiolation. BBX10 directly interacts with PIF1 and enhances its biochemical activities toward target genes *GUN5* and *APX2* (Zhou et al., 2025). GLKs are acknowledged as the key regulators of chloroplast development and have been studied across multiple species. In *Arabidopsis thaliana*, GLK1 and GLK2 operate redundantly to induce the expression of photosynthesis-associated nuclear genes (*PhANGs*) by binding to their promoter regions under light. Under light or BR deficiency, *BRZ-INSENSITIVE-PALE GREEN 4 (BPG4)* expression is transcriptionally upregulated. It acts as a chloroplast homeostasis factor, which interacts with GLKs and suppresses their transcriptional activity to promote the expression of *PhANGs*, thereby causing a decrease in the amounts of chlorophylls and the size of light-harvesting complexes. *BPG4*-deficient mutants cause enhanced reactive oxygen species (ROS) generation and damage to photosynthetic activity under excessive/high intensity light conditions. PIFs are suggested to be involved in the transcriptional activation of *BPG4* in the light, but further research needs to be done for better understanding (Tachibana et al., 2024). In *Arabidopsis*, *BPG4* has 3 paralogs: *BPG4 HOMOLOGOUS GENE 1, 2, and 3*, which correspond to *BGH1*, *BGH2*, and *BGH3*, respectively. *BGH2* is accumulated under dark by transcriptional activation by PIFs, and it suppresses excessive proto chlorophyllide accumulation via interaction with GOLDEN2-LIKE 1 (GLK1) and GLK2 promoting cotyledon greening during de-etiolation (Figure 2) (Tachibana et al., 2025).

During seedling establishment, ethylene, which is a gaseous hormone, is triggered as a response to the mechanical pressure experienced by the seedlings. ETHYLENE-INSENSITIVE 3/1 (EIN3/EIL1) are key regulators of chlorophyll biosynthesis, which are regulated by ethylene via EIN2 and ETHYLENE-INSENSITIVE-BINDING F BOX PROTEIN 1/2 (EBF1/2). In the dark, EIN3 and EIL1 markedly repress accumulation of Pchlde and directly associate with the promoters of *PORA* and *PORB* to prevent cotyledons from photooxidative damage. Ethylene suppresses the activity of EBF1/EBF2 to stabilize EIN3 and activate ethylene responses. Upon light perception, active phyB directly associates with EIN3 and targets it to the E3 Ubiquitin ligase EBF1/2, which rapidly degrades it. EIN3 and PIF3 act interdependently in regulating the chloroplast development by inhibiting the transcription of most *LIGHT HARVESTING COMPLEX (LHC)* genes to repress chloroplast development. Recently, BBX32 has been identified as an important regulator that protects seedlings against severe photobleaching damage. Upon light perception, BBX32 directly interacts with EIN3, PIF3, and EBF1/2 and reduces the interactions of EIN3 and PIF3 with their E3 ligase EBF1/2, thus attenuating degradation (Wang et al., 2025). Also, BBX32 has been reported to enhance seedling soil emergence by enhancing PIF3 on *HLS1 (HOOKLESS1)* promoter (Ravindran et al., 2025). Taken together, while the molecular knowhow about cotyledon opening and greening has expanded we still need a better understanding of the whole process. We have summarized the identified molecular components regulating the early seedling

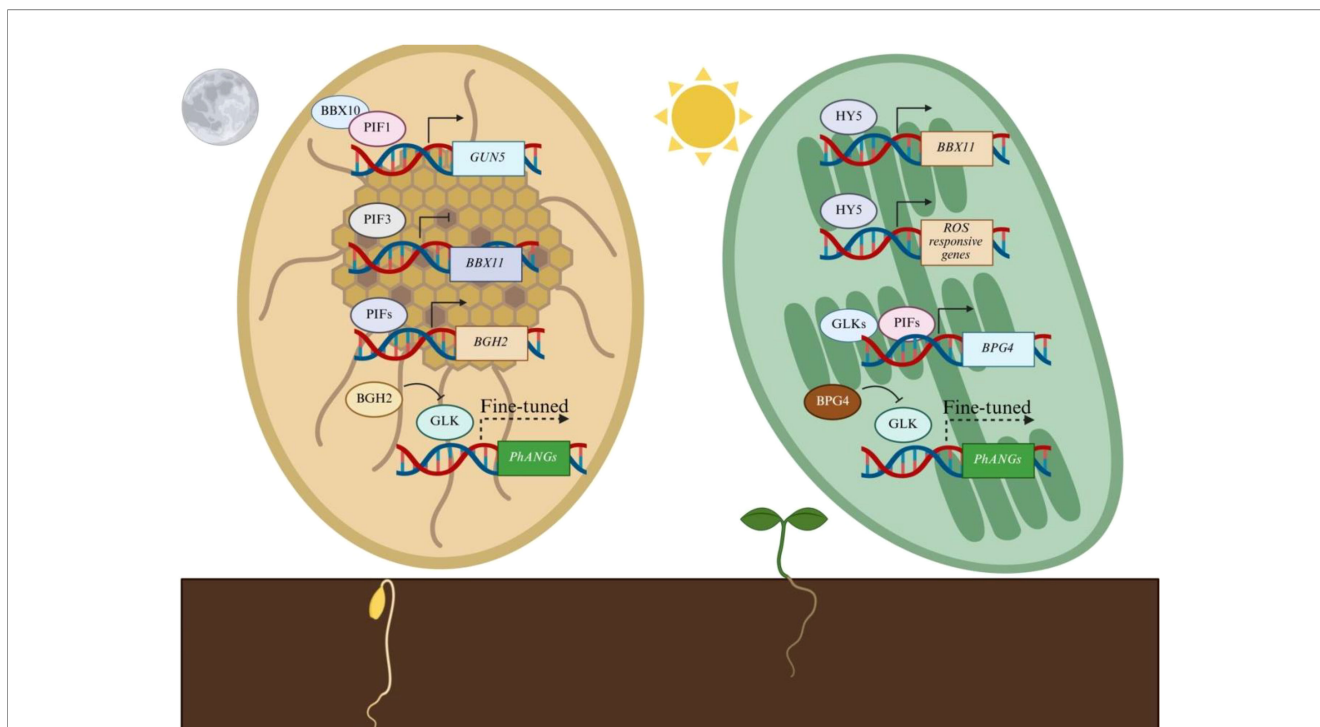


FIGURE 2

Model representing light regulated transcription factors involved in regulating the process of greening. PIFs (PHYTOCHROME INTERACTING FACTORS) and HY5 (ELONGATED HYPOCOTYL 5) antagonistically regulate protochlorophyllide accumulation under dark and light. BBX10 positively regulates greening by interacting with PIF1 and activating its binding on the promoter of GUN5 (*GENOME UNCOUPLED 5*) and APX2 (*ASCORBATE PEROXIDASE*). BBX11 on the contrary, represses greening. PIF3 binds to the promoter of *BBX11* under dark and represses its expression, while under light HY5 promotes BBX11 transcriptionally. In light *BPG4* (*BRZ-INSENSITIVE-PALE GREEN 4*) is activated, which maintains chloroplast homeostasis by inhibiting the expression of GLKs. PIFs also transcriptionally regulates BGH2 (*BPG4* HOMOLOGOUS GENE 2), BGH2 inhibits the binding of GLKs (*GOLDEN 2-LIKE*) on the promoters of PhANGs (Photosynthesis-Associated Nuclear Genes). Pointed arrows indicate positive regulation and blunt arrows indicate negative regulation.

development in *Arabidopsis* in Figure 3 depicting the possible connection and crosstalk between the signaling molecules regulated by light and phytohormones.

Light signaling in early land plants: *Chlamydomonas reinhardtii*

Chlamydomonas reinhardtii belongs to the division chlorophyta in Kingdom Plantae which serves as a unicellular model organism for studying photosynthesis, the development and function of cilia/flagella, and evolution of the complex structure of the chloroplast. Its haploid genome makes it an ideal candidate for genetic studies (Salomé and Merchant, 2019). Light signalling in *Chlamydomonas reinhardtii* is coordinated via a specialized organelle called the eyespot and an array of photoreceptors like channel rhodopsins, cryptochromes, UVR8 photoreceptors, phototropins. These help the algae to sense the photon stimulus and regulate its physiological and developmental processes in response to changes in light intensity and direction. *Chlamydomonas reinhardtii* can show either positive phototaxis (movement towards light source) or negative phototaxis (movement away from light source) and these movements are caused due to change in flagellar motion upon perception of light by eyespot (Hegemann, 2008). These changes in

flagellar motion are primarily caused due to plasma membrane depolarization mediated by influx of cations through channel rhodopsins (Hegemann, 2008).

Chlamydomonas reinhardtii possesses two channel rhodopsin proteins (CHR1 and CHR2) localised in the eyespot where they function as light gated ion channels mediating phototactic and photophobic responses (Hegemann, 2008). Both of them possess distinct spectral responsiveness with CHR1 showing maximum absorption in the green region of the spectrum and CHR2 shows maximum absorption in the blue region of spectrum (Hegemann, 2008). Activated CHR1 causes influx of cations leading to depolarisation causing light triggered changes in flagellar motion that enable directional movement in response to light (Hegemann, 2008). CHR2 similarly functions as a light gated cation selective ion channel that is involved in the photoreception specifically under low light intensities (Nagel et al., 2003). Moreover at higher intensities CHR1 gets degraded leaving CHR2 as a major contributor to photocurrent generation under these climatic conditions (Nagel et al., 2003).

Beyond the realm of visible light signalling, *Chlamydomonas reinhardtii* displays UVB signalling transduction mechanism which is conserved in accordance with complex life forms like angiosperms (Tilbrook et al., 2016). It possesses an UV-B sensing protein called Cr-UVR8 which contains crucial tryptophan residues

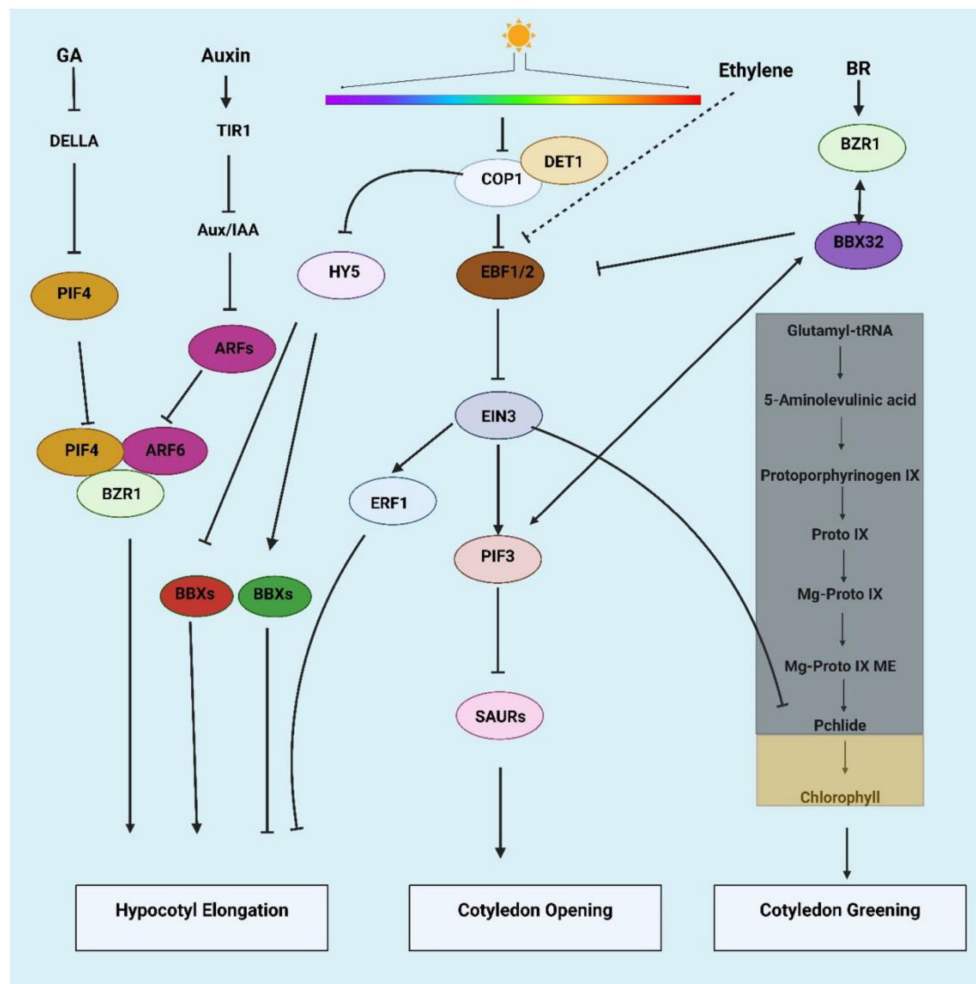


FIGURE 3

A comprehensive model showing molecular interactions between light and hormonal signalling pathways during early seedling development. EIN3-Binding F-Box Proteins 1 and 2 (EBF1/2) acts as the central convergence point for integrating light and ethylene signalling. EBF1/2 inhibit Ethylene-Insensitive 3 (EIN3) which regulates downstream genes to modulate hypocotyl elongation, cotyledon opening and greening. Brassinazole-Resistant 1 (BZR1) regulates hypocotyl elongation and cotyledon opening in brassinosteroid signaling. Elongated Hypocotyl 5 (HY5) is a light activated transcription factor which regulates certain BBXs either positively (green) or negatively (red) to regulate hypocotyl elongation. Phytochrome Interacting Factors (PIFs) are inhibited upon light perception which are known to interact with BZR1 and Auxin Responsive Factor 6 (ARF6) to regulate hypocotyl length. GA inhibits DELLA repressor which inhibits PIF4, PIF4 with BZR1 can promote the hypocotyl elongation.

for UV-B perception, similar to the AtUVR8. When exposed to UV-B, Cr-UVR8 monomerizes to interact with Cr-COP closely paralleling the UV-B signalling mechanism described for angiosperms (Tilbrook et al., 2016) (Figure 4). The ability of Cr-UVR8 to functionally complement UV-B mediated signaling in *Atuvr8* null mutants further supports the functional conservation (Tilbrook et al., 2016). In *Arabidopsis thaliana*, downstream to AtUVR8 and AtCOP1, AtHY5 acts as key transcription factor to promote UV responsive genes but the role of downstream components in the UV signalling pathway is not well explored in *Chlamydomonas* (Tilbrook et al., 2016).

Chlamydomonas reinhardtii possess both plant-like and animal-like cryptochromes and two DASH cryptochromes which makes it a suitable model for studying cryptochrome evolution and function (Müller et al., 2017). The gene CPH1 (CHLAMYDOMONAS PHOTOLYASE HOMOLOG 1) encodes

a putative plant-like cryptochrome protein of 867 amino acids with a predicted molecular mass of 91 kD (Small et al., 1995; Reisdorph and Small, 2004). This Cr-CPH1 gets accumulated under dark and as soon as it is exposed to blue or red light, it starts getting degraded which suggests a light dependent regulation of CrCPH1 (Reisdorph and Small, 2004). Functionally CrCPH1 is shown to be a positive regulator of zygote germination but a negative regulator of mating indicating its dual role in the sexual life cycle (Müller et al., 2017). On the other hand, aCRY (an animal-like cryptochrome of *Chlamydomonas reinhardtii*) shows broad spectral responsiveness as it can respond to more than one wavelength, such as blue and red light (Beel et al., 2012). Interestingly, aCRY can exist in three redox states, a feature that might be responsible for its ability to respond to multiple wavelengths. Expression of aCRY is found to be dynamically regulated throughout the life cycle playing an important role in sexual reproduction. It positively influences the

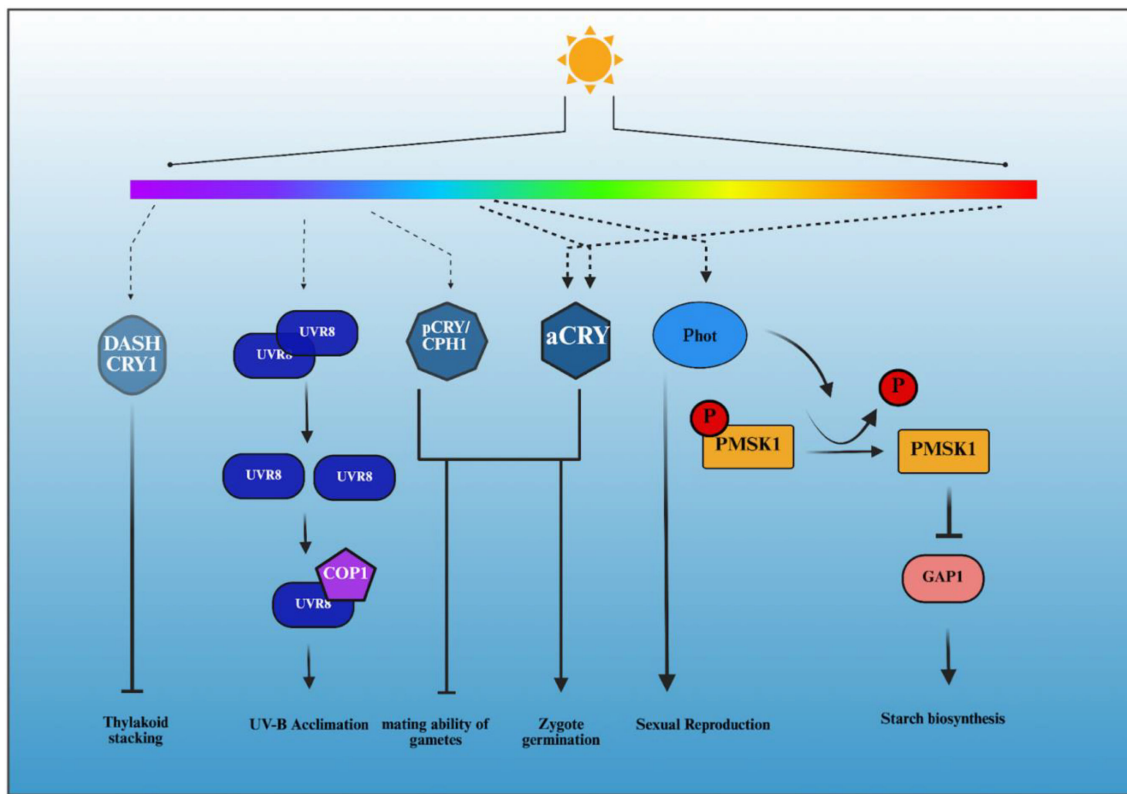


FIGURE 4

Light signalling in *Chlamydomonas reinhardtii*. DASH-CRY1 (CRYPTOCHROME-DROSOPHILA, ARABIDOPSIS, SYNECHOCYTIS, HUMAN) perceives UV and inhibits thylakoid stacking. Upon perception of UV, CrUVR8 (UV-B RESISTANCE LOCUS 8) gets monomerised and interacts with CrCOP1. This module promotes UV-B acclimatization. pCRY/CPH1 (PLANT-LIKE CRYPTOCHROME PHOTORECEPTOR) and aCRY (ANIMAL-LIKE CRYPTOCHROME RECEPTOR) perceive blue light and inhibit mating mobility and promote zygote germination. aCRY also perceives red light. Phot (PHOTOTROPIN) perceives blue light and dephosphorylates PMSK1 (PHOTOTROPIN-MEDIATED SIGNALING KINASE 1). Dephosphorylated PMSK1 inhibits GAP1 (GLYCERALDEHYDE-3-PHOSPHATE DEHYDROGENA) which promotes starch biosynthesis. Pointed arrows indicate positive regulation and blunt arrows indicate negative regulation. Dotted arrows indicate light perception by respective photoreceptors.

germination of the alga, during which the zygote undergoes meiosis, akin to the regulation by blue light receptors such as phototropin and plant cryptochrome (pCRY). Nonetheless, aCRY functions alongside pCRY as a negative regulator for both mating capability and mating persistence, contrasting with the role of phototropin in these processes (Zou et al., 2017) (Figure 4). aCRY role has also been found in DNA repair (Franz et al., 2018).

Out of the two CrCRY-DASH proteins identified in *C. reinhardtii* CRY-DASH1 shows similarity to DASH-cryptochrome subfamily members like CrCRY3 of *Arabidopsis* (Rredhi et al., 2021). It is localised in the plastid and does maximum absorption in the UV-A range with MTHF(5,10-methenyltetrahydrofolate) serving as its chromophore. Functional analysis of *cry-dash1* mutants show increased stacking of thylakoids and increased levels of chlorophyll and carotenoid suggesting a probable role in preventing excess grana formation and regulating pigmentation (Rredhi et al., 2021).

Chlamydomonas reinhardtii contains a single phototropin gene *CrPhot* which shows high sequence similarity with arabidopsis *PHOT1* and *PHOT2* consisting of two LIGHT, OXYGEN and VOLTAGE domains (LOVE1 and LOVE2) at its N-terminal and a ser/thr kinase domain at C-terminal (Huang et al., 2002). CrPhot

is important for sexual reproduction in *Chlamydomonas reinhardtii*. Its life cycle involves germination of a zygote to give rise to four independent vegetative cells. These vegetative cells develop as pre-gametes upon nitrogen starvation under dark. Further, these cells turn into mature gametes upon blue light illumination, indicating the importance of blue light in sexual reproduction. These gametes lose their mating competence under dark but this is photo-reversible. CrPhot is essential for all these three processes: gamete formation, the maintenance of mating competence in gametes, and zygote germination. Knock down of *CrPhot* results in defects in all these three events. Taken together CrPhot has a pivotal role in *Chlamydomonas reinhardtii* sexual reproduction. *Chlamydomonas reinhardtii* accumulates starch during the day, and breaks it down at night. Light regulates the starch metabolism as well. In a recent study, blue light mediated starch metabolism has been uncovered. PHOTOTROPIN-MEDIATED SIGNALING KINASE 1 (PMSK1) in its phosphorylated state promotes GLYCERALDEHYDE- 3-PHOSPHATE DEHYDROGENASE (GAP1) which in turn leads to starch accumulation (Figure 4). Blue light activated CrPhot dephosphorylates the PMSK1 which further inhibits GAP1 to reduce the starch accumulation. Hence the *crphot* mutants are

hyper starch accumulators (Yuan et al., 2025). CrPhot has its own mark in dynamic maintenance of the eyespot size. Dark increases the eyespot size whereas light decreases it. The knockout strain lacking *CrPhot* has a larger eyespot irrespective of presence or absence of light. CrPhot regulates channelrhodopsin-1(ChR1) levels which is a key receptor in the eye spot for tuning photo-taxis (Trippens et al., 2012). CrPhot localises in the axoneme of flagella to serve as a cargo mediating the intra-flagellar transport (Huang et al., 2004). Taken together the light signalling components for UVB signalling, cryptochromes, and phototropins are well conserved in *Chlamydomonas* but the phytochromes are not reported yet. Table 1 contains the light signaling genes characterised in *Chlamydomonas*. Apart from these photoreceptors, *Chlamydomonas* also possess channel rhodopsins to facilitate its locomotion towards the light.

Light signaling mechanisms regulating growth and development of *Marchantia polymorpha*

Marchantia polymorpha is considered to be an ideal model system to study the signaling mechanisms among the thallophytes. Sequenced genome of Tak-1 contains 8 pairs of autosomes and a single X/Y sex chromosome. Its haploid dominant phase in the lifecycle is one of the greatest advantages of studying *Marchantia*. *Marchantia polymorpha* has only one copy for most of the light signaling factors studied in *Arabidopsis* like a single copy for cryptochrome (MpCRY), phytochrome (MpPHY) and for UVR8 (MpUVR8) (Inoue et al., 2016; Zhang et al., 2022; Liang et al., 2025). MpCRY protein forms homodimers under blue light (Figure 5). MpCRY inhibits ABA signaling genes that inhibit gemma dormancy in blue light (Figure 5) (Liao et al., 2023). Blue light also promotes several secondary metabolites accumulation in *Marchantia* by enhancing the expression of chalcone synthase (*CHS*), cellulose synthase (*CELL*), and L-ascorbate peroxidase (*APOX3*) (Zhang et al., 2022a). Downstream to MpCRY, the

MpCOP1-MpSPA complex acts as a central regulatory network for skotomorphogenic responses (Figure 5). *MpSPA* knockout mutants exhibit asymmetrical thallus growth. *MpCRY* knockout mutant mimics the *MpSPA* knockout mutant phenotype with respect to thallus asymmetric growth. MpSPA interacts with MpCRY in a blue light independent way whereas MpSPA interacts with MpCOP1 in a blue light dependent way. MpCOP1 along with MpSPA ubiquitinates MpHY5 (Figure 5). In *Arabidopsis*, CRY1 and CRY2 inhibit COP1-SPA mediated ubiquitination of HY5, whereas in *Marchantia*, MpCRY does not regulate the MpCOP1-MpSPA mediated MpHY5 ubiquitination (Figure 5). This suggests that the COP1/SPA mediated HY5 regulation is conserved in *Marchantia polymorpha* but MpCRY does not inhibit the MpHY5 ubiquitination under blue light (Figure 5) (Zhang et al., 2022a). In *Marchantia*, MpHY5 also regulates chloroplast development although there is still a lot to be explored (Yelina et al., 2024). *Marchantia* perceives blue light by phototropins (MpPHOT) as well. Phototropins are known to regulate chloroplast movement in angiosperms. Under low blue light, phototropins enhance chloroplast accumulation to maximise the photosynthesis while high intensity blue light promotes chloroplast avoidance for photoprotection. This mechanism is conserved in *Marchantia* which has a single copy of the phototropin gene, *MpPHOT*. *MpPHOT* knock out mutants don't show any chloroplast movements. MpPHOT successfully rescued chloroplast movement defects in fern *Adiantum capillus-veneris* and also the angiosperm *Arabidopsis thaliana*. In *Marchantia*, MpPHOT undergoes cis-autophosphorylation that leads to the chloroplast accumulation under low blue light; whereas it undergoes both cis-autophosphorylation and trans-autophosphorylation ultimately leading to chloroplast avoidance response under high light and cold stress (Komatsu et al., 2014; Noguchi et al., 2025).

MpPHY5 regulates only a few genes in the UV-B signaling pathway in *Marchantia polymorpha*, whereas in *Arabidopsis* HY5/HYH module regulate the majority of UV-B signaling genes (Liang et al., 2025). *Marchantia polymorpha* possesses a single ortholog of

TABLE 1 Light signalling factors in *Chlamydomonas reinhardtii*.

Photoreceptors/light perception apparatus	Light sensitivity	Identified functions	References
Channelrhodopsin-1 (ChR1)	Blue/Green	Phototaxis and photophobic responses	(Hegemann, 2008)
Channelrhodopsin-2 (ChR2)	Blue light	Phototaxis and photophobic responses	(Nagel et al., 2003)
Phototropin (PHOT)	Blue light	Sexual reproduction, starch biosynthesis, phototaxis	(Huang et al., 2002; Trippens et al., 2012; Yuan et al., 2025)
Animal like Cryptochrome (aCRY)	Blue/Red light/Yellow light	Positive regulation zygote germination and negative regulation of mating. Plays role in DNA repair.	(Beel et al., 2012; Zou et al., 2017; Franz et al., 2018)
Cryptochrome DASH1 (CRY-DASH)	Blue/UV-A light	Balancing photosynthetic machinery and detecting UV-A light.	(Rredhi et al., 2021)
Plant like Cryptochrome (pCRY)	Blue light	Circadian regulation. Positive regulation of zygote germination and negative regulation of mating.	(Reisdorph and Small, 2004; Immeln et al., 2007; Müller et al., 2017)
CrUVR8	UV-B light	UV-B stress response and acclimatization.	(Tilbrook et al., 2016)

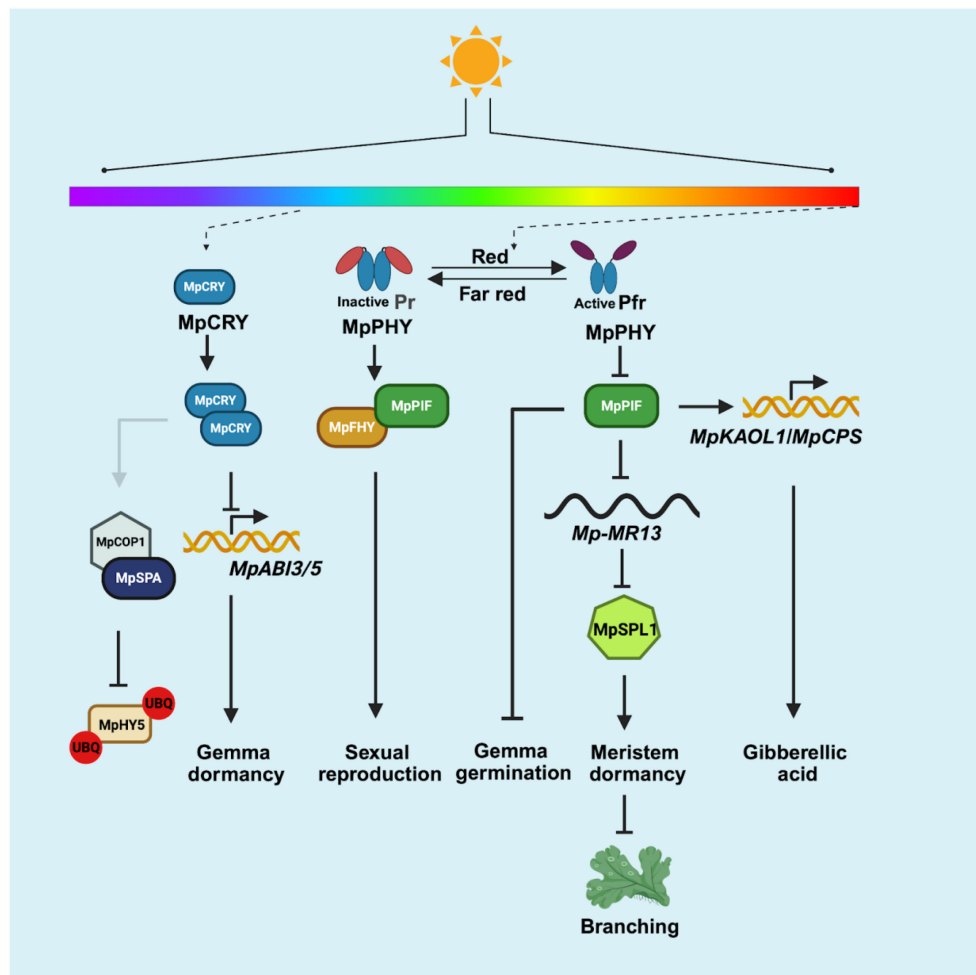


FIGURE 5

Light signalling in *Marchantia polymorpha*. The blue light receptor MpCRYs get dimerised under blue light. The shaded arrow indicates that the MpCRY (CRYPTOCHROME) does not rescue MpHY5 from MpCOP1/MpSPA mediated degradation. MpCRY inhibits the expression of MpABI3 (ABA INSENSITIVE 3)/MpABI5 (ABA INSENSITIVE 5) to release gemma dormancy. Red light is perceived by the MpPHY (PHYTOCHROME). MpPHY switches from Pr to Pfr form upon red light irradiation. The Pr form of MpPHY promotes MpPIF (PHYTOCHROME INTERACTING FACTOR)-MpPHY (FAR-RED ELONGATED HYPOCOTYL1) dimerization which activates sexual reproduction. Pfr form of MpPHY inactivates MpPIF to promote gemma germination. MpPIF inhibits Mp-MR13 to activate MpSPL1 (Clade III SQUAMOSA PROMOTER BINDING PROTEIN-LIKE) which promotes meristem dormancy to regulate thalli branching. Also, MpPIF promotes GA biosynthesis by activating MpCPS (COPALYL DIPHOSPHATE SYNTHASE), MpKAOL1 (KAURENOIC ACID OXIDASE-LIKE PROTEIN). Pointed arrows indicate positive regulation and blunt arrows indicate negative regulation.

AtUVR8 i.e. MpUVR8. MpUVR8 also forms UV-B mediated homodimers similar to AtUVR8. MpUVR8 monomers interact with MpCOP1 in nuclei under UV-B irradiation. MpRUP favours MpUVR8 dimerization to inhibit the signaling. Interestingly, *Mpspa* mutants are hyper-responsive to UV-B, indicating MpSPA act divergently from *Arabidopsis* (Liang et al., 2025). Upon exposure to the red or far-red (R/FR) light, *Marchantia* phytochrome (MpPHY) shows photo-reversibility between P_r and P_{fr} forms (Figure 5). In *Marchantia* the gemma germination is red light dependent and MpPHY is required for the gemma germination (Inoue et al., 2016, 2019) (Figure 5). Constitutive expression of *MpPHY* enhances the gemmae germination. Downstream to MpPHY, there is only a single copy of PIF, MpPIF. MpPIF acts as a negative factor and inhibits germination and under light MpPHY causes the degradation of MpPHY, similar to that of *Arabidopsis* (Figure 5) (Inoue et al., 2019). This indicates the

PHY-PIF module is functionally conserved in the liverworts. MpPIF also inhibits the expression of light responsive genes e.g. - *LIGHT-HARVESTING CHLOROPHYLL A/B BINDING PROTEIN* (*MpLHCB*) and *PROTOCHLOROPHYLLIDE OXIDOREDUCTASE* (*MpPOR*) in *Marchantia* (Inoue et al., 2016).

The thallus architecture of *Marchantia* is tightly regulated by its meristem activity. The active meristem develops dichotomous branching in *Marchantia*. Interestingly, the light signalling components especially MpPIF signals the meristem activity to control overall architecture of *Marchantia*. Clade III SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL) transcription factor MpSPL1 promotes meristem dormancy to orchestrate the apical branching in liverworts (Streubel et al., 2023) (Figure 5). A liverwort-specific *Mpo-MR13*, miRNA inhibits MpSPL1. Mp-MR13 is further negatively controlled by the MpPIF (Figure 5). Under white light, lower levels of MpPIF leads to the

accumulation of *Mp-MR13* which strongly inhibits MpSPL1 that breaks the meristem dormancy and promotes branching (Streubel et al., 2023) (Figure 5). Under shade conditions, MpPIF levels are up and strongly inhibits *MP-MR13* which favours the accumulation of MpSPL1. This promotes meristem dormancy and inhibits branching. Hence, light modulates meristem dormancy to control MpPHY-MpPIF mediated branching through *Mpo-MR-13* and MpSPL1 cascade (Streubel et al., 2023).

The MpPHY-MpPIF module is also required for the FR responses. One of such FR response is, MpPIF positively regulates GA biosynthetic genes like (*MpCPS*) *COPALYL DIPHOSPHATE SYNTHASE*, (*MpKAOL1*) *KAURENOIC ACID OXIDASE-LIKE PROTEIN 1* under FR enriched conditions (Sun et al., 2023). MpPIF also interacts with a major gibberellic acid signaling inhibitor MpDELLA to regulate growth under stress. Oxidative stress induces the accumulation of MpDELLA that inhibits MpPIF to promote sexual reproduction. MpPIF also favours gemma dormancy under stress to halt the growth. It inhibits production of the flavonoids which are required for stress tolerance (Hernández-García et al., 2021). Additionally, MpPHY regulates chloroplast development under FR enriched conditions. It promotes agranal chloroplasts with starch content which results in reduction in photosynthetic efficiency of the thalli (Pashkovskiy et al., 2023). Another FR-HIR (FAR RED-HIGH IRRADIANCE RESPONSE) response is gametangiophore formation, which is a sign of induction of sexual reproduction. Apart from its canonical role, MpPHY along with MpFH1 (FAR-RED ELONGATED HYPOCOTYL1) regulate induction of the sexual reproduction program in *Marchantia*. Knockout of MpPIF, abolished the FR-HIR-dependent gametangiophore formation, while its overexpression enhances this response. This indicates that a single MpPHY mediates both LFR and FR-HIR response (Inoue et al., 2019).

During spore germination, light promotes anisotropic division in early meristem to build auxin minima in the upper cell mass. This favours the prothallus development. In the absence of light, early cell mass undergoes isotropic cell division which disrupts the lower auxin minimum in upper cell mass which ultimately aborts the growth (Wallner et al., 2025). Further investigations to uncover the involvement of any specific monochromatic light in the vegetative and reproductive development are required. We have concisely mentioned the light signalling factors and their involvement in the molecular mechanisms regulating growth and development in *Marchantia* in Table 2.

Light signaling components regulating growth and development in *Physcomitrium patens*

Physcomitrium patens is one of the well-studied model Bryophytes. Its life cycle oscillates between dominant haploid gametophytic phase and a diploid sporophytic stage. They undergo various developmental changes during their life cycle which are light regulated. *P. patens* has phytochromes and

cryptochromes whose amino acid sequences are highly homologous to their counterparts in *A. thaliana*, suggesting conserved light-sensing mechanisms in the plant kingdom (Yamawaki et al., 2011). It has two orthologs of cryptochrome e.g.- *PpCRY1a* and *PpCRY1b*, seven orthologs of phytochrome (*PpPHY1*, *PpPHY2*, *PpPHY3*, *PpPHY4* and *PpPHY5a/b/c*), nine orthologs of COP1 *PpCOP1a/b/c/d/e/ff/g/h/i*, two orthologs of SPA1 (*PpSPAa* and *PpSPAb*) and two orthologs of HY5 i.e. *PpHY5a* and *PpHY5b* (Yamawaki et al., 2011).

Phytochromes in *P. patens* are grouped into 3 clades i.e. *PHY1/3*, *PHY2/4* and *PHY5a/b/c* (Yuan et al., 2023). Phytochromes regulate various aspects of development in *P. patens* such as and protonemal branching in juvenile phase and gametophore growth, induction in later stages of development (Yuan et al., 2023). PpPHYs show sensitivity to both red (20uM/m²sec) and blue (12uM/m²sec) light (Yuan et al., 2023). In the wild type (Grandsen) moss grown under blue and white light, the number of gametophores is more and protonemal filaments are green. However, phytochrome septuple mutant shows decrease in number of gametophores and a brown appearance (Yuan et al., 2023). The *Phy5abc* triple mutants show reduced induction of gametophores while *Ppphy1234* quadruple mutants showed a reduction in protonemata growth under blue light (Yuan et al., 2023). These suggest a crucial role of phytochromes in gametophore development and chlorophyll biosynthesis under blue light. *PpPHY5abc* clade is primarily responsible for mediating red light triggered responses (Figure 6) as the mutants for the other phytochromes i.e. *Ppphy1/3* and *Ppphy2/4* do not show any phenotype under red light conditions. But in the *PpPHY5abc* mutants reduction in the number of gametophores induced were low, protonemal branching is also inhibited and the chloronema to caulonema transition hampered as well under red light, suggesting their major role in perception of red light (Yuan et al., 2023). Among the members of PpPHY5 clade, PpPHY5a is the central player and required for the red and blue light triggered responses, studies carried out with single and double mutants showed that PpPHY5a/b/c play a redundant role (Yuan et al., 2023). PHY1/3 are responsible for perceiving far-red light (Figure 6) and regulate the branching of protonemata and induction of gametophore under far-red light (Yuan et al., 2023). *Physcomitrium patens* respond to the canopy shade conditions as well, by elongating the gametophores. PpPHY1/2/3/4 play a redundant role in sensing low red: far-red ratio in light and elongating the gametophores. The nuclear localisation of the PpPHYs are conserved in *Physcomitrium patens* as PpPHY1/2/3/4 get localised to the nuclei upon exposure to light, while PpPHY1 requires FAR-RED ELONGATED HYPOCOTYL 1 (PpFH1) for getting localised to the nucleus (Possart and Hiltbrunner, 2013) (Figure 6). In the perspective of evolutionary conserved roles PpPHYs stand out as they respond to the blue light irradiations while their role in regulating protonema growth and branching, chloronema to caulonema transition as well as responsiveness to the shade conditions are well conserved in other organisms. PpPHYs are also responsible for red light mediated movement in *Physcomitrium patens* (Kasahara et al., 2004).

In *Physcomitrium patens*, there are two orthologs of AtCRYs i.e. *PpCRY1a* and *PpCRY1b*. Both PpCRY1a and PpCRY1b contain

TABLE 2 Light signaling factors and their identified roles in *Physcomitrium* and *Marchantia*.

Light signalling factor	Orthologs found in <i>Physcomitrium patens</i>	Functional roles in <i>Physcomitrium patens</i>	References	Orthologs found in <i>Marchantia polymorpha</i>	Functional roles in <i>Marchantia polymorpha</i>	References
Phytochrome	<i>PpPHY1-4</i> , <i>PpPHYa</i> , <i>PpPHYb</i> , <i>PpPHYc</i> (7 orthologs)	PHY1/3 clade phytochromes act as primary far-red light receptors, while PHY5 clade phytochromes are the primary red-light receptors. PHY2/4 clade phytochromes have functions in both red and far-red light	(Yuan et al., 2023)	<i>Mpphy</i>	Gemma germination, sexual reproduction, gametangiophore development, agranal chloroplast development	(Inoue et al., 2019; Hernández-García et al., 2021; Pashkovskiy et al., 2023; Streubel et al., 2023)
Cryptochrome	<i>PpCRY1a</i> and <i>PpCRY1b</i>	Induction of side branching on protonema and gametophore induction and development	(Imaizumi et al., 2002)	<i>MpCRY</i>	Negatively regulates gemma dormancy through ABA signalling, promotes secondary metabolites, regulates thalli structure	(Zhang et al., 2022a; Liao et al., 2023),
UVR8	<i>PpUVR8.1</i> and <i>PpUVR8.2</i>	Both of the proteins complement the impaired UV-B response of the <i>uvr8-1</i> mutant as observed in transgenic studies with <i>Arabidopsis</i> . Mediate HY5 transcript expression and Chalcone synthase (CHS) protein accumulation in response to UV-B	(Soriano et al., 2018)	<i>MpUVR8</i>	UV-B stress tolerance	(Liang et al., 2025)
HY5 (elongated hypocotyl 5)	<i>PpHY5a</i> <i>PpHY5b</i>	Regulator of photomorphogenesis, caulonemata development and gametophore development	(Yamawaki et al., 2011)	<i>MpHY5</i>	Chloroplast development through MpGLK, UV protection	(Yelina et al., 2024; Liang et al., 2025)
COPI (constitutive photomorphogenic 1)	<i>Ppcop1a-I</i> (9 orthologs)	Gametophore elongation. Protonemata branching. Suppression of chlorophyll accumulation in darkness	(Kreiss et al., 2023)	<i>MpCOPI</i>	Regulates thalli structure, promotes gemma germination, negatively regulate photomorphogenesis, negatively regulates UV tolerance	(Zhang et al., 2022a; Liang et al., 2025)
SPA (SUPPRESSOR OF PHA-105)	<i>PpSPAa</i> <i>PpSPAb</i>	Gametophore elongation. Protonemata branching. Negatively regulates protonemal growth in light. Suppression of chlorophyll accumulation in darkness	(Kreiss et al., 2023)	<i>MpSPA</i>	Symmetry of the thalli, repressor of photomorphogenesis, negatively regulates UV tolerance	(Zhang et al., 2022a; Liang et al., 2025)
PIF (Phytochrome interacting factor)	<i>PpPIF1-4</i> (4 orthologs)	Activate G-box containing promoters and expression of light regulated genes	(Xu et al., 2020)	<i>MpPIF</i>	Promotes dichotomous branching for thalli architecture, promotes sexual reproduction, promotes gemma dormancy, regulates thalli branching	(Inoue et al., 2019; Hernández-García et al., 2021; Streubel et al., 2023)

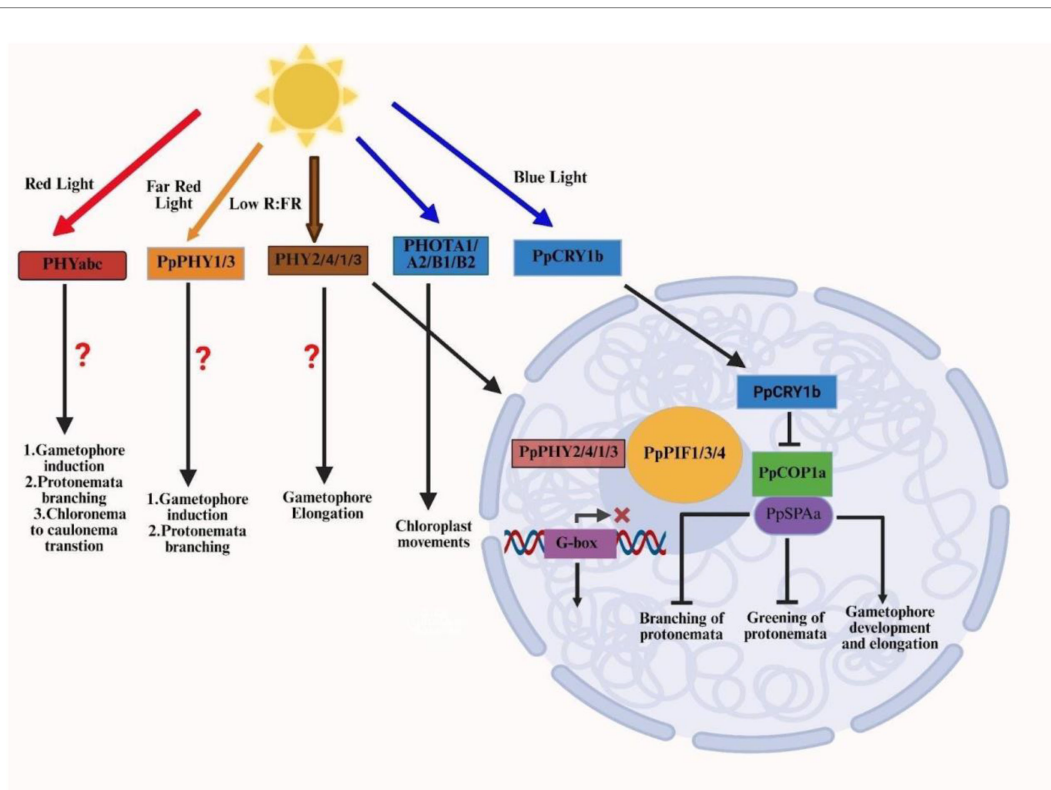


FIGURE 6

Light signaling mechanism in *Physcomitrium patens*. PpPHYabc (PHYTOCHROMEabc) photoreceptors mainly perceive red light and regulate gametophore induction, protonemata branching and chloronema to caulonema transition by an unidentified pathway indicated by (?). PpPHY1/3 (PHYTOCHROME 1/3) perceive the far-red light and regulate gametophore induction and protonemata branching, while the pathway unknown marked by (?). PHY1/3 and PHY2/4 (PHYTOCHROME2/4) sense low red:far red ratio and regulate gametophore elongation. PHY1/3/2/4 are localised to the nucleus upon light exposure, where they interact with PpPIF1/3/4 (PHYTOCHROME INTERACTING FACTORS 1/3/4) which prevents the transcriptional activity of PpPIF1/3/4. PpPHOTA1/A2/B1/B2 (PHOTOTROPINS) perceive blue light and regulate chloroplast movements. PpCRY1b (CRYPTOCHROME b) perceives blue light and gets localised to the nucleus and inhibits PpCOP1a/SPAa (CONSTITUTIVE PHOTOMORPHOGENIC1a/SUPPRESSOR OF PHY-105) to regulate greening & branching of protonemata and gametophore development.

nuclear localization signals (NLS) at their C-terminus and localise to the nucleus (Imaizumi et al., 2002) (Figure 6). PpCRY1a and PpCRY1b play redundant role in regulating certain developmental steps throughout the moss life cycle, including induction of side branching on protonema as well as the gametophore induction and development (Imaizumi et al., 2002). PpCRYs inhibit the auxin signaling leading to the regulation of developmental steps (Imaizumi et al., 2002). PpCrys negatively regulate SQUAMOSA PROMOTER BINDING PROTEIN (SBP) domain transcription factors *PpSBP1* and *PpSBP4*, which act as negative regulators of side branch formation in the protonema.

Four orthologs of AtPHOTs are identified in *Physcomitrium patens* and are grouped into two categories *PpPHOTA1*, *PpPHOTA2* and *PpPHOTB1*, *PpPHOTB2* on the basis of their amino acid sequences (Kasahara et al., 2004) (Figure 6). *PpPHOTA2*, *PpPHOTB1* and *PpPHOTB2* are expressed under both light and dark conditions. Expression of *PpPHOTA1* is specific to blue light illumination and gets inhibited under dark (Kasahara et al., 2004). *PpphotA2-1* mutants lack the chloroplast avoidance movement in the basal cells of protonema while the tip cells of protonema lacked chloroplast movement in *PpphotA1PpphotA2-1*, suggesting that the group PpPHOTA is

responsible for mediating photo avoidance response under blue light and are the functional ortholog of AtPHOT2 (Kasahara et al., 2004). At higher fluence rates *photB1B2* double mutants showed avoidance response indicating a functional redundancy (Kasahara et al., 2004). Phototropins also have a role in mediating phytochrome dependent chloroplast movements as *PpphotA2PpphotB1PpphotB2* triple mutants lack red light driven avoidance and accumulation response (Kasahara et al., 2004). Since PpPHY5abc are mainly responding to red light, it is speculated that PpPHOTA2, PpPHOTB1 and PpPHOTB2 are downstream to unexplored pathway involving PHYabc.

The two orthologs of HY5 in *Physcomitrium patens* i.e. PpHY5a and PpHY5b play crucial role in caulonemal cells development under light and dark conditions as the double mutants for *PpHY5a/b* are defective in caulonemal development (Yamawaki et al., 2011). Examination of diurnal transcriptional profiles revealed that expression of *PpHY5a* was light inducible, and it also showed strong induction when exposed to red and blue light after a brief incubation in dark (Yamawaki et al., 2011). Although both the orthologs are share their amino acid sequence similarity, but differ in terms of expression upon exposure to light. This suggests *PpHY5a* is more important for light signaling. Overexpressing

PpPHY5a in *A. thaliana* recovered the elongated hypocotyl phenotype of *Athy5* mutants suggesting functional redundancy and evolutionary conservation between *AtHY5* and *PpPHY5a*. Further studies can unravel the signaling mechanism connecting *PpPHY5* and *PpPHYs* as well as *PpCRYs*.

(Kreiss et al., 2023) COP1 orthologs in *Physcomitrium* (*PpCOP1a/b/c/d/e/f/g/h/i*) share approximately 54-64% sequence similarity with *AtCOP1* and have at least one ring finger motif, coiled coiled domain and WD40 repeat domain. Out of the 9 orthologs *COP1a* is the closest ortholog of *AtCOP1* (Ranjan et al., 2014). *PpCOP1a* is only able to partially rescue the constitutive photomorphogenic phenotype shown by *Atcop1-4* (Ranjan et al., 2014). The phenotype of *PpCOP1* nonuple mutants resembles that of *Ppspa* mutants (Kreiss et al., 2023). Most importantly, both mutants produce green chloroplasts in complete darkness. They also exhibit dwarfed gametophores, disturbed branching of protonemata under different light conditions. *PpCOP1* and *PpSPA* proteins form a complex and they interact via their WD repeat domains, also both show interaction with *PpCRY1b* under blue light (Kreiss et al., 2023). This suggests that *PpCOP1/PpSPA* complex regulates various developmental and physiological aspects in *Physcomitrium patens* such as branching and greening of protonema and gametophore development in blue light dependent manner downstream to *CRY1b* (Figure 6). This resembles the interaction of *AtSPA1* with *AtCRY1* (Lian et al., 2011). *PpCOP1* nonuple mutants continued normal gametophore growth in dark and grew to a larger size than wildtype with leaflets that were slightly expanded than wildtype and *Ppspa* mutant (Kreiss et al., 2023). RNA-sequencing (RNA-seq) analysis of wild-type, *PpCOP1_9x*, and *Ppspa_ab* mutant grown in darkness or subjected to 24 hours of white light indicated that *PpCOP1* and *PpSPA* repress light-responsive genes in darkness. However, light-regulated gene expression in *PpCOP1* and *Ppspa* is only partially constitutive, suggesting that *PpCOP1* and *PpSPA* proteins may not be the sole repressor of light-responsive genes in darkness (Kreiss et al., 2023).

The predicted domain structures of *Physcomitrium* SPA proteins are similar to SPA proteins in *Arabidopsis*. They both contain an N-terminal kinase-like domain, a coiled-coil domain, and seven WD40-repeats. Both *PpSPAa* and *PpSPAb* show similarity to *AtSPA1* (Ranjan et al., 2014). However, *PpSPAb* gene driven by *AtSPA1* and *AtSPA4* promoters failed to rescue the phenotype of *Atspa1/3/4* triple mutant and *Atspa1/2/3* triple mutants (Ranjan et al., 2014). *PpSPAa* and *PpSPAb* double mutants develop smaller gametophores than wildtype while *PpSPAa* single mutants also show reduction in the length of the gametophores (Artz et al., 2019). This suggests that *PpSPA* genes contribute to gametophore development redundantly with *PpSPAa* being the major contributor as the mutants of *PpSPAb* exhibited insignificant dwarfing of gametophores. In *Ppspaa/b* double mutants, the leaflet formation is impaired hence show an etiolated phenotype which is strikingly different from *spaQ* which shows constitutive photomorphogenesis. The protonema grows faster in *Ppspaa/b* double mutant, suggesting that *PpSPA* genes negatively regulate protonemal growth (Artz et al., 2019). Transcriptomic analysis carried out in *Ppspaa/b* background for 3

strongly light regulated genes *PpPOR*, *PpFNR* and *PpFEDa* also confirmed that partial constitutive light signaling prevails in *Ppspa* double mutants which can be due to the action of COP1 orthologs in *P. patens* (Artz et al., 2019).

Physcomitrium patens contains four orthologs for PIFs named *PpPIF1/2/3/4* (Possart et al., 2017). There exist some significant variations in the *PpPIFs* for motif-dependent PHY interaction, similar to *AtPIFs* in terms of protein domain structure, molecular characteristics, and physiological consequences (Possart et al., 2017). *Physcomitrium patens* contains potential PIF homologues and they complement the constitutively photomorphogenic phenotype of the *pifQ* mutant in *Arabidopsis* (Xu et al., 2020). *PpPIFs* have a function in the expression of light-regulated genes, similar to PIFs in *Arabidopsis thaliana*. *PpPIF1/3/4* interact with *PpPHY1/3/2/4* in a light dependent manner suggesting that the function of PIFs in phytochrome downstream signaling might be conserved in land plants (Possart et al., 2017). This interaction prevents *PpPIF* mediated transcriptional regulation but. On analyzing the gametophore induction and development in different *Pppif* mutants, no significant deviation from the wild type was observed (Xu et al., 2020). These genes are down regulated in both wild-type and mutant under continuous white light conditions. This suggests that *PpPIFs* have discrete roles to play in light mediated responses under specific conditions. We have concisely mentioned all the light signalling factors in *Physcomitrium* in Table 2. A recent report identifies that blue light facilitates the regeneration in *P. patens*, this cellular reprogramming is mediated through SHMT1, which accumulate more under bluelight (Zhao et al., 2025). Though the photoreceptors, and their downstream components are identified but there exist a few non canonical functions such as both red and blue light perception by *PpPHYs*, red light mediated chloroplast movement and etiolated phenotypes of *Ppspaa/b* mutants. However further studies can reveal the complete understanding of the mechanisms.

Concluding remarks

Light is one of the external cues regulating growth and development of terrestrial plants. While the light signaling mechanism regulating early plant development is well studied in *Arabidopsis thaliana*, its role in early plant development is increasingly being investigated. In *Arabidopsis* the activation of the light signaling takes place by the light perception by the photoreceptors. The downstream signaling cascades involve PIFs, HY5, COP-DET-FUS etc. signalling components which regulate a wide range of physiological functions including seed germination, apical hook opening, hypocotyl elongation, cotyledon opening and greening (Figure 3). The temporal and spatial localization of some of the key regulators mentioned above and their stability modulate the transcription of the downstream genes. The connection between the light signaling and phytohormones regulating the early seedling establishment continuously expanding. The hypocotyl length regulation by the BBXs (*BBX14/15/16*), the CRY-mediated

regulation of auxin and GA signaling and the SAURs interaction with TMK regulating the alkalization of the extracellular matrix are a few examples of novel findings in this area.

There are many studies that identified light perception and phototactic behaviour in *Chlamydomonas reinhardtii*. It utilizes the light cues by converting light as an electrical signal to orchestrate the flagella beating pattern. Using the model organisms *Marchantia polymorpha* and *Physcomitrium patens* scientists have recently started developing a better understanding of the light signaling mechanisms in bryophytes. The core module of light perception, signal transduction and response seems to be quite conserved throughout the lineage starting from *Chlamydomonas*, *Marchantia*, *Physcomitrium* and *Arabidopsis*. However, presence or absence of photoreceptors and some downstream components and responses are quite divergent. In *Chlamydomonas*, light perception takes place by the eyespot, and the membrane localized photoreceptors. Channel rhodopsins which act as ion channels causing depolarisation of membranes, perceive blue and green light to mediate the phototactic movements. It also possesses orthologs of cryptochromes, and a single copy of phototropin for the blue light perception and signalling. In addition to photosynthesis, light regulates sexual reproduction, starch biosynthesis and UV acclimation. The established mechanisms of CrPhot mediated regulation of *PMSK1* in starch biosynthesis and CrUVR8 mediated promotion of UV acclimation by CrCOP1 accumulation is established but the downstream HY5 mediated gene networking is not well explored in *Chlamydomonas*. Orthologs of AtRUP1 and AtRUP2 also need to be characterised in *Chlamydomonas*.

In *Marchantia*, light perception shares both similarities as well as differences from *Physcomitrium* and *Arabidopsis*. The conventional phytochrome P_r and P_{fr} conversion is well conserved in *Marchantia*. Since *Marchantia* has single phytochrome, it takes over both red and far-red light perception and signaling mechanisms which is different from *Physcomitrium* and *Arabidopsis*. Downstream to MpPHY, MpPIF regulates gemma germination, sexual reproduction and meristem dormancy. In case of blue light perception and signaling, the CRY mediated inhibition of COP1 is absent in *Marchantia*. However, MpCRY inhibits ABA responsive genes to inhibit gemma dormancy. Further studies are required in *Marchantia* to completely understand light signaling in this liverwort.

In *Physcomitrium patens*, the genome is more complex than *Chlamydomonas*, and *Marchantia*. It has multiple copies of photoreceptors and light signaling genes. It has even higher copies of genes than *Arabidopsis* for some of the signaling pathways particularly light signaling. Red light is perceived by PpPHYabc whereas far red light is perceived by the PpPHY1/3. Blue light is perceived by PpPHOTs and PpCRYs. CRY mediated inhibition of HY5 by COP1 is conserved in *Physcomitrium patens*. PpCOP has nine copies in *Physcomitrium* whereas there is only one AtCOP1. However, interestingly *Physcomitrium* has only two SPA proteins, but *Arabidopsis* has 4 SPAs. And COP and SPA proteins are not solely skotomorphogenic promoters in *Physcomitrium*, since the absence of *COP* and *SPA* could not abolish expression of all light regulated genes in dark. Also, *Ppccpn* develop green chloroplast in dark which is not usual in the *Arabidopsis*. *Physcomitrium* possess

four orthologs of phototropins which mediate red and blue light mediated chloroplast movements. Interestingly PHYabc are mainly responsible for perceiving red light therefore we speculate that PpPHOTA2, PpPHOTB1, PpPHOTB2 are key players of red light mediated chloroplast movements involving PHYabc since the triple mutants for the above mentioned three phototropins don't show red light mediated chloroplast movements. All these together suggest that while the core light perception and signaling is well conserved among these species there is a lot of difference in the number copies of the light signaling genes and their functional divergence during evolution.

Genes regulating the photoreceptors and other light signaling pathway components have evolved during the process of land invasion by plants. Further characterization of the light signaling components in green algae, and bryophytes like *Physcomitrium* and *Marchantia* will enhance our understanding of the role of light in shaping plant development over time. The use of technologies like single cell and spatial transcriptomics, long-read RNA sequencing, live imaging methods and hormonal bio-sensors might help enhance our knowledge about the evolution of light signaling in plants. These studies might further facilitate the use of optogenetic methods and genome editing tools in modulating light-mediated development for enhanced resilience under changing climatic conditions.

Author contributions

AP: Data curation, Conceptualization, Visualization, Writing – review & editing, Writing – original draft. KR: Visualization, Conceptualization, Writing – original draft, Writing – review & editing, Data curation. SS: Data curation, Writing – original draft, Visualization, Conceptualization, Writing – review & editing. NS: Conceptualization, Visualization, Data curation, Writing – review & editing, Writing – original draft. UZ: Conceptualization, Writing – review & editing, Visualization, Data curation, Writing – original draft. SD: Writing – original draft, Data curation, Supervision, Investigation, Conceptualization, Visualization, Writing – review & editing, Validation.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Abbas, M., Alabadi, D., and Blázquez, M. A. (2013). Differential growth at the apical hook: all roads lead to auxin. *Front. Plant Sci.* 4, 441. doi: 10.3389/fpls.2013.00441
- Alem, A. L., Gonzalez, D. H., and Viola, I. L. (2025). TCP10 acts downstream of light and retrograde signaling pathways to promote Arabidopsis cotyledon de-etiolation in concert with GLK1. *New Phytol.* 248, 265–281. doi: 10.1111/nph.70407
- Artz, O., Dickopf, S., Ranjan, A., Kreiss, M., Abraham, E. T., Boll, V., et al. (2019). Characterization of spa mutants in the moss *Physcomitrella* provides evidence for functional divergence of SPA genes during the evolution of land plants. *New Phytol.* 224, 1613–1626. doi: 10.1111/nph.16004
- Beel, B., Prager, K., Spexard, M., Sasso, S., Weiss, D., Müller, N., et al. (2012). A flavin binding cryptochrome photoreceptor responds to both blue and red light in *Chlamydomonas reinhardtii*. *Plant Cell* 24, 2992–3008. doi: 10.1105/tpc.112.098947
- Blanco-Touriñán, N., Legris, M., Minguet, E. G., Costigliolo-Rojas, C., Nohales, M. A., Iniesto, E., et al. (2020). COP1 destabilizes DELLA proteins in Arabidopsis. *Proc. Natl. Acad. Sci.* 117, 13792–13799. doi: 10.1073/pnas.1907969117
- Buhr, F., El Bakkouri, M., Valdez, O., Pollmann, S., Lebedev, N., Reinbothe, S., et al. (2008). Photoprotective role of NADPH: protochlorophyllide oxidoreductase A. *Proc. Natl. Acad. Sci.* 105, 12629–12634. doi: 10.1073/pnas.0803950105
- Bustamante, J. A., Miller, N. D., and Spalding, E. P. (2025). Separate sites of action for cry1 and phot1 blue-light receptors in the Arabidopsis hypocotyl. *Curr. Biol.* 35, 100–108. doi: 10.1016/j.cub.2024.11.021
- Cao, J., Liang, Y., Yan, T., Wang, X., Zhou, H., Chen, C., et al. (2022). The photomorphogenic repressors BBX28 and BBX29 integrate light and brassinosteroid signaling to inhibit seedling development in Arabidopsis. *Plant Cell* 34, 2266–2285. doi: 10.1093/plcell/koac092
- Cao, J., Yuan, J., Zhang, Y., Chen, C., Zhang, B., Shi, X., et al. (2023). Multi-layered roles of BBX proteins in plant growth and development. *Stress Biol.* 3, 1. doi: 10.1007/s44154-022-00080-z
- Casal, J. J. (2013). Photoreceptor signaling networks in plant responses to shade. *Annu. Rev. Plant Biol.* 64, 403–427. doi: 10.1146/annurev-arplant-050312-120221
- Chen, D., Xu, G., Tang, W., Jing, Y., Ji, Q., Fei, Z., et al. (2013). Antagonistic basic helix-loop-helix/bZIP transcription factors form transcriptional modules that integrate light and reactive oxygen species signaling in Arabidopsis. *Plant Cell* 25, 1657–1673. doi: 10.1105/tpc.112.104869
- Dong, J., Sun, N., Yang, J., Deng, Z., Lan, J., Qin, G., et al. (2019). The transcription factors TCP4 and PIF3 antagonistically regulate organ-specific light induction of SAUR genes to modulate cotyledon opening during de-etiolation in Arabidopsis. *Plant Cell* 31, 1155–1170. doi: 10.1105/tpc.18.00803
- Dong, J., Tang, D., Gao, Z., Yu, R., Li, K., He, H., et al. (2014). Arabidopsis DE-ETIOLATED1 represses photomorphogenesis by positively regulating phytochrome-interacting factors in the dark. *Plant Cell* 26, 3630–3645. doi: 10.1105/tpc.114.130666
- Fan, X.-Y., Sun, Y., Cao, D.-M., Bai, M.-Y., Luo, X.-M., Yang, H.-J., et al. (2012). BZS1, a B-box protein, promotes photomorphogenesis downstream of both brassinosteroid and light signaling pathways. *Mol. Plant* 5, 591–600. doi: 10.1093/mp/sss041
- Franz, S., Ignatz, E., Wenzel, S., Zielosko, H., Ngurah Putu, E. P. G., Maestre-Reyna, M., et al. (2018). Structure of the bifunctional cryptochrome aCRY from *Chlamydomonas reinhardtii*. *Nucleic Acids Res.* 46, 8010–8022. doi: 10.1093/nar/gky621
- Gallego-Bartolomé, J., Arana, M. V., Vandenbussche, F., Žádníková, P., Minguet, E. G., Guardiola, V., et al. (2011). Hierarchy of hormone action controlling apical hook development in Arabidopsis. *Plant J.* 67, 622–634. doi: 10.1111/j.1365-313X.2011.04621.x
- Galvão, R. M., Li, M., Kothadia, S. M., Haskel, J. D., Decker, P. V., Van Buskirk, E. K., et al. (2012). Photoactivated phytochromes interact with HEMERA and promote its accumulation to establish photomorphogenesis in Arabidopsis. *Genes Dev.* 26, 1851–1863. doi: 10.1101/gad.193219.112
- Gangappa, S. N., and Kumar, S. V. (2017). DET1 and HY5 control PIF4-mediated thermosensory elongation growth through distinct mechanisms. *Cell Rep.* 18, 344–351. doi: 10.1016/j.celrep.2016.12.046
- Gendreau, E., Traas, J., Desnos, T., Grandjean, O., Caboche, M., and Hofte, H. (1997). Cellular basis of hypocotyl growth in Arabidopsis thaliana. *Plant Physiol.* 114, 295–305. doi: 10.1104/pp.114.1.295
- Griffiths, J., Rizza, A., Tang, B., Frommer, W. B., and Jones, A. M. (2024). GIBBERELLIN PERCEPTION SENSOR 2 reveals genesis and role of cellular GA dynamics in light-regulated hypocotyl growth. *Plant Cell* 36, 4426–4441. doi: 10.1093/plcell/koae198
- Gyula, P., Schäfer, E., and Nagy, F. (2003). Light perception and signalling in higher plants. *Curr. Opin. Plant Biol.* 6, 446–452. doi: 10.1016/S1369-5266(03)00082-7
- Han, X., Chang, X., Zhang, Z., Chen, H., He, H., Zhong, B., et al. (2019). Origin and evolution of core components responsible for monitoring light environment changes during plant terrestrialization. *Mol. Plant* 12, 847–862. doi: 10.1016/j.molp.2019.04.006
- Hao, Y., Zeng, Z., Zhang, X., Xie, D., Li, X., Ma, L., et al. (2023). Green means go: Green light promotes hypocotyl elongation via brassinosteroid signaling. *Plant Cell* 35, 1304–1317. doi: 10.1093/plcell/koad022
- Hegemann, P. (2008). Algal sensory photoreceptors. *Annu. Rev. Plant Biol.* 59, 167–189. doi: 10.1146/annurev-arplant.59.032607.092847
- Hernández-García, J., Sun, R., Serrano-Mislata, A., Inoue, K., Vargas-Chávez, C., Esteve-Bruna, D., et al. (2021). Coordination between growth and stress responses by DELLA in the liverwort *Marchantia polymorpha*. *Curr. Biol.* 31, 3678–3686.e11. doi: 10.1016/j.cub.2021.06.010
- Hernández-Muñoz, A., Agreda-Laguna, K. A., Ramirez-Bernabé, I. E., Oltehua-López, O., Arteaga-Vázquez, M. A., and Leon, P. (2024). *Marchantia polymorpha* GOLDEN2-LIKE transcriptional factor: a central regulator of chloroplast and plant vegetative development. *New Phytol.* 243, 1406–1423. doi: 10.1111/nph.19916
- Huang, K., Kunkel, T., and Beck, C. F. (2004). Localization of the blue-light receptor phototropin to the flagella of the green alga *Chlamydomonas reinhardtii*. *Mol. Biol. Cell* 15, 3605–3614. doi: 10.1091/mbc.E04
- Huang, K., Merkle, T., and Beck, C. F. (2002). Isolation and characterization of a *Chlamydomonas* gene that encodes a putative blue-light photoreceptor of the phototropin family. *Physiol. Plant* 115, 613–622. doi: 10.1034/j.1399-3054.2002.1150416.x
- Imaizumi, T., Kadota, A., Hasebe, M., and Wada, M. (2002). Cryptochrome light signals control development to suppress auxin sensitivity in the moss *Physcomitrella patens*. *Plant Cell* 14, 373–386. doi: 10.1105/tpc.010388
- Immeln, D., Schlesinger, R., Heberle, J., and Kottke, T. (2007). Blue light induces radical formation and autophosphorylation in the light-sensitive domain of

Chlamydomonas cryptochrome. *J. Biol. Chem.* 282, 21720–21728. doi: 10.1074/jbc.M700849200

Inoue, K., Nishihama, R., Araki, T., and Kohchi, T. (2019). Reproductive induction is a far-red high irradiance response that is mediated by phytochrome and phytochrome interacting factor in *Marchantia polymorpha*. *Plant Cell Physiol.* 60, 1136–1145. doi: 10.1093/pcp/pcz029

Inoue, K., Nishihama, R., Kataoka, H., Hosaka, M., Manabe, R., Nomoto, M., et al. (2016). Phytochrome signaling is mediated by PHYTOCHROME INTERACTING FACTOR in the liverwort *Marchantia polymorpha*. *Plant Cell* 28, 1406–1421. doi: 10.1105/tpc.15.01063

Jenkins, G. I. (2014). The UV-B photoreceptor UVR8: from structure to physiology. *Plant Cell* 26, 21–37. doi: 10.1105/tpc.113.119446

Job, N., and Datta, S. (2021). PIF3/HY5 module regulates BBX11 to suppress protochlorophyllide levels in dark and promote photomorphogenesis in light. *New Phytol.* 230, 190–204. doi: 10.1111/nph.17149

Kami, C., Lorrain, S., Hornitschek, P., and Fankhauser, C. (2010). Light-regulated plant growth and development. *Curr. Top. Dev. Biol.* 91, 29–66. doi: 10.1016/S0070-2153(10)91002-8

Kasahara, M., Kagawa, T., Sato, Y., Kiyosue, T., and Wada, M. (2004). Phototropins mediate blue and red light-induced chloroplast movements in *Physcomitrella patens*. *Plant Physiol.* 135, 1388–1397. doi: 10.1104/pp.104.042705

Kauss, D., Bischof, S., Steiner, S., Apel, K., and Meskauskiene, R. (2012). FLU, a negative feedback regulator of tetrapyrrole biosynthesis, is physically linked to the final steps of the Mg²⁺-branch of this pathway. *FEBS Lett.* 586, 211–216. doi: 10.1016/j.febslet.2011.12.029

Kim, J., Yi, H., Choi, G., Shin, B., Song, P.-S., and Choi, G. (2003). Functional characterization of phytochrome interacting factor 3 in phytochrome-mediated light signal transduction. *Plant Cell* 15, 2399–2407. doi: 10.1105/tpc.014498

Kobayashi, K., and Masuda, T. (2016). Transcriptional regulation of tetrapyrrole biosynthesis in *Arabidopsis thaliana*. *Front. Plant Sci.* 7, 1811. doi: 10.3389/fpls.2016.01811

Komatsu, A., Terai, M., Ishizaki, K., Suetsugu, N., Nishihama, R., Yamato, K. T., et al. (2014). Phototropin encoded by a Single-Copy gene mediates chloroplast photorelocation movements in the liverwort *Marchantia polymorpha*. *Plant Physiol.* 166, 411–427. doi: 10.1104/pp.114.245100

Krahmer, J., and Fankhauser, C. (2024). Environmental control of hypocotyl elongation. *Annu. Rev. Plant Biol.* 75, 489–519. doi: 10.1146/annurev-arplant-062923-023852

Kreiss, M., Haas, F. B., Hansen, M., Rensing, S. A., and Hoecker, U. (2023). Co-action of COP1, SPA and cryptochrome in light signal transduction and photomorphogenesis of the moss *Physcomitrium patens*. *Plant J.* 114, 159–175. doi: 10.1111/tj.16128

Larner, V. S., Franklin, K. A., and Whitelam, G. C. (2018). Photoreceptors and light signalling pathways in plants. *Annu. Plant Rev. Online* 21, 107–131. doi: 10.1002/9781119312994.apr0210

Lee, J., He, K., Stolc, V., Lee, H., Figueroa, P., Gao, Y., et al. (2007). Analysis of transcription factor HY5 genomic binding sites revealed its hierarchical role in light regulation of development. *Plant Cell* 19, 731–749. doi: 10.1105/tpc.106.047688

Legris, M., Ince, Y. Ç., and Fankhauser, C. (2019). Molecular mechanisms underlying phytochrome-controlled morphogenesis in plants. *Nat. Commun.* 10, 5219. doi: 10.1038/s41467-019-13045-0

Li, Q.-F., and He, J.-X. (2016). BZR1 interacts with HY5 to mediate brassinosteroid- and light-regulated cotyledon opening in *Arabidopsis* in darkness. *Mol. Plant* 9, 113–125. doi: 10.1016/j.molp.2015.08.014

Li, J., Li, G., Wang, H., and Deng, X. W. (2011). Phytochrome signaling mechanisms. *Arabidopsis. Book/American. Soc. Plant Biol.* 9, e0148. doi: 10.1199/tab.0148

Li, K., Yu, R., Fan, L.-M., Wei, N., Chen, H., and Deng, X. W. (2016). DELLA-mediated PIF degradation contributes to coordination of light and gibberellin signalling in *Arabidopsis*. *Nat. Commun.* 7, 11868. doi: 10.1038/ncomms11868

Lian, H.-L., He, S.-B., Zhang, Y.-C., Zhu, D.-M., Zhang, J.-Y., Jia, K.-P., et al. (2011). Blue-light-dependent interaction of cryptochrome 1 with SPA1 defines a dynamic signaling mechanism. *Genes Dev.* 25, 1023–1028. doi: 10.1101/gad.202511

Liang, Y., Podolec, R., Chappuis, R., Defossez, E., Glauser, G., Rötzer, J., et al. (2025). Conservation and divergence of UVR8-COP1/SPA-HY5 signaling in UV-B responses of *Marchantia polymorpha*. *bioRxiv*, 2025-07. doi: 10.1101/2025.07.16.665153

Liao, J., Deng, B., Yang, Q., Li, Y., Zhang, Y., Cong, J., et al. (2023). Insights into cryptochrome modulation of ABA signaling to mediate dormancy regulation in *Marchantia polymorpha*. *New Phytol.* 238, 1479–1497. doi: 10.1111/nph.18815

Li KunLun, L. K., Gao ZhaoXu, G. Z., He Hang, H. H., Terzaghi, W., Fan LiuMin, F. L., Deng XingWang, D. X., et al. (2015). *Arabidopsis* DET1 represses photomorphogenesis in part by negatively regulating DELLA protein abundance in darkness. *Molecular Plant*, 8, 622–630. doi: 10.1016/j.molp.2014.12.017

Lin, W., Zhou, X., Tang, W., Takahashi, K., Pan, X., Dai, J., et al. (2021). TMK-based cell-surface auxin signalling activates cell-wall acidification. *Nature* 599, 278–282. doi: 10.1038/s41586-021-03976-4

Lopez-Pozo, M., Adams, W. W. III, Polutchko, S. K., and Demmig-Adams, B. (2023). Terrestrial and floating aquatic plants differ in acclimation to light environment. *Plants* 12, 1928. doi: 10.3390/plants12101928

Matsumoto, F., Obayashi, T., Sasaki-Sekimoto, Y., Ohta, H., Takamiya, K., and Masuda, T. (2004). Gene expression profiling of the tetrapyrrole metabolic pathway in *Arabidopsis* with a mini-array system. *Plant Physiol.* 135, 2379–2391. doi: 10.1104/pp.104.042408

Meskauskiene, R., Nater, M., Goslings, D., Kessler, F., op den Camp, R., and Apel, K. (2001). FLU: a negative regulator of chlorophyll biosynthesis in *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci.* 98, 12826–12831. doi: 10.1073/pnas.221252798

Mochizuki, N., Tanaka, R., Grimm, B., Masuda, T., Moulin, M., Smith, A. G., et al. (2010). The cell biology of tetrapyrroles: a life and death struggle. *Trends Plant Sci.* 15, 488–498. doi: 10.1016/j.tplants.2010.05.012

Monte, E., Tepperman, J. M., Al-Sady, B., Kaczorowski, K. A., Alonso, J. M., Ecker, J. R., et al. (2004). The phytochrome-interacting transcription factor, PIF3, acts early, selectively, and positively in light-induced chloroplast development. *Proc. Natl. Acad. Sci.* 101, 16091–16098. doi: 10.1073/pnas.0407107101

Müller, N., Wenzel, S., Zou, Y., Künzel, S., Sasso, S., Weiß, D., et al. (2017). A plant cryptochrome controls key features of the *Chlamydomonas* circadian clock and its life cycle. *Plant Physiol.* 174, 185–201. doi: 10.1104/pp.17.00349

Nagel, G., Szellas, T., Huhn, W., Kateriya, S., Aideshvilvi, N., Berthold, P., et al. (2003). Channelrhodopsin-2, a directly light-gated cation-selective membrane channel. *Proc. Natl. Acad. Sci. U.S.A.* 100, 13940–13945. doi: 10.1073/pnas.1936192100

Nasim, Z., Karim, N., Susila, H., and Ahn, J. H. (2024). *Arabidopsis* B-BOX DOMAIN PROTEIN14/15/16 form a feedback loop with ELONGATED HYPOCOTYL 5 and PHYTOCHROME-INTERACTING FACTORS to regulate hypocotyl elongation. *Curr. Plant Biol.* 40, 100395. doi: 10.1016/j.cpb.2024.100395

Noguchi, M., Noda, S., Matsubayashi, Y., and Kodama, Y. (2025). Phototropin switches between cis- and trans-autophosphorylation in light-induced chloroplast relocation in *Marchantia polymorpha*. *Plant J.* 121, 1–16. doi: 10.1111/tj.17183

Oh, E., Zhu, J.-Y., and Wang, Z.-Y. (2012). Interaction between BZR1 and PIF4 integrates brassinosteroid and environmental responses. *Nat. Cell Biol.* 14, 802–809. doi: 10.1038/ncb2545

op den Camp, R. G. L., Przybyla, D., Ochsenbein, C., Laloi, C., Kim, C., Danon, A., et al. (2003). Rapid induction of distinct stress responses after the release of singlet oxygen in *Arabidopsis*. *Plant Cell* 15, 2320–2332. doi: 10.1105/tpc.014662

Oyama, T., Shimura, Y., and Okada, K. (1997). The *Arabidopsis* HY5 gene encodes a bZIP protein that regulates stimulus-induced development of root and hypocotyl. *Genes Dev.* 11, 2983–2995. doi: 10.1101/gad.11.22.2983

Park, E., Kim, Y., and Choi, G. (2018). Phytochrome B requires PIF degradation and sequestration to induce light responses across a wide range of light conditions. *Plant Cell* 30, 1277–1292. doi: 10.1105/tpc.17.00913

Park, E., Park, J., Kim, J., Nagatani, A., Lagarias, J. C., and Choi, G. (2012). Phytochrome B inhibits binding of phytochrome-interacting factors to their target promoters. *Plant J.* 72, 537–546. doi: 10.1111/j.1365-3113X.2012.05114.x

Pashkovskiy, P., Khalilova, L., Vereshchagin, M., Voronkov, A., Ivanova, T., Kosobryukhov, A. A., et al. (2023). Impact of varying light spectral compositions on photosynthesis, morphology, chloroplast ultrastructure, and expression of light-responsive genes in *Marchantia polymorpha*. *Plant Physiol. Biochem.* 203, 1–10. doi: 10.1016/j.plaphy.2023.108044

Ponnu, J., and Hoecker, U. (2021). Illuminating the COP1/SPA ubiquitin ligase: fresh insights into its structure and functions during plant photomorphogenesis. *Front. Plant Sci.* 12, 662793. doi: 10.3389/fpls.2021.662793

Possart, A., and Hiltbrunner, A. (2013). An evolutionarily conserved signaling mechanism mediates far-red light responses in land plants. *Plant Cell* 25, 102–114. doi: 10.1105/tpc.112.104331

Possart, A., Xu, T., Paik, I., Hanke, S., Keim, S., Hermann, H.-M., et al. (2017). Characterization of phytochrome interacting factors from the moss *Physcomitrella patens* illustrates conservation of phytochrome signaling modules in land plants. *Plant Cell* 29, 310–330. doi: 10.1105/tpc.16.00388

Ranjan, A., Dickopf, S., Ullrich, K. K., Rensing, S. A., and Hoecker, U. (2014). Functional analysis of COP1 and SPA orthologs from *Physcomitrella* and rice during photomorphogenesis of transgenic *Arabidopsis* reveals distinct evolutionary conservation. *BMC Plant Biol.* 14, 178. doi: 10.1186/1471-2229-14-178

Ravindran, N., Ramachandran, H., Job, N., Yadav, A., Vaishak, K. P., and Datta, S. (2021). B-box protein BBX32 integrates light and brassinosteroid signals to inhibit cotyledon opening. *Plant Physiol.* 187, 446–461. doi: 10.1093/plphys/kiab304

Ravindran, N., Rao, K. V., and Datta, S. (2025). BBX32 integrates ethylene and light signaling to delay apical hook opening and optimize seedling soil emergence. *New Phytol.* 248, 758–775. doi: 10.1111/nph.70236

Rehmani, M. S., Xian, B., Wei, S., He, J., Feng, Z., Huang, H., et al. (2023). Seedling establishment: The neglected trait in the seed longevty field. *Plant Physiol. Biochem.* 200, 107765. doi: 10.1016/j.plaphy.2023.107765

Reinbothe, S., Reinbothe, C., Apel, K., and Lebedev, N. (1996). Evolution of chlorophyll biosynthesis—the challenge to survive photooxidation. *Cell* 86, 703–705. doi: 10.1016/S0092-8674(00)80144-0

Reisdorph, N. A., and Small, G. D. (2004). The CPH1 gene of *Chlamydomonas reinhardtii* encodes two forms of cryptochrome whose levels are controlled by light-induced proteolysis. *Plant Physiol.* 134, 1546–1554. doi: 10.1104/pp.103.031930

Reyes-Hernández, B. J. (2025). Guided by light, microtubules choreograph the directional expansion of cotyledons. *Plant Physiology*, 198, 1–3. doi: 10.1093/plphys/kiaf234

- Rredhi, A., Petersen, J., Schubert, M., Li, W., Oldemeyer, S., Li, W., et al. (2021). DASH cryptochrome 1, a UV-A receptor, balances the photosynthetic machinery of *Chlamydomonas reinhardtii*. *New Phytol.* 232, 610–624. doi: 10.1111/nph.17603
- Salomé, P. A., and Merchant, S. S. (2019). A series of fortunate events: Introducing *Chlamydomonas* as a reference organism. *Plant Cell* 31, 1682–1707. doi: 10.1105/tpc.18.00952
- Shin, J., Kim, K., Kang, H., Zulfugarov, I. S., Bae, G., Lee, C.-H., et al. (2009). Phytochromes promote seedling light responses by inhibiting four negatively-acting phytochrome-interacting factors. *Proc. Natl. Acad. Sci.* 106, 7660–7665. doi: 10.1073/pnas.0812219106
- Small, G. D., Min, B., and Lefebvre, P. A. (1995). Characterization of a *Chlamydomonas reinhardtii* gene encoding a protein of the DNA photolyase/blue light photoreceptor family. *Plant Mol. Biol.* 28, 443–454. doi: 10.1007/BF00020393
- Song, Z., Ye, W., Jiang, Q., Lin, H., Hu, Q., Xiao, Y., et al. (2024). BBX9 forms feedback loops with PIFs and BBX21 to promote photomorphogenic development. *J. Integr. Plant Biol.* 66, 1934–1952. doi: 10.1111/jipb.13746
- Soriano, G., Cloix, C., Heilmann, M., Núñez-Oliviera, E., Martínez-Abaigar, J., and Jenkins, G. I. (2018). Evolutionary conservation of structure and function of the UVR8 photoreceptor from the liverwort *Marchantia polymorpha* and the moss *Physcomitrella patens*. *New Phytologist* 217, 151–162.
- Spartz, A. K., Lee, S. H., Wenger, J. P., Gonzalez, N., Itoh, H., Inzé, D., et al. (2012). The SAUR19 subfamily of SMALL AUXIN UP RNA genes promote cell expansion. *Plant J.* 70, 978–990. doi: 10.1111/j.1365-313X.2012.04946.x
- Spartz, A. K., Ren, H., Park, M. Y., Grandt, K. N., Lee, S. H., Murphy, A. S., et al. (2014). SAUR inhibition of PP2C-D phosphatases activates plasma membrane H⁺-ATPases to promote cell expansion in Arabidopsis. *Plant Cell* 26, 2129–2142. doi: 10.1105/tpc.114.126037
- Stephenson, P. G., Fankhauser, C., and Terry, M. J. (2009). PIF3 is a repressor of chloroplast development. *Proc. Natl. Acad. Sci.* 106, 7654–7659. doi: 10.1073/pnas.0811684106
- Streubel, S., Deiber, S., Rötzer, J., Mosiolek, M., Jandrasits, K., and Dolan, L. (2023). Meristem dormancy in *Marchantia polymorpha* is regulated by a liverwort-specific miRNA and a clade III SPL gene. *Curr. Biol.* 33, 660–674.e4. doi: 10.1016/j.cub.2022.12.062
- Sullivan, J. A., and Deng, X. W. (2003). From seed to seed: The role of photoreceptors in Arabidopsis development. *Dev. Biol.* 260, 289–297. doi: 10.1016/S0012-1606(03)00212-4
- Sun, R., Okabe, M., Miyazaki, S., Ishida, T., Mashiguchi, K., Inoue, K., et al. (2023). Biosynthesis of gibberellin-related compounds modulates far-red light responses in the liverwort *Marchantia polymorpha*. *Plant Cell* 35, 4111–4132. doi: 10.1093/plcell/koad216
- Sun, N., Wang, J., Gao, Z., Dong, J., He, H., Terzaghi, W., et al. (2016). Arabidopsis SAURs are critical for differential light regulation of the development of various organs. *Proc. Natl. Acad. Sci.* 113, 6071–6076. doi: 10.1073/pnas.1604782113
- Tachibana, R., Abe, S., Marugami, M., Yamagami, A., Akema, R., Ohashi, T., et al. (2024). BPG4 regulates chloroplast development and homeostasis by suppressing GLK transcription factors and involving light and brassinosteroid signaling. *Nat. Commun.* 15, 370. doi: 10.1038/s41467-023-44492-5
- Tachibana, R., Akema, R., Yoshihara, A., Ujihara, C., Nishida, K., Ri, S., et al. (2025). Dark-inducible BGH2 suppresses GLK transcription factors and maintains plastid homeostasis to promote light adaptation. *Plant Cell* 37, koaf180. doi: 10.1093/plcell/koaf180
- Tanaka, R., and Tanaka, A. (2007). Tetrapyrrole biosynthesis in higher plants. *Annu. Rev. Plant Biol.* 58, 321–346. doi: 10.1146/annurev.arplant.57.032905.105448
- Tilbrook, K., Arongaus, A. B., Binkert, M., Heijde, M., Yin, R., and Ulm, R. (2013). The UVR8 UV-B photoreceptor: perception, signaling and response. *Arabidopsis. Book/American. Soc. Plant Biol.* 11, e0164. doi: 10.1199/tab.0164
- Tilbrook, K., Dubois, M., Crocco, C. D., Yin, R., Chappuis, R., Allorent, G., et al. (2016). UV-B perception and acclimation in *Chlamydomonas reinhardtii*. *Plant Cell* 28, 966–983. doi: 10.1105/tpc.15.00287
- Trippens, J., Greiner, A., Schellwat, J., Neukam, M., Rottmann, T., Lu, Y., et al. (2012). Phototropin influence on eyespot development and regulation of phototactic behavior in *Chlamydomonas reinhardtii*. *Plant Cell* 24, 4687–4702. doi: 10.1105/tpc.112.103523
- Von Wettstein, D., Gough, S., Kannagara, C. G., et al. (1995). Chlorophyll Biosynthesis. *The Plant Cell* 7, 1039–1057. doi: 10.1105/tpc.7.7.1039
- Wagner, D., Przybyla, D., op den Camp, R., Kim, C., Landgraf, F., Lee, K. P., et al. (2004). The genetic basis of singlet oxygen induced stress responses of Arabidopsis thaliana. *Sci. (1979)*. 306, 1183–1185. doi: 10.1126/science.1103178
- Wallner, E.-S., Edelbacher, N., and Dolan, L. (2025). *De novo* meristem development in *Marchantia* requires light and an apical auxin minimum. *Current Biology* 36, 1–12. doi: 10.1016/j.cub.2025.11.016
- Wang, Z.-Y., Bai, M.-Y., Oh, E., and Zhu, J.-Y. (2012). Brassinosteroid signaling network and regulation of photomorphogenesis. *Annu. Rev. Genet.* 46, 701–724. doi: 10.1146/annurev-genet-102209-163450
- Wang, P., Fouracre, J., Kelly, S., Karki, S., Gowik, U., Aubry, S., et al. (2013). Evolution of GOLDEN2-LIKE gene function in C3 and C4 plants. *Planta* 237, 481–495. doi: 10.1007/s00425-012-1754-3
- Wang, K., Meng, Y., Tian, Q., Zhou, R., Wu, S., Wu, J., et al. (2025). BBX32 dampens E3 ligase activity to promote greening in emerging seedlings. *J. Integr. Plant Biol.* 67, 2078–2099. doi: 10.1111/jipb.13939
- Wang, Y., Peng, Y., and Guo, H. (2023). To curve for survival: Apical hook development. *J. Integr. Plant Biol.* 65, 324–342. doi: 10.1111/jipb.13441
- Wang, J., Sun, N., Zhang, F., Yu, R., Chen, H., Deng, X. W., et al. (2020). SAUR17 and SAUR50 differentially regulate PP2C-D1 during apical hook development and cotyledon opening in Arabidopsis. *Plant Cell* 32, 3792–3811. doi: 10.1105/tpc.20.00283
- Waters, M. T., Wang, P., Korkaric, M., Capper, R. G., Saunders, N. J., and Langdale, J. A. (2009). GLK transcription factors coordinate expression of the photosynthetic apparatus in Arabidopsis. *Plant Cell* 21, 1109–1128. doi: 10.1105/tpc.108.065250
- Wei, Y., Wang, S., and Yu, D. (2023). The role of light quality in regulating early seedling development. *Plants* 12, 2746. doi: 10.3390/plants12142746
- Wolf, S., Hématy, K., and Höfte, H. (2012). Growth control and cell wall signaling in plants. *Annu. Rev. Plant Biol.* 63, 381–407. doi: 10.1146/annurev-arplant-042811-105449
- Xin, X., Chen, W., Wang, B., Zhu, F., Li, Y., Yang, H., et al. (2018). Arabidopsis MKK10-MPK6 mediates red-light-regulated opening of seedling cotyledons through phosphorylation of PIF3. *J. Exp. Bot.* 69, 423–439. doi: 10.1093/jxb/erx418
- Xu, T., Yuan, J., and Hiltbrunner, A. (2020). PHYTOCHROME INTERACTING FACTORS in the moss *Physcomitrella patens* regulate light-controlled gene expression. *Physiol. Plant* 169, 467–479. doi: 10.1111/ppl.13140
- Yadav, A., Ravindran, N., Singh, D., Rahul, P. V., and Datta, S. (2020a). Role of Arabidopsis BBX proteins in light signaling. *J. Plant Biochem. Biotechnol.* 29, 623–635. doi: 10.1007/s13562-020-00597-2
- Yadav, A., Singh, D., Lingwan, M., Yadukrishnan, P., Masakapalli, S. K., and Datta, S. (2020b). Light signaling and UV-B-mediated plant growth regulation. *J. Integr. Plant Biol.* 62, 1270–1292. doi: 10.1111/jipb.12932
- Yamawaki, S., Yamashino, T., Nakanishi, H., and Mizuno, T. (2011). Functional characterization of HY5 homolog genes involved in early light-signaling in *Physcomitrella patens*. *Biosci. Biotechnol. Biochem.* 75, 1533–1539. doi: 10.1271/bbb.110219
- Yang, M., Li, C., Cai, Z., Hu, Y., Nolan, T., Yu, F., et al. (2017). SINAT E3 ligases control the light-mediated stability of the brassinosteroid-activated transcription factor BES1 in Arabidopsis. *Dev. Cell* 41, 47–58. doi: 10.1016/j.devcel.2017.03.014
- Yang, N., Zhang, Y., Liu, J., Liu, Y., Chen, Q., Wang, H., et al. (2020). Network during light-induced cotyledons opening and greening in *Astragalus membranaceus*. *J. Plant Interact.* 15, 358–370. doi: 10.1080/17429145.2020.1831088
- Yelina, N. E., Frangedakis, E., Wang, Z., Schreier, T. B., Rever, J., Tomaselli, M., et al. (2024). Streamlined regulation of chloroplast development in the liverwort *Marchantia polymorpha*. *Cell Rep.* 43, 1–24. doi: 10.1016/j.celrep.2024.114696
- Yuan, Y., Iannetta, A. A., Kim, M., Sadecki, P. W., Arend, M., Tschila, A., et al. (2025). Phototropin connects blue light perception to starch metabolism in green algae. *Nat. Commun.* 16, 1–15. doi: 10.1038/s41467-025-57809-3
- Yuan, J., Xu, T., and Hiltbrunner, A. (2023). Phytochrome higher order mutants reveal a complex set of light responses in the moss *Physcomitrium patens*. *New Phytol.* 239, 1035–1050. doi: 10.1111/nph.18977
- Zhang, L., Li, T., Su, S., Peng, H., Li, S., Li, K., et al. (2022a). Functions of COP1/SPA E3 ubiquitin ligase mediated by MpcRY in the liverwort *Marchantia polymorpha* under blue light. *Int. J. Mol. Sci.* 23, 1–18. doi: 10.3390/ijms23010158
- Zhang, Z., Xu, C., Zhang, S., Shi, C., Cheng, H., Liu, H., et al. (2022b). Origin and adaptive evolution of UV RESISTANCE LOCUS 8-mediated signaling during plant terrestrialization. *Plant Physiol.* 188, 332–346. doi: 10.1093/plphys/kiab486
- Zhao, M., Huang, X., Lu, W., Wang, S., Zheng, H., Luo, C., et al. (2025). Light-regulated reprogramming in moss: SHMT1 mediates blue light enhancement of cell regeneration. *Plant Cell Environ.* 48, 7759–7774. doi: 10.1111/pce.70044
- Zhao, L., Peng, T., Chen, C.-Y., Ji, R., Gu, D., Li, T., et al. (2019). HY5 interacts with the histone deacetylase HDA15 to repress hypocotyl cell elongation in photomorphogenesis. *Plant Physiol.* 180, 1450–1466. doi: 10.1104/pp.19.00055
- Zhao, X., Wang, Y.-L., Qiao, X.-R., Wang, J., Wang, L.-D., Xu, C.-S., et al. (2013). Phototropins function in high-intensity blue light-induced hypocotyl phototropism in Arabidopsis by altering cytosolic calcium. *Plant Physiol.* 162, 1539–1551. doi: 10.1104/pp.113.216556
- Zheng, Y., Cui, X., Su, L., Fang, S., Chu, J., Gong, Q., et al. (2017). Jasmonate inhibits COP 1 activity to suppress hypocotyl elongation and promote cotyledon opening in etiolated Arabidopsis seedlings. *Plant J.* 90, 1144–1155. doi: 10.1111/tpj.13539
- Zhong, M., Zeng, B., Tang, D., Yang, J., Qu, L., Yan, J., et al. (2021). The blue light receptor CRY1 interacts with GID1 and DELLA proteins to repress GA signaling during photomorphogenesis in Arabidopsis. *Mol. Plant* 14, 1328–1342. doi: 10.1016/j.molp.2021.05.011
- Zhou, L., Bian, Y., Song, Z., Chen, X., Wang, Y., Chu, L., et al. (2025). BBX10 interacts with PIF1 to prevent photo-oxidation and to promote the greening process. *Cell Rep.* 44, 1–17. doi: 10.1016/j.celrep.2025.116268
- Zou, Y., Wenzel, S., Müller, N., Prager, K., Jung, E. M., Kothe, E., et al. (2017). An animal-like cryptochrome1 controls the *Chlamydomonas* sexual cycle. *Plant Physiol.* 174, 1334–1347. doi: 10.1104/pp.17.00493