



Dark-Induced Hormonal Regulation of Plant Growth and Development

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The sessile nature of plants has made them extremely sensitive and flexible toward the constant flux of the surrounding environment, particularly light and dark. The light is perceived as a signal by specific receptors which further transduce the information through the signaling intermediates and effector proteins to modulate gene expression. Signal transduction induces changes in hormone levels that alters developmental, physiological and morphological processes. Importance of light for plants growth is well recognized, but a holistic understanding of key molecular and physiological changes governing plants development under dark is awaited. Here, we describe how darkness acts as a signal causing alteration in hormone levels and subsequent modulation of the gene regulatory network throughout plant life. The emphasis of this review is on dark mediated changes in plant hormones, regulation of signaling complex COP/DET/FUS and the transcription factors PIFs which affects developmental events such as apical hook development, elongated hypocotyls, photoperiodic flowering, shortened roots, and plastid development. Furthermore, the role of darkness in shade avoidance and senescence is discussed.

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INTRODUCTION

Light and dark, both act as environmental cues that regulate plant growth and development from seedling emergence till senescence. Plant development begins in the soil where darkness acts as a signal for etiolation which is characterized by elongated hypocotyl and shortened roots, apical hook of closed cotyledons covering shoot apical meristem and impaired chloroplast development (Arsovski et al., 2012; Mazzella et al., 2014; Gommers and Monte, 2018). This mode of plant growth is known as skotomorphogenesis. It is an evolutionary advanced program in angiosperms to safely get seedling through the soil to light (Seluzicki et al., 2017). Nonetheless, exposure of seeds to continuous light during early development causes seedling de-etiolation (photomorphogenesis) characterized by attenuated hypocotyl growth, root growth acceleration, apical hook straightening and chloroplast maturation.

Being photoautotrophs, plants have evolved with the diverse set of photoreceptors. *Arabidopsis* photoreceptors have been classified as phytochromes (phyA-E, red/far-red light), cryptochromes (cry1-2), phototropins (phot1-2) and zeitelupe family members (*ZTL*, blue/UV-A light and *UVR8*; UV-B light) (Galvao and Fankhauser, 2015; Mishra and Khurana, 2017; Podolec and Ulm, 2018). Light-mediated activation of different photoreceptors and subsequent release of the dark-mediated photomorphogenic repression leads to light-dependent plant development. Some of the major mechanisms that play important role in photomorphogenic

development are phosphorylation of phytochrome interacting factors (PIFs), ubiquitin-mediated proteolysis (UMP), and modulation of CONSTITUTIVE PHOTOMORPHOGENIC/DE-ETIOLATED/FUSCA (COP/DET/FUS) complex activity, organization and subcellular localization of positive regulators of light signaling like ELONGATED HYPOCTYL 5 (HY5), LONG AFTER FAR-RED LIGHT1 (LAF) and LONG HYPOCOTYL AFTER FAR-RED LIGHT1 (HFR1) (Huang et al., 2014; Pham et al., 2018). Dark germinated seedlings become sensitive to fluctuations of the day/night cycles when they are first exposed to light. Therefore, growth and development of seedling comes under the control of circadian clock components. Ample amount of information is available about how plants sense and respond to the complex light spectra, but the information is missing about their behavior under darkness, and light and dark signal interaction. Since, light simply reverses the dark-mediated development by activation of the photoreceptors, it has been speculated that the inactive photoreceptors might act as dark receptors and mediate the dark-triggered signal transduction (Seluzicki et al., 2017; Gommers and Monte, 2018; Armarego-marriott and Sandoval-ibañez, 2020). Nonetheless, exact mechanism of dark sensing and perception is still unknown, and the idea of darkness perception by the inactive light receptors is a matter of debate. Though, regulation of seedling establishment by the light and dark signaling in *Arabidopsis* was recently reviewed (Gommers and Monte, 2018), enough literature is not available for light and dark signal integration and consequent phenotypic alterations.

In this review, an update about how plants make sense of darkness and use it as a signal during different phases of skotomorphogenic development e.g., apical hook formation, hypocotyl elongation, shortened roots, photoperiodic flowering, and plastid development is provided. Moreover, how endogenous clock integrates plant growth and development with photoperiods, and the effect of darkness on the plant responses such as, shade avoidance and dark-mediated senescence is discussed.

DARKNESS AS A SIGNAL

As mentioned earlier, it is presumed that darkness might be perceived by the inactive light receptors that could activate the COP/DET/FUS complex proteins and the PIFs. The proteins of COP/DET/FUS complex are encoded by a group of pleiotropic genes. These proteins are assembled in three different functional complexes, i.e., SUPPRESSOR OF PHYA105 (COP1-SPA), COP10-DET1-DDB1 (CDD), and COP9 signalosome complex (CSN), all of them are connected by a scaffold protein CULLIN4 (CUL4) (Chen et al., 2010; Pokhilko et al., 2011; Dong et al., 2014; Huang et al., 2016). In darkness, COP1-SPA and CDD complex act together to degrade positive regulators of photomorphogenesis like HY5, LAF and HFR1 via UMP. However, these complexes also prevent degradation of PIFs (PIF3 and 4) by inhibiting a brassinosteroid (BR) signaling component BRASSINOSTEROID-INSENSITIVE 2 (BIN2) (Dong et al., 2014; Huang et al., 2016; Wang and Guo, 2018; **Figure 1**). The

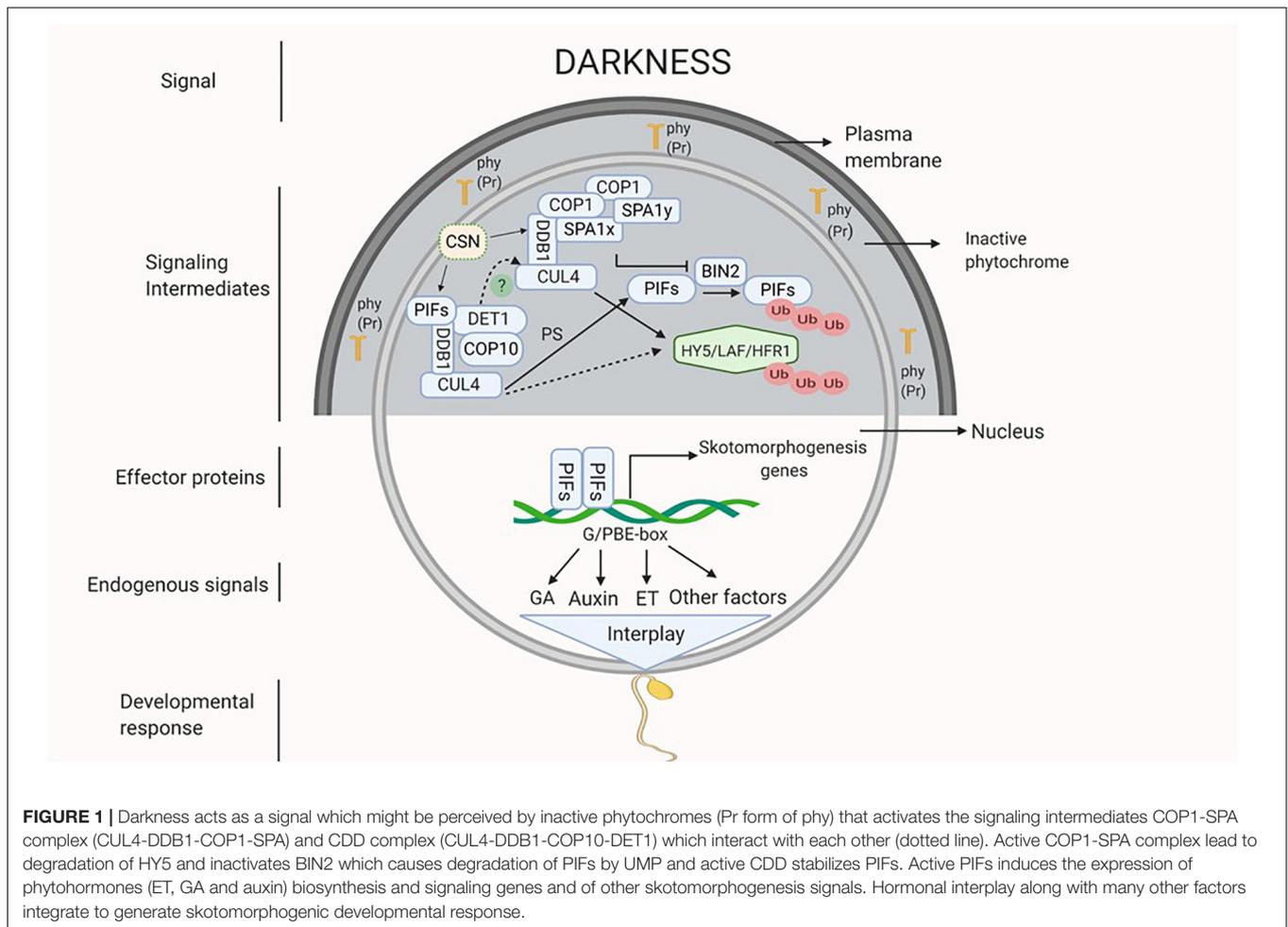
function of CSN complex is to derubylate and thus positively regulates the activity of CUL4 which is present on both COP1-SPA and CDD complexes (Chen et al., 2010; Dong et al., 2014). Additionally, DET1 interacts with PIFs under darkness to stabilize them (Dong et al., 2014; Pham et al., 2018). PIFs in turn activate a diverse set of hormone biosynthetic and signaling genes that promote etiolation and repression of photomorphogenic response (Leivar et al., 2008; Paik et al., 2017). In *Arabidopsis*, PIF1, 3, 4, and 5 are involved in skotomorphogenesis, as indicated by normal light-grown seedling like growth of quadruple mutant *pif1pif3pif4pif5* (*pifq*) under complete darkness (Dong et al., 2014; Pfeiffer et al., 2014).

In the forthcoming sections, how darkness regulates development of specific skotomorphogenic structures such as, apical hook, elongated hypocotyls, and shortened roots is discussed.

HORMONAL REGULATION OF PLANT DEVELOPMENT IN DARK

Apical Hook Development

Within 24 h of seed germination, after hypocotyl elongation, darkness induces the development of an apical hook (Mazzella et al., 2014) with curvature formation by modulating several hormonal pathways (de Wit et al., 2016). An asymmetrical distribution of auxin (auxin concentration increases at concave side and inhibit cell expansion) causes differential cell expansion and division at both the sides of the hypocotyl. This leads to faster growth at the outer side compared to inner side, which culminates in the hook formation (Béziat and Kleine-Vehn, 2018; Gommers and Monte, 2018; Wang and Guo, 2018). Asymmetric distribution of auxin is facilitated by the influx and efflux carriers on the cell membrane. In *Arabidopsis*, influx carriers AUXIN1 (AUX1) and LIKE AUXIN (LAX3) localize at the epidermal cells and vascular cylinder of the hook. These carriers facilitate the polar and basipetal flow of auxin from shoot apical meristem and cotyledons to hypocotyl. Efflux carrier PIN1 facilitates the outward flow of auxin through vascular cylinder and inner epidermis. PIN3 facilitates the auxin flow from vascular tissues to outer cortex and epidermis, whereas PIN4 and 7 support the auxin flow from vascular tissue to cortex and epidermis. In addition, ABCB transporter 1 and 19 which are localized at inner epidermal cells of the hook, steer the auxin transport to the convex side (Vandenbussche et al., 2010; Wu et al., 2010; Žádníková et al., 2010, 2016; Farquharson, 2017; Wang and Guo, 2018). The maintenance of differential auxin gradient involves the co-ordination of auxin synthesis, transport and signaling. YUCs and TAR2 are the flavin monooxygenases and tryptophan aminotransferase related enzymes, which, respectively, catalyze two initial steps in the auxin biosynthesis pathway. These genes are differentially expressed in the apical hook region and their mutants (*yuc1/2/4/6*, *tar2*) display impaired hook phenotype due to developmental defects (Stepanova et al., 2008, 2011; Vandenbussche et al., 2010; Abbas et al., 2013; Cao et al., 2019). The auxin signaling mutants like *iaa3*, *iaa12* and *iaa13* lack apical hook, suggesting the involvement of auxin signaling in apical



hook formation. Moreover, AUX/IAAs regulate auxin signaling effector proteins; auxin response factors (ARFs) (Žádníková et al., 2010, 2016; Abbas et al., 2013).

The apical hook development is tightly regulated by signals from cell wall and root-hypocotyl interaction. The cell wall status affects apical hook bending by transcriptional regulation of *PINs* and *AUX1* through ARF2 (Aryal et al., 2020; Sampathkumar and Eng, 2020). Recently, it was shown that auxin gradient formed at the root tip by PIN2 is required for root growth in response to gravity (Zhu and Gallem, 2019). The root auxin gradient gradually extends toward hypocotyl and might trigger the hypocotyl bending resulting in hook formation. A balanced concentration of hormones ABA and GA has been shown to be essential for a close interaction between root and hypocotyl (Baral et al., 2020).

PIFs have been involved in different aspects of gradient formation such as, auxin synthesis and polar auxin transport (PAT). In *Arabidopsis*, PIF4 and PIF5 induce the expression of *YUCCA* genes (Pfeiffer et al., 2014) and PIN localization regulatory kinase *WAG2* (Willige et al., 2012; Mazzella et al., 2014). Darkness induced phytohormones such as, GA and ethylene (ET) affect PAT indirectly by modulating the expression of *WAG2* (Willige et al., 2012) and *ETHYLENE INSENSITIVE*

3/EIN3-LIKE1 (EIN3/EIL1) (Wabnik et al., 2016; Wang and Guo, 2018). PIFs and EIN3/EIL1 co-regulate the curvature formation by directly binding to *HOOKLESS 1 (HLS1)* promoter. *HLS1*, which codes for a putative N-acetyltransferase and transcriptionally regulated by EIN3/EIL1 is a key regulator of apical hook development (Wang and Guo, 2018). Markedly, PIFs enhance the expression of *HLS1* by binding to its promoter at a site different from that of EIN3/EIL1. In addition, PIFs work in tandem with EIN3/EIL1 to integrate hormonal signals such as, GA, JA, and physical factors including, light and mechanical pressure (Zhang et al., 2018). Besides acting along with PIFs, EIN3 also induces the expression *PIF3* (Zhong et al., 2012). Also, divergent roles of ET in the light- and dark- mediated seedling growth are recently shown (Yu and Huang, 2017; Harkey et al., 2018, 2019; Gu et al., 2019).

In response to darkness, GA accumulates and binds to its receptor gibberellin insensitive dwarf 1 (GID1) and targets DELLAs (GAI, RGA), the negative regulators of GA signaling for UMP degradation (de Lucas et al., 2008). GA is essential for skotomorphogenesis as GA mutant *ga1* seedlings and GA biosynthesis inhibitor Paclobutrazol (PAC) treated seedlings show light-grown phenotype and are unable to form hook even when grown in the complete darkness (Achard et al.,

2007; Feng et al., 2008; Arana et al., 2011; Zhang et al., 2018). Antagonistic to auxin, GA promotes cell expansion and division on the convex side of hypocotyl (Alabadí et al., 2008; Arana et al., 2011).

In darkness, ET synthesis is enhanced by the transcriptional activation of ACS8 by PIF5 in GA dependent manner (Arana et al., 2011). In addition to darkness, physical factors such as, soil depth and compactness, mechanical pressure generated by hypocotyl against soil induce ET production (Zhong et al., 2014; de Wit et al., 2016). ET positively regulates skotomorphogenesis as dark-grown seedlings when treated with exogenous ET, produces exaggerated hooks (Mazzella et al., 2014). Similar to auxin and GA, ET also regulates cell division but at the apical basal parts of the hook. In addition, ET maintains auxin gradient by regulating its synthesis, transport and signaling (An et al., 2012; Chang et al., 2013; Wang et al., 2014; Wabnik et al., 2016; Zhang et al., 2018). JA and SA both are negative regulators of apical hook formation, and both of them act by disrupting ET signaling. JA activated MYC2 promotes the degradation of EIN3/EIL1. Also, MYC2 and NON-EXPRESSION OF PR GENES1 (NPR1, SA signaling mediator) individually interact with EIN3 and inhibits its binding to the promoter of *HLS1* (Zhang et al., 2018; Bertoni, 2020; Huang et al., 2020).

Hypocotyl Elongation

Another remarkable phenotype observed under darkness is an elongated hypocotyl. Darkness leads to this phenotype by modulating the levels of phytohormones such as, auxin, BR, ET, and GA (Reed et al., 2018). Irreversible increase in the plant organ size is primarily caused by cell expansion. Expansion of a cell is characterized by the vacuole enlargement and selective cell wall loosening, which releases the wall pressure and allows the water to flow inside (Cosgrove, 2016a,b). Consistently, the up-regulation of several auxin responsive cell wall loosening related genes such as, *EXPANSINs* (*EXPA4,11*), *EXPANSIN- LIKE* (*EXLA3*) and *XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE* (*XTH18,19*) was found in dark-grown seedlings (Cosgrove, 2005; Orden et al., 2010; Majda, 2018). Auxin acidifies the wall matrix by stimulating the activity of epidermal cell H⁺-ATPases and K⁺ channels, thereby, generating the turgor pressure (Ivakov et al., 2017; Majda, 2018; Duman et al., 2020). Therefore, cell wall remodeling by auxin and cell wall generated signals promotes hypocotyl elongation. PIFs maintain auxin gradient and induce the expression of wall loosening enzymes (Rougemont et al., 2012; Leivar and Monte, 2014). PIF4 remains functional under darkness by binding directly to BR stabilized protein BZR1 (Wang et al., 2012). Active PIF4-BZR1 module positively regulates the synthesis of GA by targeting DELLAs. Thus, darkness acts through the functional PIF4-BZR1 by regulating the level of phytohormones. ABA has been found to be a negative regulator of hypocotyl elongation in the dark-grown seedlings. ABA induces the expression of DELLAs (*GAI* and *RGA*) and inhibits the expression of auxin biosynthetic genes and membrane H⁺-ATPases (Hayashi et al., 2014; Lorrai et al., 2018).

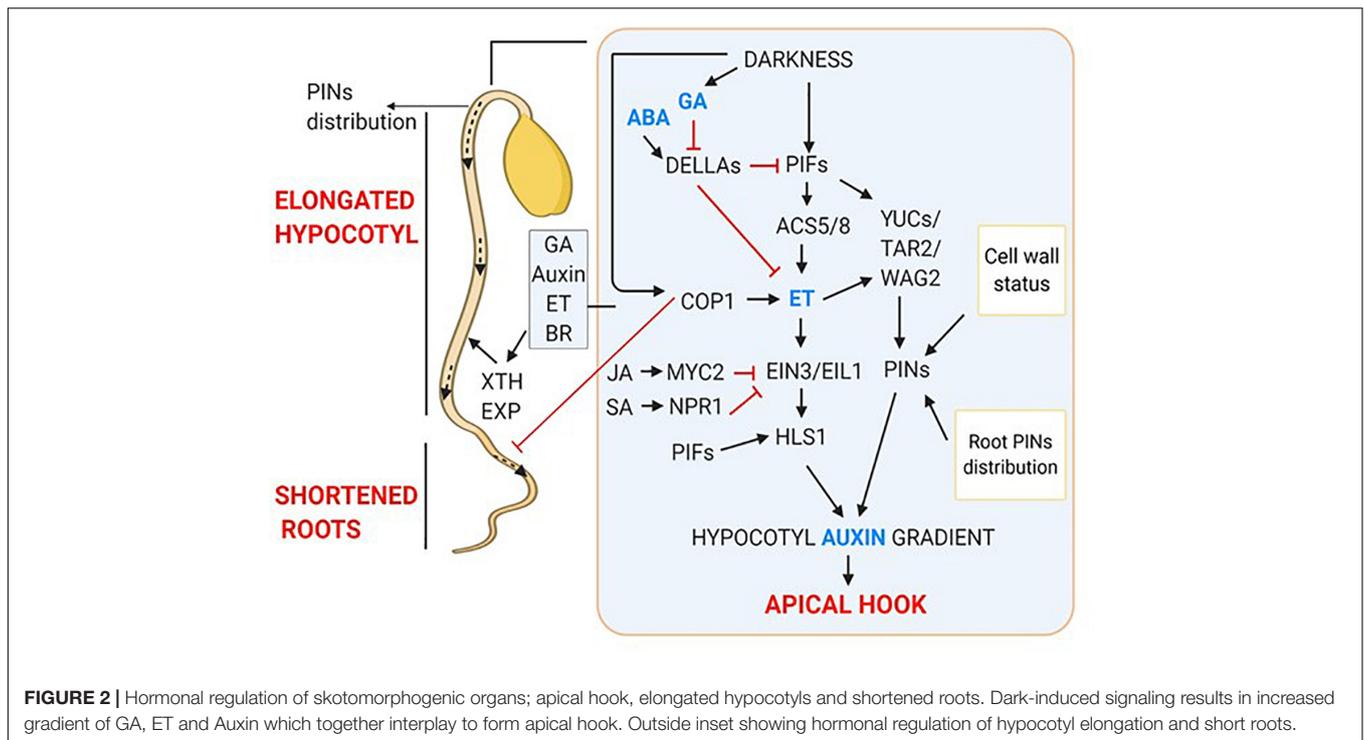
Shortened Roots

Like shoots, roots also sense light, consequently, root morphology is altered after light perception (Lee et al., 2017). Dark-germinated seedlings have short and thin primary roots with reduced lateral roots, whereas, the phenotype is reversed after light exposure (Dyachok et al., 2011). So, how the dark signaling represses root growth, and the light perceived at axial end of the plant alters root morphology is a curious question?

When light grown seedlings were decapitated or treated with PAT inhibitors, they showed inhibition of lateral root development (Salisbury et al., 2007), like the etiolated seedlings. This indicated that auxin synthesized in cotyledons in response to light acts as a positive regulator of lateral root emergence. Also, light facilitates auxin transport from apical part of shoot to root (Lee et al., 2016, 2017). In darkness, COP1 inhibits *PIN1* gene expression in shoot. *PIN1* is essential for shoot to root PAT therefore, repression of its expression leads to the root growth suppression. But, when shoot is exposed to light, COP1 moves out from the nucleus, relieving the suppression of *PIN1* gene expression (Sassi et al., 2012; Gangappa and Botto, 2016). The *HY5* deficient mutant also exhibits defects in lateral root elongation and growth, suggesting the involvement of *HY5* in maintaining shoot to root continuum (Sibout et al., 2006). Light activates photoreceptors which interact with COP1, leading to its inactivation. Light-dependent inactivation of COP1 inhibits COP1 mediated degradation of *HY5* thereby, promoting *HY5* activity. Interestingly, light stabilized *HY5* targets COP1 for degradation, thereby, shoot to root PAT is resumed that leads to altered root morphology (Mazzella et al., 2014). Moreover, *HY5* translocation from shoot to root promotes root growth (Zhang et al., 2017). The dark-induced hormonal regulation of skotomorphogenic development is summarized in **Figure 2**.

Photoperiodic Flowering

Plants sense diurnal variations which affect flowering and accordingly are classified as short- day, long-day and day neutral plants. Importance of darkness in short-day plants is evident from the fact that disruption of dark period with light significantly affects flowering (Andrés and Coupland, 2012; Johansson and Staiger, 2015; Cao et al., 2016). Under long-day condition, light inhibits the expression of flowering genes; *HEADING DATE 3A* (*HD3A*) and *RICE FT-LIKE1* (*RFT1*) in rice by activating an inhibitor *HEADING DATE 1* (*HD1*), whereas, under short-days, *HD1* induces the expression of *HD3A* and *RFT1* (Ishikawa et al., 2005). Interruption of long duration of darkness with short exposure of light induces *PHOTOPERIOD1* (*PPD1*) mediated activation of *FT1*, which after moving from leaves into shoot apical meristem promotes accelerated flowering in wheat (Pearce et al., 2017). Moreover, a night break (NB) causes transcriptional up-regulation of *PPD1* in wheat, levels of which increases with multiple NB and length of darkness. Thus, a period of darkness plays an important role in regulating photoperiodic flowering in plants.



Light- and Dark-Dependent Plastid Development

Development of plastids could be understood by the studies on the dark-grown seedlings. Plastids could be of various types like, proplastids, eoplasts, etioplasts, chloroplasts and chromoplasts based on their morphological characters, function and tissue location (Liebers et al., 2017). In the cotyledon of the dark-grown seedlings, eoplasts develop into etioplast and at this stage, the development of a prolamellar body (PLB) occurs (Bastien et al., 2016). A PLB is made up of regular arrangements of NADPH, the chlorophyll precursor protochlorophyllide (Pchlde), protochlorophyllide-oxido-reductase (POR), and the thylakoid membrane lipids monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG). In light, various nuclear genes which code for chloroplast biogenesis related proteins are expressed. This results in thylakoid membrane development and POR induced chlorophyll biosynthesis. The proplastids in the shoot apical meristem are directly converted to chloroplast during primary leaf development (Liebers et al., 2017).

Molecular Aspects of Plastid Development

TFs involved in early developmental process regulate the expression of plastid development related genes. PIF1 and PIF3 accumulate in dark-grown seedlings and repress the chlorophyll biosynthesis genes, whereas, in response to red light PIFs undergo active phy (Pfr) mediated degradation (Gommers and Monte, 2018; Hernández-Verdeja et al., 2020). Similarly, in light, EIN3 is directly targeted and degraded by crys and phys (Gommers and Monte, 2018).

In an early response to light the expression of *HY5*, which regulates the downstream components of chloroplast development, is induced. In dark *COP1* mediates the degradation of *HY5* and stabilization of *PIF* and *EIN3*. Under blue light, cryptochrome represses the expression of *COP1* leading to enhanced *HY5* activity, which is required for chloroplast development (Hernández-Verdeja et al., 2020). *PIFs* and *HY5* act as negative and positive regulators, respectively, of chlorophyll and carotenoid synthesis. Therefore, *PIFs* and *HY5* compete for the same binding site (G-box) on the promoter of common target genes, and eventually they regulate chloroplast development antagonistically (Toledo-Ortiz et al., 2014). In addition, *HY5-PIF* module controls the photosynthetic gene transcription by regulating *PHYTOENE SYNTHASE (PSY)* gene, which catalyzes a rate limiting step in carotenoid biosynthesis pathway (Toledo-Ortiz et al., 2014). Thus, the *PIF-HY5* regulatory mechanism is crucial for the proplastid development. Golden2-Like (GLK) nuclear TFs which work independently of phytochromes and *PIFs* are also the key regulators of plastid biogenesis (Liu et al., 2020). *GLKs* strongly activate the chlorophyll biosynthesis enzymes and light-harvesting chlorophyll binding proteins including, GlutRNA reductase (*HEMA1*), magnesium chelatase (*CHLH*), pchlde oxidoreductase (*POR-B*) and chlidea oxygenase (*CAO*).

Two RNA polymerases; nuclear encoded RNA polymerase (*NEP*) and plastid encoded RNA polymerases (*PEP*) are involved in the proplastid biogenesis (Hernández-Verdeja et al., 2020). In dark, plastid gene transcription is driven by *NEP* whereas, upon light exposure, transition of *NEP* to *PEP* occurs leading to *PEP* driven transcription. In light, the main transcriptional activity is taken-up by *PEP*, thus, the transcription of *PEP* associated genes

increases. PRIN2, a plastid localized redox regulated protein is required for PEP activity. In dark, PRIN2 forms a homo-dimer via di-sulfide bonds, however, upon exposure to light it get reduced to PRIN2 monomers, and contributes to PEP activity (Díaz et al., 2018). PEP mediated increase in transcription and light induced communication between developing chloroplast and nucleus through antero-retrograde signaling results in completion of chloroplast biogenesis (Pogson et al., 2015).

Hormonal Regulation of Plastid Development

Some phytohormones control the chlorophyll biosynthesis, thereby, regulate the chloroplast biogenesis. For example, in the dark-grown *Arabidopsis* seedlings cytokinin treatment induces the formation of prothylakoids whereas, these thylakoid membranes developed after about 6 h of light treatment in cytokinin untreated seedlings (Cortleven and Schmölling, 2015). The chlorophyll biosynthesis begins with the conversion of glutamate to 5-aminolevulinic acid (ALA), followed by the production of chlorophyll precursor, Pchlide. POR catalyzes the conversion of Pchlide into chlorophyllide which after esterification forms chlorophyll. Cytokinin promotes ALA synthesis and enhances POR activity to support the chloroplast biogenesis (Liu et al., 2017). GA regulated DELLA proteins are involved in the induction of *PORA* and *PORB* genes (Cheminant et al., 2011). Involvement of ET signaling has also been found in plastid development. In the double mutant of ET signaling; *ein3eil1* expression of Pchlide/chlorophyll synthesis genes *HEMA1*, *GUN4*, and *GUN5* was increased under darkness. PIF3 has been known to inhibit the expression of these genes (Stephenson et al., 2009; Shin et al., 2009), consistently, their expression was higher in *pif3* mutant. Moreover, *ein3eil1mutant* but not *pif3* had reduced expression of *PORA* and *PORB* genes. Thus, EIN3/EIL1 negatively regulate Pchlide/chlorophyll biosynthesis through PIF3, but stimulate *PORA* and *PORB* independently of PIF3 (Zhong et al., 2014). These observations clearly suggest the crucial role of phytohormones in plastid development.

Shade Avoidance: An Intermediate Response Between Light and Dark

Due to their sessile nature, plants face shade arising from the neighboring vegetation canopies. In the shade, plants compete for their resources particularly red/far-red (R:FR) photon flux ratio. In response to shade, plants channelize their energy toward hypocotyl and stem elongation, enhanced apical dominance and early flowering, all of them collectively termed as shade avoidance syndrome (SAS) (de Wit et al., 2016). Along with photoreceptors, phytohormones like ET, GA, Auxin, and BR are implicated in shade-induced plant responses (Das et al., 2016; Yang and Li, 2017).

In the past decade, shade related research was carried out mainly in *Arabidopsis*, and indicated a crucial role of auxin in the shade avoidance response (Sessa et al., 2018). In the *Arabidopsis* seedlings, auxin accumulates in response to shade resulting in hypocotyl cells elongation (Ma and Li, 2019).

A low R:FR ratio (as in case of shade) has been found to promote petiole elongation in *Arabidopsis* (Roig-Villanova and Martínez-García, 2016). Phytochrome B (phyB) is the key shade avoidance response regulating photoreceptor, whereas, phyD and phyE function redundantly in promoting shade-induced elongation (Franklin et al., 2003). In contrast, phyA represses the elongation response induced by low R/FR light (Martínez-García et al., 2014). phyB becomes active in the presence of light having high R:FR ratio. Upon activation, it translocates into the nucleus and interacts with PIFs. This interaction causes phosphorylation and subsequent inactivation of PIFs leading to their degradation via UMP (de Wit et al., 2016). Hence, PIF-dependent transcriptional activation of auxin homeostasis and cell wall remodeling related genes is inhibited (Courbier and Pierik, 2019). While, under light of low R:FR, phyB remains inactive, thus allowing PIFs to accumulate and induce the transcription of *YUCCA* genes (Müller-Moulé et al., 2016), resulting in enhanced auxin concentration in the cell. PIF4, 5, and 7 directly regulate several auxin biosynthesis and signaling genes in response to shade (Hornitschek et al., 2012; Li et al., 2012). A HomeoBox2 (ATHB2) TF acts as a positive regulator and Long Hypocotyl in Far-red 1/Slender In Canopy Shade 1 (HFR1/SICS1) (an atypical bHLH protein), acts as a negative regulator of PIFs controlled shade avoidance response (Sessa et al., 2018). Cryptochromes (*cry1* and *cry2*) are involved in low blue light (LBL)-induced shade avoidance response. CRY1 and CRY2 physically interact with PIFs and regulates their activity for LBL induced hypocotyl growth (Ma et al., 2016; Sessa et al., 2018).

Phytohormones in Shade Avoidance Response

Upon low R: FR exposure, bioactive GA levels increases and the accumulated GA inhibits the DELLAs. The DELLA proteins directly interact with PIFs and this interaction prevents PIFs binding to DNA, thereby, negatively regulating the expression of cell elongation related genes (Li et al., 2016). Moreover, GA is implicated in shade-induced flowering, as silencing *GA20ox2* expression results in delayed flowering in *Arabidopsis* under far-red light conditions (Yang and Li, 2017). In addition, ET is proposed to be a positive regulator of shade-induced petiole elongation, and is involved in organ specific shade avoidance response (Yang and Li, 2017). ABA biosynthesis mutants, *nced3-2* and *aba2-1* show increased branching under low R:FR suggesting that ABA suppresses branching under shade (Yang and Li, 2017). NPR1 also plays a crucial role in petiole elongation in shade (Nozue et al., 2018). Interestingly, elevated auxin and BR production in response to PIFs activation under low R:FR light costs both SA and JA based defenses (Martínez et al., 2018).

Day-Night Transitions

The rhythmic behavior of the biological processes is maintained by an endogenous oscillator/pacemaker called the circadian clock. This clock, under natural conditions maintains a period of 24 h, regulated by transitions from day to night (light/dark) and vice versa. As the clock is tightly coupled with diurnal cycles, it modulates many gene regulatory networks (GRNs) based on

time of the day. When an organism is subjected to constant light or dark for a longer time, the rhythms dampen out and require transition from the existing environment. Since, plant life begins under complete darkness, the seedling growth during this period is clock independent, till it experiences light/dark (photoperiod) cycles (Salome et al., 2008). The fact that *Arabidopsis* seedling growth becomes photoperiod sensitive after de-etiolation was established by growing plants in continuous light and dark, separately. Until 12 h, similar hypocotyl length was observed in both conditions, and only prolonged exposure of darkness (> 12 h) resulted in elongated hypocotyls, suggesting the process to be short-day specific (Niwa et al., 2009; Seluzicki et al., 2017). Then, how clock is integrated with photoperiod after de-etiolation, was disclosed by the growth pattern of WT and clock mutants (*CCA1-ox* and *elf3*) seedlings in short-day conditions. WT seedlings elongated normally after prolonged darkness, but in both the clock mutants seedling elongation started at the beginning of the dark period and continued till it prolonged, indicating an inhibitory effect of clock genes during initial hours of darkness (Fankhauser et al., 2007). Interestingly, temporal transcriptional induction of *PIF1*, 3, 4, and 5 was also observed during late-night hours coinciding with the seedling etiolation (Leivar et al., 2012). PIFs are degraded during the day through PHY mediated photobodies, and are kept in check during early-night by clock evening complex (EC) genes (Huang et al., 2016). Another clock complex gene, *TIMING OF CAB EXPRESSER 1* (*TOC1*) represses PIFs level during early- and mid-night (Soy et al., 2016; Paik et al., 2017). Therefore, clock exerts its effect by controlling the temporal expression of *PIF* genes under darkness.

Dark-Induced Senescence

Senescence is an age triggered developmental process characterized by an ordered and programmable degradation. The degradation involves the mobilization of building blocks at various levels of organization e.g., cell, tissue, organ and the organism, culminating in plant death (Lim et al., 2007). Its initiation, progression and completion are tightly linked to various external and internal cues (Kim et al., 2016; Law et al., 2018). Darkness is one of the external cues that positively regulate leaf senescence, and the process is called dark-induced senescence (DIS). DIS is physiologically quite different from an age-triggered leaf senescence (Kiddle et al., 2011). Interestingly, darkness only promotes senescence of individual plant organs, and inhibits senescence at the whole plant level (Keech et al., 2010; Sakuraba et al., 2014; Law et al., 2018), suggesting the involvement of other factors for death of the whole plant.

PIFs involvement in DIS became evident when *PIF* single and quadruple (*pifq*) mutants exhibited delayed leaf senescence, and their overexpressing plants showed the opposite phenotype (Song et al., 2014). Moreover, *PIF3*, 4 and 5 were significantly up-regulated in both age triggered senescence and DIS. Evidences indicate that PIFs mediate transcriptional activation of many SENESCENCE ASSOCIATED GENES (SAGs), i.e., *STAY GREEN 1* (*SGR1*) and *NON-YELLOW COLORING1* (*NYC1*) and other senescence promoting TFs such as *WRKY22* and *NAC* (Zhang et al., 2015). Additionally, *PIF4/5* have

been shown to transcriptionally enhance the expression of *ABSCISIC ACID 5* (*ABI5*) and *ENHANCED EM LEVELS* (*EEL*) (Qi et al., 2020). *ABI5*, *EEL*, and PIFs act together in a coherent feed forward loop to increase the expression of *ORESARA1* (*ORE1*), a master regulator of senescence. Subsequently, PIFs, *ORE1*, *ABI5*, and *EIN3* interplay to activate SAGs which finally lead to breakdown of chlorophyll, degradation of photosynthetic machinery culminating in leaf senescence (Sakuraba et al., 2014; Qiu et al., 2015; Liebsch and Keech, 2016).

CONCLUSION AND FUTURE DIRECTIONS

Dark and light independently activate diverse signaling pathways which alter the levels of plant growth regulators consequently leading to a specific response. Efforts made in the past two decades in the area of skotobiology have advanced our understanding of how plant behaves and make sense of the dark period. The role of multifunctional dark signaling intermediates COP/DET/FUS and transcription factor PIF has been explored in diverse areas. We have provided the latest information about darkness acting as a signal during various plant growth processes such as, skotomorphogenesis, day-night transitions, shade avoidance, and senescence. Differential accumulation of several phytohormones, their regulatory effects on diverse molecular components and, in turn, the interplay of molecular players that determines the pattern of growth and development in dark has been elaborated. However, a complete understanding of the dark and light signaling integration needs exploration of the inter-organ communication mechanisms, necessary for establishment/transfer of hormonal gradients. Also, the hormonal interplay and regulatory mechanism underlying the integration of other subterranean environmental cues such as, soil compactness, temperature, biotic and abiotic factors with dark signaling, is still enigmatic and requires in-depth exploration in future.

AUTHOR CONTRIBUTIONS

AS conceptualized and designed the study. Deepika, Ankit, and SS compiled the data. Deepika, Ankit, and AS wrote the manuscript. All authors read and approved the final version of the manuscript.

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Conflict of Interest: The authors declare that the research 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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