Proceedings of the International Conference on Plant Developmental Biology

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PREFACE

Plant developmental biology has emerged as an area of tremendous significance in the fields of basic research, agriculture, health, industry, and environmental protection. Plants, being sessile, must cope with their environment and the changes associated with it. Light is apparently the most important environmental cue for a developing plant. In addition to photosynthesis, light regulates plant growth and development. With the advent of genomics-based technology, it is now possible to address biological questions or altered phenotypes, which was previously unimaginable. Recent advances in developmental biology, molecular techniques along with computational biology have resulted in incredible information related to molecular processes and attenuations that occur in various conditions of biotic and abiotic stress. The objective of the International Conference on Plant Developmental Biology was to review and put together the knowledge gained from the various developmental research programs happening all over the world with special focus on photomorphogenesis. The seminar comprised of keynote addresses from The Director, National Institute of Science Education and Research (NISER), The Director, Institute of Life Sciences (ILS) and The Chairperson along with plenary lectures, invited talks, oral presentation sessions from students and young scientists, and poster presentations on various plant developmental biology related topics. The seminar provided a platform for sharing knowledge, to help arriving at many definite conclusions on several developmental processes and to sensitize young researchers and budding biotechnologists to promote laboratory research. The Proceedings bring together review articles and research papers from the registered participants of the conference. We hope that this book of proceedings will help students, teachers, researchers, and scientists to gain knowledge as well as to make new research plans in the field of plant developmental biology. We are extremely grateful to the contributing authors for their support in bringing out these proceedings. We are also thankful to our well-wishers for their constant support and encouragement to conduct the conference. We are thankful to The Director of NISER, Professor S. Panda for the constant encouragement. We are thankful to the government and private sector funding agencies for sponsoring the

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REVIEW ARTICLES

REVIEW PAPER 1

INFLUENCE OF LIGHT-HORMONE INTERACTION ON SEEDLING DEVELOPMENT IN *ARABIDOPSIS THALIANA*

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Abstract

Root and hypocotyl development is influenced by various extrinsic and intrinsic factors. Extrinsically, the quality and quality of light impacts plant development in a variety of ways, while phytohormones act as intrinsic factors regulating the development. Besides, each phytohormone affects the development of root and hypocotyl differently. In the current review, the interactive role of light and phytohormones in root and hypocotyl development has been summarized. Phytohormones play different roles in root and hypocotyl development based on the availability, intensity, and wavelength type of light. Further, light and phytohormones affect the root development and hypocotyl development differently.

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Abbreviations

ET	Ethylene
HY5	Elongated hypocotyl
PHYB	Phytochrome B
TIR1	Transport inhibitor response 1

Introduction

Plant growth and development includes various processes beginning with seed germination and stretching up to senescence and death. Different stages of plant life cycle depend on various internal and external factors. Phytohormones are the intrinsic/internal factors, which regulate the plant growth, whereas environmental aspects such as light, water, gravity, temperature are the extrinsic/external factors. Among the environmental factors, light plays the most crucial role in the proper plant growth and development.

Phytohormones are plant growth regulators and are of various types, such as auxin (IAA), cytokinin (CK), gibberellin (GA), abscisic acid (ABA), ethylene (ET), strigolactone (SL), jasmonic acid (JA), brassinosteroid (BR), and salicylic acid (SA). These phytohormones play different roles in plant development and regulate processes such as seed germination, root development, hypocotyl growth, fruit development, etc.

Plants have developed different photoreceptors, which can sense the quality as well as the quantity of light. The major photoreceptors present in plants are phytochromes (*PHYs*), cryptochromes (*CRYs*), phototropins (*PHOTs*) and *UVR8*. Phytochromes are primarily red and far-red light photoreceptors, cryptochromes and phototropins are meant for perceiving blue light, and *UVR8* is involved in perceiving ultraviolet B (UV-B) light. These photoreceptors control various developmental processes occurring throughout the plant life cycle.

Photomorphogenesis and skotomorphogenesis are the most important aspects of seedling development regulated by light. Photomorphogenesis is defined as the light-mediated plant development, whereas skotomorphogenesis refers to the developmental processes occurring in the absence or low intensity of light. In the early seedling stages, these developmental aspects control the root and hypocotyl generation and development.

Light regulates root and hypocotyl development by promoting primary root growth, lateral root branching, and inhibiting hypocotyl elongation. Under darkness, hypocotyl elongation is enhanced and root development is hampered. Different photoreceptors control these aspects by regulating the downstream light-signaling components.

The phytochrome family consists of five members: phytochromes A to E (*PHYA–E*). It has been established that *PHYA, PHYB,* and *PHYE* promote lateral root generation, while *PHYD* hampers this activity. Additionally, *PHYA* and *PHYB* have been found to enhance the rate of lateral root growth (Salisbury *et al.* 2007). The transcription factors downstream to *PHYs,* such as elongated hypocotyl 5 (*HY5*) and its homolog elongated hypocotyl H (*HYH*) have been reported to inhibit the root growth (Sibout *et al.* 2006).

There are two types of cryptochromes present in plants, namely *CRY1* and *CRY2*. They have been found to act in opposite ways to affect primary root elongation, i.e., *CRY1* promotes primary root elongation whereas *CRY2* inhibits this (Canamero *et al.* 2006). Recently, *UVR8* has been found to inhibit primary and lateral root development (Fasano *et al.* 2014).

Phytohormones are also involved in root and hypocotyl development, i.e., IAA, CK, GA, ET, JA, and BR play a primary role in root and hypocotyl development under normal conditions. Under stress, SA, ABA, and SL influence plant development. IAA promotes hypocotyl elongation, lateral root, and adventitious root formation (Chae *et al.* 2012; Aloni *et al.* 2006). CK inhibits hypocotyl growth in the dark, but no significant impact has been observed in light (Su and Howell 1995). CK acts antagonistically to IAA in root development, as it inhibits lateral root growth (Aloni *et al.* 2006). GA promotes hypocotyl elongation and suppresses photomorphogenesis under darkness (Alabadí 2004), but it has the least significant influence on root growth (Tanimoto 2005).

ET suppresses hypocotyl elongation in the dark and promotes it under light (Yu *et al.* 2013). In the presence of light, root growth is suppressed by ET, but it promotes the size and number of root hairs (Feng *et al.* 2017). Further, JA has a negative impact on hypocotyl elongation and primary root growth (J. Chen *et al.* 2013; Staswick, Su, and Howell 1992) while BR positively regulates hypocotyl growth and has dose-dependent effects on root development (Tanaka *et al.* 2003). It promotes root elongation and increases the number of lateral root numbers in lower doses, but has inhibitory effects in higher concentrations (Wei and Li 2016; González-Garcí a *et al.* 2011). SA promotes shoot growth and root length (Gutiérrez-

Coronado, Trejo-López, and Larqué-Saavedra 1998), while ABA affects the hypocotyl growth in a dose-dependent manner, has a positive effect on hypocotyl elongation in the dark, and a negative effect under light. Further, it plays an inhibitory role in primary root elongation (Xingju Luo *et al.* 2014). Finally, SL suppresses hypocotyl development and adventitious root formation in the hypocotyl (Jia *et al.* 2014; Rasmussen *et al.* 2012).

Both light and phytohormone are involved in the development of root and hypocotyl; it has been demonstrated that light and phytohormone signal cross talk at various stages, affecting these development aspects. The current review specifically focuses on the interactive role of light and phytohormones in the regulation of root and hypocotyl growth in thale cress (*Arabidopsis thaliana)*, a flowering plant.

Auxin and light interaction in regulating root and hypocotyl growth

Light regulates the synthesis, signaling, and transport of auxins. Auxin biosynthetic genes, *YUCCA*, have been found to be involved in end-of-the-day far-red (EOD-FR) response and shade-avoidance response (SAR) of plants. Shade or low R:FR treatment and EOD-FR treatment promote hypocotyl elongation. It has been reported that hypocotyl elongation is due to the upregulation of *YUCCA 2, 5, 8*, and *9* genes under the above-mentioned conditions. *YUCCA 2, 5, 8* and *9* genes come together in this response and they also enhance auxin signaling (Müller-Moulé *et al*. 2016).

Prolonged shade promotes the rate of hypocotyl elongation and under this condition, the activity of *PHYB* is reduced. As a result, there is an upregulation of downstream signaling component phytochrome interacting factor 4 (*PIF4*). Furthermore, the *PIF4* targets, such as indole-3-acetic acid 19 (*IAA19*) and *IAA29* are also induced. PIF4 is known to positively regulate hypocotyl elongation and inhibit photomorphogenesis. It has been found that transport inhibitor response 1 (*TIR1*), auxin signaling F-box protein 2 (*ABF2*), and auxin receptor (*TAAR*) genes are upregulated under shade, which further induces *IAA19* and *IAA29* genes; whereas, auxin response factor 6 (*ARF6*) is downregulated. The microRNA 393 (miR393), which is involved in maintaining auxin signaling, is also downregulated under shade. Therefore, prolonged shade enhances hypocotyl growth through altered auxin signaling and perception (Pucciariello *et al.* 2018).

It has been demonstrated that blue and red light-mediated inhibition of hypocotyl growth occurs through *CRY1*, *CRY2*, and *PHY*s, which directly

interact with auxin inducible genes *AUX/IAA*. Hence, blue and red light inhibit the auxin response and also prevent *TIR1/AFB*-mediated *AUX/IAA* degradation. *AUX/IAA* has been found to act downstream in the light-signaling pathway and is a common component where light and auxin signaling interact with one another (Xu *et al.* 2018). It was reported that the N-terminal domain of *CRY1* interacts with *AUX/IAA* to stabilize it, while the C-terminal domain of *CRY1* interacts with the *COP1-SPA1* complex to inhibit it, which further stabilizes *HY5*. These processes are involved in blue-mediated inhibition of hypocotyl elongation (Huq 2018).

Constitutive photomorphogenic 1 (*COP1*) was found to regulate the transcription of pin-formed1 (*PIN1*) in the shoot and *PIN2* and *PIN2* in the root. In dark conditions, *COP1* suppresses the *PIN1* expression in the shoot and hence inhibits shoot-to-root polar auxin transport (PAT). The decreased auxin level in the root reduces *PIN1* and *PIN2* in the plasma membrane and therefore alters the root development. Hence, *COP1* regulates root and shoot development by modulating *PIN* localization (Sassi *et al.* 2012).

Response to auxins and gibberellins 1 (*RAG1*) is a small auxin up *RNA 36* (*SAUR36*), which promotes hypocotyl elongation in the dark, but its expression is hampered in light. *RAG1* regulation is dependent on the GA and auxin signaling during hypocotyl elongation (Stamm and Kumar 2013).

Erecta (ER) is one of the receptor-like kinases that play a role in the shade-avoidance syndrome. It promotes hypocotyl elongation under shade through *PHYB* and is regulated by GA and auxin signaling (Du *et al.* 2018).

Blue and red light-mediated hypocotyl inhibition occurs through the downregulation of ATP binding cassette B19 (*ABCB19*). Therefore, the inhibition of hypocotyl is a result of the altered auxin level in the hypocotyl (Wu *et al.* 2010).

Cytokinin and light regulating root and hypocotyl growth

It has been reported that CK inhibits hypocotyl elongation in darkness and has no significant effect under light. Further, it has been observed that under white light, when ET action is hindered and IAA transport is disturbed, CK recovers the hypocotyl growth and induces hypocotyl elongation (Smets *et al.* 2005).

CK has been known to inhibit hypocotyl elongation in the dark, but also suppresses this growth under blue light. The blue light-mediated inhibition

of hypocotyl elongation occurs as CK prevents the degradation of *HY5* by *COP1*. However, *CRY*-mediated hypocotyl inhibition acts as an additional pathway, along with which other signaling pathways that are also involved in this phenomenon (Vandenbussche *et al.* 2007). In one of the reports, it has been demonstrated that a CK-insensitive mutant, grown fast on cytokinin 1 *(gfc1)* shows a de-etiolated phenotype of shorter hypocotyl in darkness, whereas under other light there is no obvious difference in hypocotyl elongation (Wu *et al.* 2015). CK induces root hair formation, causes reduced root growth, and results in a small root apical meristem (RAM). In phytochrome mutants, these phenomena are altered because of modulated CK signaling. Cytokinin independent 1 (*CKI1*) is upregulated in these mutants, which causes a reduction in the RAM activity and hence the altered root phenotype (Dobisova *et al.* 2017). Degradation of periplasmic proteins 9 (*DEG9*) is a serine protease and causes degradation of Arabidopsis response regulator 4 (*ARR4*). It is a member of the ARR family of cytokinin signaling. *DEG9* and *ARR4* are reported to play a role in the same CK signaling pathway and *DEG9* is present upstream of *ARR4*. *DEG9* has been shown to negatively control the *ARR4*-regulated hypocotyl and root growth and this occurs significantly under red light. Hence, *DEG9* acts as a connecting link between cytokinin and the red light-signaling pathway, regulating hypocotyl and root growth (Chi *et al.* 2016).

Ethylene and light crosstalk regulating root and hypocotyl growth

ET has been shown to affect hypocotyl elongation in different ways, depending on the availability and intensity of light. It promotes elongation of hypocotyl under light and inhibits its growth under darkness (Smalle *et al.* 1997; Zhong *et al.* 2012). The ET-mediated hypocotyl growth has been reported specifically under red light (Yu *et al.* 2013). In this differential effect of ET various transcription factors are involved, where a few belong to ET signaling and others are from the light-signaling pathways. Light-signaling components, such as *PHYB*, *PIF3, COP1,* and *HY5* have been found to control ET-mediated hypocotyl growth (Yu and Huang 2017). Ethylene response factor 1 (*ERF1*) is one of the elements belonging to the E3 ubiquitin ligase complex that has been shown to regulate this growth phenomenon. *PIF3* and *ERF1* are the major regulators playing important roles in the ET-mediated promotion of hypocotyl elongation under light and inhibition under dark respectively (Zhong *et al.* 2012). These two factors are regulated by ethylene insensitive 3 (*EIN3*) and the levels of *PIF3* and *ERF1* determine the differential hypocotyl elongation. ET promotes *COP1*

nuclear localization in the presence of light and hence causes *HY5* degradation, which in turn results in hypocotyl elongation. ET-mediated *COP1* nuclear localization and *HY5* degradation have been shown to be regulated by *EIN3*. It has also been reported that *COP1* and *HY5* are downstream to *EIN3*. In the dark, *ERF1* and wave-dampened 5 (*WDL5*) are responsible for the inhibition of hypocotyl elongation by ET (Yu *et al*. 2013). Light-activated *PHYB* binds with *EIN3* and F-box proteins; *EIN3*-binding F-box protein 1/2 (*EBF1/2*) increases the *EBF1/2-EIN3* interaction and results in the degradation of *EIN3* (Yu *et al.* 2013).

Coronatine insensitive 1 (*COI1*), one of the components of JA signaling and coronatine insensitive 1 (COI1-1), is a JA-insensitive null mutant. *COI1* forms an E3 ubiquitin ligase complex. It has been reported that in hook formation, JA acts as an antagonist to ET and this phenomenon is COI dependent. In ACC-mediated root development, *COI1* has been shown to play an important role. It has been shown that ACC-induced and *COI1*-mediated reduction in root growth is independent of JA biosynthesis and perception. This reduction in the root growth occurs in the presence of light, but not in darkness (Adams and Turner 2010).

Gibberellin and light regulating root and hypocotyl growth

GA promotes hypocotyl elongation in the dark, which occurs through the regulation of *PIFs* and *HY5*. GA negatively regulates *HY5* stability and this takes place through the altered activity of *COP1*. GA has also been found to positively regulate the *PIFs* in the dark. Decreased *HY5* stability and enhanced PIF activity promote hypocotyl growth in dark conditions (Alabadí *et al.* 2008).

In the presence of light, hypocotyl elongation is suppressed because of the inactivation of *PIF4* and *PIF5* as well as the reduction of GA. *PHYB* promotes degradation of *PIF4* through the 26S proteasome pathway and *DELLA* protein has been shown to suppress PIFs by binding with the bHLH DNA-recognition domain of *PIF* (de Lucas *et al.* 2008).

The response to auxins and gibberellins 1 (*RAG1*) is a small auxin upregulated *RNA 36* (*SAUR36*) gene, which is also an auxin and gibberellin integrator. *RAG1* has been found to positively regulate hypocotyl elongation under dark conditions whereas in light, the *RAG1* expression level goes down and suppresses the hypocotyl growth, exhibiting a de-etiolated phenotype (Stamm and Kumar 2013).

It has been reported that *CRYs* suppress GA accumulation under blue light and inhibit hypocotyl elongation. In the presence of blue light, *CRYs* are involved in promoting the expression of gibberellin 2-beta-dioxygenase 1(*GA2ox1*), which regulates the catabolism of GA and GA precursor. *CRYs* also downregulate *GA20ox1* and *GA3ox1* expression, which are involved in the synthesis of bioactive GAs (Zhao *et al.* 2007).

ABA and light regulating root and hypocotyl growth

ABA insensitive 5 (*ABI5*), an ABA signaling regulator, has been shown to promote a de-etiolated response with shorter hypocotyl in the presence of blue, red, and far-red light. This de-etiolated phenotype is because of *HY5* accumulation in the presence of light. *HY5* has also been involved in ABA-regulated suppression of lateral root growth and promotion of primary root growth. ABA regulates the root and hypocotyl growth by affecting *HY5* expression through *ABI5* (Chen *et al.* 2008).

A bifunctional regulator of abiotic stress and ABA signaling, *FIERY1* (*FRY1*) acts antagonistically to *HY5* with regard to light response of hypocotyl elongation as well as ABA sensitivity in lateral root growth. This shows the probability of *HY5* and *FRY1* playing a role in a common or overlapping pathway, and *HY5* acts downstream of *FRY1* (Chen and Xiong 2011).

Roots produce the reactive oxygen species (ROS) when exposed to light, which enhances root growth. Prolonged exposure to light causes oxidative stress in the root. Research studies have reported that *PHYB* induces ABA synthesis in the shoot and this ABA signal induces ROS detoxification in the root. Further, it has been demonstrated that ABA signaling interacts with the *PHYB*-mediated light perception and ROS equilibrium in the root which leads to proper root growth (Ha *et al.* 2018).

Brassinosteroids and light regulating root and hypocotyl growth

Brassinazole-resistant 1 (*BZR1*) is a positive regulator of the BR signaling pathway. It suppresses photomorphogenesis by interacting with GATA 2 (transcription factor in the light-signaling pathway) and inhibiting its transcription (Luo *et al.* 2010). *BZR1* has also been found to interact with *PIF4* to promote etiolated phenotype (Oh, Zhu, and Wang 2012). It also interacts with *COP1* which degrades the inactive form of *BZR1* and

enhances its active form, which leads to hypocotyl growth promotion though BR signaling (Kim *et al.* 2014).

The antagonistic role of *BZR1* and *HY5* in hypocotyl elongation was demonstrated by Li and He (2016). *BZR1* was found to interact with *HY5*, which in turn binds itself to the dephosphorylated active form of *BZR1* and suppresses its transcriptional activity. Under darkness, *BZR1* exists mostly in its active form and a little amount of *HY5* is present. These evidences support that *BZR1* promotes skotomorphogenesis and shows that *BZS1* along with *BZR1* is a BR signaling component, which connects the light and BR signaling pathways. *BZS1*, a repressor of BR response, promotes photomorphogenesis. It interacts with *COP1* and light regulates *BZS1* through a *COP1*-mediated degradation pathway (Fan *et al*. 2012). BR-enhanced expression (*BEE*) and *BES1*-interacting myc-like (*BIM*) are the BR signaling components that interact with phytochrome rapidly regulated 1 (*PAR1*) and are involved in shade-regulated hypocotyl elongation. *BEE* and *BIM* have been shown to positively regulate the shade-avoidance syndrome (SAS) mediated hypocotyl growth. They act synergistically in shaded or non-shaded light conditions (Cifuentes-Esquivel *et al.* 2013). Cogwheel 1 (*COG1*) encodes a DOF transcription factor and is involved in the development of the seed coat. Cogwheel 1-3D (*COG1-3D*) is involved in BR response and was previously found to act as a suppressor of the phytochrome signaling pathway. *COG1* interacts with *PIF4* and *PIF5,* and induces its expression. They upregulate BR biosynthetic genes, such as DWARF4 (*DWF4*) and brassinosteroid-6-oxidase 2 (*BR6OX2*). Therefore, *PIF4* and *PIF5* promote hypocotyl elongation through BR synthesis (Wei *et al.* 2017). Phytochrome B activation-tagged suppressor 1 (*BAS1*) encodes P450 mono-oxygenase, which is upregulated by light signaling. It deactivates BRs and promotes photomorphogenesis (Turk *et al.* 2003). Suppressor of *PHYB-4 7 (SOB7)*, one of the analogs of *BAS1*, was found to act in a redundant manner with *BAS1* in regulating the light-mediated suppression of hypocotyl elongation (Turk *et al.* 2005). *SOB3* is involved in proper hypocotyl growth and along with BR signaling, it regulates the transcription of the *SAUR19* family member. The *SAUR19* family controls the cell expansion and was found to be repressed by light and *SOB3*. *SAUR19* is induced by auxin and is upregulated by BRs. Hence, *SOB3* and BR signaling have antagonistic roles in the hypocotyl elongation and are dependent on *SAUR19* expression (Favero *et al.* 2017).

Jasmonic acid and light regulating root
and hypocotyl growth

In the presence of light, exogenous JA causes the inhibition of root growth and hypocotyl growth. Coronatine insensitive 1 (*COI1*) is known to play role in JA perception and far-red light-mediated hypocotyl growth inhibition. Downstream genes of JA signaling pathways, such as *JAI/JAZ3* and *MYC2,* and the JA biosynthetic genes, such as jasmonic acid-amido synthetase 1 (*JAR1*) and allene oxide synthase (*AOS*), have been reported to have increased SAS under low R:FR light and are involved in FR-induced hypocotyl growth inhibition. Hence, both JA synthesis and signaling are involved in far-red light-mediated hypocotyl growth inhibition (Robson *et al*. 2010). Under FR light, *MYC2* acts as positive regulator in *PHYA*-mediated photomorphogenesis. *MYC2* is required for JA-mediated hypocotyl inhibition under darkness, but not under continuous red light conditions. *COI1* participates in hypocotyl elongation under both R and FR light (Kazan and Manners 2011). JA inhibits hypocotyl growth in the dark and continuous red light, and it depends on SCFCOI1. *MYC2* is also involved in the hypocotyl growth inhibition in dark conditions but under red light *PHYB* plays a major role (Chen *et al.* 2013). Far-red insensitive 219/jasmonate resistance 1 (*FIN219/JAR1*) is a JA-conjugating enzyme which acts as a connecting link of JA and FR light signaling. *FIN219/JAR1* interacts with *COP1* to inhibit its function under darkness, as well as under continuous FR light. It suppresses the shade-induced hypocotyl growth and downregulates the shade-induced gene expression (Swain, Jiang, and Hsieh 2017). JA inhibits the activity of *COP1* and stabilizes its target genes to ultimately suppress the hypocotyl elongation. *PAR1* and *PAR2* have been reported to positively regulate JA-mediated hypocotyl growth inhibition. *HY5* and *HYH* are also possibly involved in this phenomenon. Light positively regulates the JA-mediated suppression of hypocotyl growth and it occurs through light-dependent enhanced accumulation of JA through the promotion of JA biosynthetic genes (Zheng *et al.* 2017). Along with *FIN219*, *FIN219*-interacting protein 1 (*FIP1*) was also found to play a role in FR-mediated hypocotyl elongation (Chen *et al.* 2007).

Strigolactone and light regulating root
and hypocotyl growth

SL has been found to suppress hypocotyl and adventitious root growth. SL inhibits hypocotyl elongation under light and darkness. More axillary growth 2 (*MAX2*) is involved in the synthesis and signaling of SL, as it

promotes photomorphogenesis under red, far-red, and blue light. GR24, an analog of SL, suppresses hypocotyl elongation in a *MAX2*-dependent manner. Under blue and red/far-red light *CRYs* and *PHYs*, along with *PIFs,* regulate GR24-mediated hypocotyl inhibition (Jia *et al.* 2014). It has been reported that inhibition of the nuclear localization of *COP1* and promotion of *HY5* accumulation is regulated by SL (Tsuchiya *et al.* 2010). SL positively regulates *HY5* expression through *MAX2* under light as well as darkness. Salt tolerance homolog 7 (*STH7*), encoding a transcription factor *BZR1*, acts as a positive regulator of photomorphogenesis (Thussagunpanit *et al.* 2017).

Hence, the SL-mediated hypocotyl growth inhibition involves *MAX2*, *PHYA, PHYB*, *CRY1*, *CRY2*, *HY5*, *COP1*, *PIFs*, and *STH7* genes. However, the role of the interaction between salicylic acid and light in root and hypocotyl development has not been studied in depth.

Conclusion

The light and phytohormone crosstalk regulates the root and hypocotyl growth differently. The quality and quantity of light along with the phytohormones involved are the major factors that determine the growth pattern of the seedling.

Under shade or EOR-FR conditions, hypocotyl elongation occurs due to upregulated gene expression of *YUCCA 2, 5, 8,* and *9* and hence enhanced auxin signaling. Under prolonged shade upregulation of *PIF4* takes place, which induces the expression of *IAA19* and *IAA29* genes. *TAAR* genes are also upregulated under prolonged shade, which again leads to upregulation of *IAA19* and *IAA29* along with the downregulation of *ARF6*. On the contrary, *MIR393* is negatively regulated under prolonged shade conditions, which causes enhanced auxin perception and signaling, ultimately leading to hypocotyl elongation. Under blue and red light, hypocotyl growth is suppressed due to the inhibition of auxin response and prevention of *TIR1*/AFB-mediated *AUX/IAA* degradation. *CRY1* has also been found to directly interact with *AUX/IAA* and stabilize it. In the dark, *COP1* regulates the expression of *PIN1* in the shoot as well as expression of *PIN1* and *PIN2* in the root, leading to coordinated shoot and root growth. In the dark, hypocotyl elongation is also controlled by *RAG1* expression. Endoplasmic reticulum (ER) has been reported to regulate hypocotyl elongation positively under shade through *PHYB*, GA, and IAA signaling. Hypocotyl growth suppression under blue and red light is also due to the downregulation of *ABCB19* gene. CK suppresses hypocotyl elongation in

darkness as well as in blue light. In the presence of blue light, this suppression takes place by way of preventing the *COP1*-mediated *HY5* degradation. Under white light, when ET action and IAA transport are altered, CK was shown to promote hypocotyl elongation. Upregulation of *CKI1* has been reported to cause reduced RAM activity along with altered root phenotype in phytochrome mutants. Under red light, *DEG9* negatively regulates the root and hypocotyl growth controlled by *ARR4*, and hence *DEG9* could be one of the entities to link light and the cytokinin signaling pathway. ET promotes the elongation of hypocotyl in light and it depends on enhanced nuclear transport of *COP1,* and hence increased *HY5* degradation. Under darkness, ET inhibits hypocotyl growth due to enhanced ERF-mediated *EIN3* degradation and altered expression of *WDL5*. In the presence of light, ACC-mediated reduction in root growth is dependent on *COI*.

GA enhances hypocotyl growth under darkness by negatively regulating *HY5* and regulating *PIFs* positively. *RAG1* is also involved in the enhancement of hypocotyl elongation in the dark. Under light, GA-mediated inhibition of hypocotyl growth takes place due to the downregulation of *PIF4* and *PIF5* genes. *PHYB* and *DELLA* proteins are involved in degradation of *PIF*s in the presence of light. Under blue light, inhibition of hypocotyl occurs due to *CRY*-mediated suppression of GA accumulation. *CRYs* have been seen to promote the *GA2ox1* (involved in regulating the catabolism of GA and its precursor) and suppress *GA20ox1* and *GA3ox1* (involved in synthesis of GA) expression. ABA inhibits hypocotyl growth in the presence of light through *ABI5*-mediated altered expression of *HY5*. Further, *FIERY1* has been identified as one of factors involved in light-mediated inhibition of hypocotyl growth.

PHYB induces ABA synthesis in the shoot in the presence of light, followed by detoxification of ROS in the root. Hence, *PHYB* is involved in the proper development of root by way of ABA signaling. BR has been shown to promote skotomorphogenesis and hypocotyl elongation. *BZR1* plays a major role in the hypocotyl growth, which is promoted by the interaction between *PIF4* and *COP1,* whereas *GATA2* and *HY5* have antagonistic roles. *BEE* and *BIM* enhance hypocotyl growth under shade conditions by interacting with *PAR1*. *COG1* also acts as a positive regulator of hypocotyl growth, as it activates *PIF4* and *PIF5* expression and upregulates BR biosynthetic genes, such as *DWF4* and *BR6OX2*. *BAS1* and *SOB7* have been found to act opposite to BRs and promote photomorphogenesis. Similarly, *SOB3* also has an antagonistic role in the BR-mediated hypocotyl elongation. In the presence of light, exogenous JA

shows suppression in root growth. Further, JA inhibits hypocotyl elongation in darkness as well as in light. *COI1* has been found to be involved in far-red light-induced inhibition of hypocotyl growth. Along with *COI1*, the *JAI/JAZ3*, *MYC2*, *JAR1*, and *AOS* genes also play important roles in hypocotyl growth inhibition. In the dark or far-red light, *FIN219* and *FIP1* act as positive regulators of hypocotyl inhibition as *FIN219* has been shown to suppress *COP1* activity. This stabilizes the *HY5*, *HYH,* and *PAR1/PAR2* transcription factors. SL inhibits the hypocotyl elongation in the light and darkness and it is dependent on the expression of genes, such as *MAX2, PHYA, PHYB, CRY1*, *CRY2*, *HY5, COP1, PIFs*, and *STH7*. However, there are no reports indicating the involvement of SA and light interaction in regulating seedling development.

Prospective

The role of light-hormone interactions in root and hypocotyl development has been thoroughly analyzed, but the light-hormone crosstalk with regard to root growth needs to be investigated in detail. Regulation of root and hypocotyl development through the interaction of light and phytohormones, such as auxin, ethylene, jasmonic acid, brassinosteroids, and gibberellin has been well explored; however, there is limited information regarding the interaction of light with phytohormones, like cytokinin, abscisic acid, and strigolactone. Further, the prospects of the interaction between salicylic acid and light with regard to root and hypocotyl growth have not been explored in detail.

Acknowledgments

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