Chapter 13
Cross Talk Between Light and ABA Signaling

Rongcheng Lin and Weijiang Tang

Abstract The endogenous phytohormone abscisic acid (ABA) and the exogenous signal light regulate both distinct and overlapping processes in plant growth and development. This review summarizes recent advances in our understanding of the cross-regulation between light and ABA signaling, and their cooperative interactions in modulating plant responses, including seed germination, seedling growth and development, stomatal movement, and hydrotropic growth.

Keywords ABA · Light · Cross talk · Modulation

13.1 Introduction

Due to their sessile nature, plants are controlled by endogenous hormones and influenced by environmental cues. As one of the most important environmental signals, light plays critical roles in regulating diverse plant growth and developmental processes, ranging from seed germination, seedling de-etiolation, phototropism, shade avoidance, stomatal opening, flowering time, and circadian rhythms. Accumulating evidence indicates that light interacts with many phytohormone signaling, including abscisic acid (ABA), gibberellin (GA), brassinosteroid, and ethylene, in controlling various plant response (for reviews, Seo et al. 2009; Alabadi and Blazquez 2009; Lau and Deng 2010). ABA regulates many plant processes that are also mediated by light, such as seed germination and seedling development. The biosynthesis and function of ABA and its regulatory network were extensively reviewed in the other chapters of this book. The scope of this chapter emphasizes advances in our understanding of interaction between light and ABA

R. Lin (✉) · W. Tang
Key Laboratory of Photobiology, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China
e-mail: rclin@ibcas.ac.cn

D.-P. Zhang (ed.), *Abscisic Acid: Metabolism, Transport and Signaling*,
DOI 10.1007/978-94-017-9424-4_13

Signaling, based largely on progress achieved so far using genetic and molecular approaches in *Arabidopsis* as a model system. In this review, we first describe a brief introduction of the light signaling pathway, and then summarize, and discuss the convergence of light and ABA Signaling in regulating plant responses.

13.2 Overview of the Light Signaling Pathway

Plants have evolved an array of photoreceptors to perceive and transduce different spectra of light that ultimately modulate the transcriptomes and trigger plant growth and development. These photoreceptors include the red and far-red light (600–750 nm)-absorbing phytochromes (phys), the blue/ultraviolet-A light (320–500 nm)-absorbing cryptochromes (cry1 and cry2), phototropins (phot1 and phot2), and three newly identified LOV/F-box/Kelch-repeat proteins ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-BOX (FKF), and LOV KELCH REPEAT PROTEIN 2 (LKP2), and UV-B light (282–320 nm)-absorbing UV RESISTANCE LOCUS8 (UVR8) (Chen et al. 2004; Christie 2007; Nagatani 2010; Yu et al. 2010; Heijde and Ulm 2012; Ito et al. 2012). Phytochromes are unique photoreceptors because they exist as two distinct but photoreversible forms in vivo. The biological active Pfr form absorbs far-red light, whereas the inactive Pr form absorbs red light (Li et al. 2011). There are five phytochromes, designated phyA to phyE in *Arabidopsis thaliana*. phyA is light labile, while phyB to phyE are light stable (Li et al. 2011).

Seedling de-etiolation is a light-controlled process that has been extensively studied in the past decades. Accumulating evidence has established that phys and crys control two main branches of light signaling during seedling de-etiolation (Lau and Deng 2010). A group of constitutive photomorphogenic/de-etiolated/fusca (COP/DET/FUS) proteins act as repressors downstream of phys and crys that define the first branch of the light signaling pathway (Lau and Deng 2012). Among these proteins, COP1 is a central repressor that targets a number of positive factors, such as ELONGATED HYPOCOTYL5 (HY5) and LONG HYPOCOTYL IN FAR-RED1 (HFR1), for 26S proteasome-mediated degradation, thus desensitizing light signaling (Henriques et al. 2009; Lau and Deng 2012). *HY5* encodes a basic domain/leucine zipper transcription factor that plays a key role in promoting photomorphogenesis in all light conditions by directly regulating the transcription of a wide range of genes (Oyama et al. 1997; Lee et al. 2007). HY5 is stabilized at the post-translational level by light and inhibits hypocotyl growth (Osterlund et al. 2000). In the second branch, a class of basic helix-loop-helix transcription factors, designated PHYTOCHROME-INTERACTING FACTORs (PIFs), accumulate in darkness and thus regulate gene expression to promote the skotomorphogenic response (Leivar et al. 2008). Under light, PIF proteins interact with photoactivated phys and result in PIFs' phosphorylation and subsequent degradation in an unknown manner (Leivar and Quail 2011). PIF proteins mainly regulate the phytochrome pathway, although they might also effect under blue light. Increasing

studies demonstrated the broad function of PIFs as integrators in mediating plant development (Leivar and Monte 2014).

Extensive studies have identified dozens of intermediates in the light signaling pathway and revealed the importance of transcriptional regulatory networks in controlling photomorphogenesis (Jiao et al. 2007; Chory 2010). For example, *FAR-RED ELONGATED HYPOCOTYL3* (*FHY3*) and *FAR-RED IMPAIRED RESPONSE1* (*FAR1*) are two positive transcription factors transducing signals in the far-red light pathway (Hudson et al. 1999; Wang and Deng 2002; Lin et al. 2007). For more information on light signaling regulation, readers may go through some recent reviewer articles (Bou-Torrent et al. 2007; Jiao et al. 2007; Demarsy and Fankhauser 2009; Li et al. 2011).

13.3 Inter-regulation Between Light and ABA

13.3.1 Light Regulates ABA Biosynthesis

The ABA metabolic pathway has been described in detail in Chap. 20. Most of the genes involved in ABA biosynthesis and catabolism have been identified genetically. The oxidative cleavage of cis-epoxycarotenoid to xanthoxin is catalyzed by 9-cis-epoxycarotenoid dioxygenase (NCED) and represents the key regulatory step of ABA biosynthesis in plants. ABA 8′-hydroxylases encoded by cytochrome P450 *CYP707A* genes catalyze the first committed step in the predominant ABA catabolic pathway (Kushiro et al. 2004; Nambara and Marion-Poll 2005). The endogenous ABA level is modulated by the precise balance between its biosynthesis and catabolism. Regulation of *NCED* and *CYP707A* has thus been proposed to significantly determine endogenous ABA level in plants (Nambara and Marion-Poll 2005).

ABA is increasingly accumulated in seeds during their maturation. Studies from seed germination have well demonstrated that light plays a crucial role in regulating ABA metabolic gene expression and subsequent ABA level. Red light decreases, whereas far-red light increases endogenous ABA level in Arabidopsis and lettuce (*Lactuca sativa* L.) seeds (Toyomasu et al. 1994; Seo et al. 2006; Sawada et al. 2008). Among *AtNCED* genes, *AtNCED6* and *AtNCED9* have been shown to play key roles in ABA biosynthesis in developing seeds (Lefebvre et al. 2006). The transcript level of *AtNCED6* remains high after pulse of far-red light irradiation and is reduced by a subsequent red light pulse in Arabidopsis seeds. In agreement with this notion, the *nced6-1* mutant showed enhanced germination ability relative to wild type when treated with FR light (Seo et al. 2006). Similarly, red light down-regulates *LsNCED2* and *LsNCED4* and increases *LsABA8ox4* (encoding ABA 8′-hydroxylase) expression (Sawada et al. 2008). As a catabolic gene, the expression pattern of *CYP707A2* undergoes an opposite manner to that of *AtNCED6* (Seo et al. 2006). However, photoreversible expression of *CYP707A1* and *CYP707A3* appears to be regulated indirectly by light (Seo et al. 2006). Thus, ABA biosynthesis is likely regulated through the photoreversible expression of *AtNCED6* and *CYP707A2* in an opposite manner.

Photoreversible regulation of ABA level during seed germination is mainly mediated by phyB photoreceptor, since reduction of ABA level after red light pulse was not observed in the *phyB* mutant (Seo et al. 2006). When phyB is activated, the ABA anabolic genes, *ABA-DEFICIENT 1* (*ABA1*), *AtNCED6*, and *AtNCED9*, are down-regulated, whereas an ABA catabolic gene, *CYP707A2,* is induced (Kim et al. 2008; Oh et al. 2007). This process is mainly controlled by the transcription factor PIL5/PIF1, which negatively regulates phyB responses (Oh et al. 2007, other ref). PIL5 indirectly regulates the transcript levels of ABA metabolic genes, including *ABA1*, *AtNCED6*, *AtNCED9,* and *CYP707A2*, and some GA metabolic genes, such as *GA3ox1* and *GA2ox2* (Oh et al. 2007). PIL5 can target *SOMNUS* (*SOM*) and directly activates its expression. In the *som* mutant, the expression levels of *ABA1* and *AtNCED6* are reduced, whereas the level of *CYP707A2* is increased compared to the wild type. Consistently, the *som* seeds contain low amount of ABA and high levels of active GA_4 (Kim et al. 2008). Therefore, PIL5 regulates endogenous ABA level largely through SOM. However, the question how SOM regulates the expression of ABA metabolic genes is still unknown.

Besides, at the seed germination stage, the expression of *CYP707A2* is also significantly up-regulated, whereas the transcript levels of *AtNCED* genes (including *AtNCED2*, *3*, *5*, and *9*) are decreased by light during seedling de-etiolation (Charron et al. 2009). Moreover, the expression patterns of tomato *LeZEP1* (encoding zeaxanthinepoxidase) and *LeNCED* are under circadian regulation (Thompson et al. 2000). In addition, the transcript level of *ABA-INSENSITIVE 3* (*ABI3*), encoding a key component in the ABA signaling pathway, is also affected by mutations in *phyB* in Arabidopsis (Mazzella et al. 2005), suggesting that phytochrome regulates both the metabolic and signaling genes of ABA.

13.3.2 ABA Modulates the Expression of Light-Responsive Genes

Light-harvesting chlorophyll a/b-binding proteins (LHCBs) are the apoproteins of the photosystem II complex that absorb and transfer light energy. Expression of these nuclear *LHCB* genes is tightly controlled by light, and therefore, *LHCB*s serve as typical light-responsive genes (Johanningmeier 1988; Johanningmeier and Howell 1984). Being a stress signal, ABA plays an important role in the regulation of *LHCB* expression under environmental stress conditions. For example, exogenously application of high concentrations of ABA inhibits *LHCB* expression in various tissues, including tomato leaves, Arabidopsis seedlings, *Lemma gibba* cells, and developing seeds of soybean (Bartholomew et al. 1991; Staneloni et al. 2008; Weatherwax et al. 1996; Chang and Walling 1991). However, low level of ABA enhances *LHCB1.2* transcript level in Arabidopsis seedlings, and *cab3* (*GmLHCB*) expression in soybean seeds (Voigt et al. 2010; Chang and Walling 1991). This is consistent with a recent study showing that physiological levels of ABA enhance *LHCB* expression in Arabidopsis (Liu et al. 2013). Liu and the

coauthors (2013) further found that ABA is required for full expression of different *LHCB* members likely via the WRKY40 transcription factor. ABA may be an inducer to fine-tune *LHCB* expression under stressful conditions in cooperation with light that allows plants to adapt to environmental changes. Moreover, a signal transduction chain consisting of GCR1 (a potential G-protein-coupled receptor), GPA1 (the sole Ga subunit), RPN1 (one of four members of an iron-containing subgroup of the cupin superfamily), and a nuclear factor Y convergences blue light and ABA signals to regulate *LHCB* expression in etiolated Arabidopsis seedlings (Warpeha et al. 2007).

In addition, ABA regulates genes involved in the light signal transduction pathway. For instance, the transcript levels of *FHY3* and *FAR1*, encoding two key positive transcription factors in the phyA pathway, are induced in Arabidopsis seedlings after ABA treatment (Tang et al. 2013).

13.4 Light and ABA Coregulate Plant Responses

Light and phytohormone ABA coordinately regulate many plant developmental processes, including seed germination, seedling growth, stomatal movement, and hydrotropic response, as reviewed below in detail. We focus on the function of signaling factors that were genetically identified in recent studies and their regulatory mechanisms on each distinct response.

13.4.1 Seed Germination

Seed germination is an adaptive trait of higher plants that is controlled by both environmental cues and internal growth regulators, including light, GA, and ABA. GA is known to break seed dormancy and promote germination, whereas ABA is involved in maintaining seed dormancy and inhibiting germination (Koornneef et al. 2002; Finch-Savage and Leubner-Metzger 2006). It is now much clear that GA promotes germination by promoting destruction of DELLA repressors, whereas ABA prevents germination by stimulating the expression of ABI repressors. Endogenous ABA biosynthesis in imbibed seeds is required for the maintenance of seed dormancy in Arabidopsis and tobacco (Ali-Rachedi et al. 2004; Grappin et al. 2000).

Light is a critical determinant environmental factor for seed germination in some small-seeded plants, such as Arabidopsis and lettuce (Shinomura 1997). In the middle of twentieth century, it was discovered that red light promotes, whereas far-red light inhibits lettuce seed germination, and the process is reversible by red and far red (Borthwick et al. 1952). The photoreceptor responsible for the reversible photoreaction was discovered from etiolated *Brassica rapa* and *Zea mays* and was named phytochrome (Butler et al. 1959). It has been well established that phyA and phyB play curical role in the light-mediated seed germination (Shinomura et al. 1994, 1996;

Casal and Sanchez 1998). phyA mediates very low-fluence response (VLFR), while phyB acts via photoreversible low-fluence response (LFR) to promote seed germination. However, continuous far-red light inhibits germination via high-irradiance response in many plant species (Botto et al. 1996).

Light controls seed germination predominantly through regulating the endogenous levels of GA and ABA. ABA inhibits germination of lettuce seeds induced by red light, whereas active GA mimics the effect of red light (Kahn et al. 1957; Sankhla and Sankhla 1968). Extensive studies have identified a number of factors that involve in light-controlled seed germination.

Giltu Choi's laboratory firstly reported that a basic helix-loop-helix transcription factor PIL5 acts as a key negative regulator in phytochrome-mediated seed germination (Oh et al. 2004). PIF5 preferentially interacts with the Pfr forms of phyA and phyB. When activated by light, phytochromes bind to and accelerate the degradation of PIL5 in both seeds and seedlings (Oh et al. 2006; Shen et al. 2005). The destabilization of PIL5 thus releases its repression of seed germination and allows seeds to germinate. As a result, loss-of-function mutant of *pil5* germinates well regardless of far-red light treatment mediated by LFR and VLFR, whereas *PIL5* overexpression transgenic lines fail to germinate under relative low intensity of red light (Oh et al. 2004). It was showed that PIL5 directly binds to the promoters of two GA repressor (DELLA) genes, *REPRESSOR OF GA1-3* (*RGA*) and *GA-INSENSITIVE* (*GAI*), and activates their expression (Oh et al. 2007). Furthermore, chromatin immunoprecipitation (ChIP) chip and microarray analyses helped to identify large amount of PIL5 direct target genes involved in hormone signaling and cell wall modification (Oh et al. 2009). Therefore, PIL5 regulates seed germination not only by mediating GA signaling and coordinating GA and ABA metabolism, but also by modulating cell wall properties in imbibed seeds. Since *pil5* could not fully restore the germination deficiency of *phyB* in the *pil5phyB* double mutant, other factors must be involved in the phyB-mediated germination process (Oh et al. 2004).

SOM was identified as another negative factor in regulating light-dependent seed germination (Kim et al. 2008). The *SOM* gene encodes a CCCH-type zinc finger protein that probably acts as an RNA-binding factor. The *som* mutants have lower levels of ABA and elevated levels of GA and germinate in darkness independently of various light regimens (Kim et al. 2008). PIL5 directly promotes the expression of *SOM* through binding to its promoter sequence, and the reduced germination rate of a PIL5 overexpression line is rescued by the *som* mutation (Kim et al. 2008). Thus, SOM functions downstream of PIL5 and the PIL5-SOM regulatory pathway likely defines an essential step in integrating ABA and light signaling to control seed germination. In addition to PIL5, ABI3 was also found to be targeted to the RY motifs present in the *SOM* promoter. ABI3 and PIL5 interact and collaboratively activate the expression of *SOM* mRNA in Arabidopsis imbibed seeds, but independently induce *SOM* expression in maturing seeds (Park et al. 2011). However, HFR1 plays a negative role on PIL5 transcriptional activity by interacting with PIL5 and preventing its binding to target DNA. Through the HFR1-PIL5 heterdimer, light regulates expression of numerous genes involved in

cell wall loosening, cell division, and hormone pathways to initiate seed germination (Shi et al. 2013). Hence, HFR1 defines a new positive regulator of phyB-dependent seed germination.

Recently, Lim et al. (2013) demonstrated that ABI3, ABI5, and DELLAs form a complex on the *SOM* promoter to activate *SOM* expression in imbibed seeds in response to high temperature. ABI5 is a bZIP transcription factor that plays important role in ABA signaling and ABA responses (Finkelstein and Lynch 2000). Two previous researches identified two types of transcription factors that directly regulate *ABI5* expression (Chen et al. 2008; Tang et al. 2013). A ChIP study indicates that HY5 directly binds to the promoter region of *ABI5*, and the binding ability was significantly enhanced by exogenous ABA treatment. Consistent with this observation, HY5 is required for the expression of ABA-inducible genes, such as *ABI3*, *RAB18*, *AtEM1*, and *AtEM6*, in seeds and during seed germination (Chen et al. 2008). Consequently, *hy5* mutant seeds are less sensitive to the inhibition of ABA and glucose on germination (Chen et al. 2008).

FHY3 is another type of transcription factor that directly binds to the promoter of *ABI5* and activates its expression (Tang et al. 2013). Disruption of *FHY3* and/or its homology gene, *FAR1,* reduces sensitivity to ABA-mediated inhibition of seed germination. Germination of the *fhy3* mutant seeds is also less sensitive to salt and osmotic stress than that of the wild type (Tang et al. 2013). Strikingly, constitutive expression of *ABI5* restores the seed germination response of *fhy3*. Furthermore, the expression of several ABA-responsive genes (e.g., *ABI1*, *ABI2*, *ABF3*, *RAB18*, *KIN2*, *COR47*, *DREB2A*, and *RD22*) is decreased in the *fhy3* and/or *far1* mutants during seed imbibition (Tang et al. 2013).

Although both phyA and phyB photoreceptors are essential for seed germination, the mechanism underlying their distinct roles has long been a mystery. Using a seed coat bedding assay system where dissected embryos are cultured on a layer of dissected seed coats, Lee and coauthors (2012) demonstrated that phyA and phyB spatially control seed germination in embryo and endosperm, respectively, in response to far-red light irradiation. The endosperm mediates far-red repression of phyB-dependent germination, whereas FR stimulation of phyA-dependent germination occurs only in the embryo. These responses specifically involve the light signaling genes PIL5 and RGL2 in the endosperm and PIL5, SOM, GAI, and RGA in the embryo, where they regulate the expression of GA and ABA biosynthetic genes in each tissue (Lee et al. 2012). Therefore, early upon seed imbibition, far-red light inactivation of phyB leads to ABA biosynthesis and releases from the endosperm to prevent phyA-dependent promotion of germination in the embryo. This involves an extended regulatory network where ABA overrides phyA signaling by interfering with the expression of light signaling genes and GA and ABA metabolic genes. Over time, a weakening of ABA-dependent responses takes place, thus allowing phyA-dependent germination after a later light treatment. This results in a phyA-dependent "explosive" germination unlike phyB-dependent germination (Lee et al. 2012). Furthermore, far-red light repression of germination involves stabilized DELLA proteins GAI, RGA, and RGL2 that stimulate endogenous ABA biosynthesis, which in turn blocks germination through ABI3 (Piskurewicz et al. 2009).

IMB1 (for imbibition-inducible 1) defines as a putative bromodomain transcription factor. The imb1 loss-of-function mutant is hypersensitive to ABA-mediated inhibition of cotyledon expansion and greening, and is deficient in the phyA-mediated VLFR of seed germination (Duque and Chua 2003). *IMB1* transcript level is elevated during seed imbibition. This study implicates that IMB1 might link phyA to ABA signaling in seed germination (Duque and Chua 2003). Interestingly, *ABI5* transcript level was up-regulated in *imb1* seed germination in ABA when compared to the wild type, suggesting that IMB1 acts upstream of ABI5 in the ABA pathway (Duque and Chua 2003).

In addition to transcription factors, two JmjC domain-containing proteins, JMJ20 and JMJ22, have been shown as positive regulators of seed germination (Cho et al. 2012). *JMJ20* and *JMJ22* encode histone arginine demethylases, and their expression is directly repressed by SOM. Upon phyB activation by red light, *JMJ20* and *JMJ22* are derepressed, resulting in increased GA levels through the removal of repressive histone arginine methylation at *GA3ox1* and *GA3ox2* loci, which in turn promote germination (Cho et al. 2012). However, the ABA metabolic genes are not regulated by JMJ20/JMJ22. This study adds an additional layer that involves repressive epigenetic mechanism during seed germination.

The F-box protein MORE AXILLARY BRANCHES2 (MAX2) plays an important role in promoting photomorphogenesis through modulating GA and ABA biosynthetic pathways (Shen et al. 2007, 2012). The *max2* mutant seeds are hyposensitive to light-induced seed germination and hypersensitive to ABA. Surprisingly, expression of ABA biosynthetic and catabolic genes and ABA-regulated genes is up-regulated by *max2* mutation (Shen et al. 2012; Bu et al. 2014). Though a genetic study indicated that the seed germination phenotype of *max2* is epistatic to *pil5* (Shen et al. 2012), the molecular mechanism between MAX2 and PIL5 remains to be elucidated.

13.4.2 Seedling Growth and Development

After seed germination, seedling growth and development are also regulated by light and ABA. It has been shown that disruption of *HY5* confers tolerance to the inhibitory effect of ABA on lateral root growth and seedling growth. The *hy5* seedlings were also more susceptible to salt and osmotic stresses than the wild-type plants (Chen et al. 2008). *ABI5::GUS* promoter activity was detected in cotyledons, hypocotyls, roots, flowers, and siliques. However, this activity was greatly reduced in the *hy5* mutant background. Furthermore, light promotes *ABI5* expression in a HY5-dependent manner (Chen et al. 2008). This is because HY5 protein is tightly controlled by the COP1-mediated 26S proteasome degradation pathway in the dark (Osterlund et al. 2000). As a consequence, overexpression of *ABI5* restores ABA sensitivity in *hy5* and enhances light response (hypocotyl elongation) in the wild type (Chen et al. 2008). Since FHY3/FAR1 also bind to *ABI5* promoter sequence, *fhy3* and/or *far1* mutants are hyposensitive to ABA-mediated

inhibition of seedling greening. *FHY3* and *FAR1* transcripts are up-regulated by ABA and abiotic stresses (Tang et al. 2013). Thus, HY5 and FHY3/FAR1 transcription activators act upstream of ABI5 to integrate light and ABA signaling during early seedling development. In addition, the *max2* mutant seedlings are hypersensitive to ABA (Shen et al. 2012).

13.4.3 Stomatal Movement

ABA is a stress signal that plays a prominent role in inducing stomatal closure to prevent water loss in response to drought stress and thereby contributes to tolerance for plants (Cutler et al. 2010; Hauser et al. 2011). It has been known that blue light receptor phototropins mediate stomatal opening (Kinoshita et al. 2001). Studies from our laboratory showed that the *fhy3* and *far1* mutants have wider stomata, lose water faster, and are more sensitive to drought than the wild type; therefore, FHY3 and FAR1 confer increased resistance to drought (Tang et al. 2013). The drought-sensitive phenotype of *fhy3* may be partly caused by the reduced sensitivity of guard cell movement under drought stress conditions, which may induce the production of ABA. In agreement with this notion, *FHY3* is highly expressed in guard cells (Tang et al. 2013). MAX2 plays a similar role as FHY3/FAR1 in modulating stomatal movement. The *max2* mutant plants are less sensitive to ABA-induced stomatal closure and display increased water loss and drought-sensitive phenotypes. The expression of ABA biosynthesis, catabolism, transport, and signaling genes was impaired in *max2*, compared to wild type in response to drought stress (Bu et al. 2014).

Down-regulation or disruption of any member of the LHCB family, *LHCB1* to *LHCB6*, reduces responsiveness of stomatal movement to ABA. By contrast, overexpression of *LHCB6* enhances stomatal sensitivity to ABA (Xu et al. 2012). These results demonstrate that LHCBs play a positive role in ABA signaling in stomatal movement and the plant response to drought. Similarly, LHCBs positively regulate seed germination and seedling growth in response to ABA (Liu et al. 2013).

Mg-chelatase catalyzes the formation of Mg-protoporphyrin IX by chelating magnesium to protoporphyrin IX in the chlorophyll biosynthesis pathway (Tanaka and Tanaka 2007). The H subunit of Mg-chelatase was identified as an ABA receptor, and it functions in the ABA signaling pathway (Shen et al. 2006; Wu et al. 2009). ABA specifically binds to CHLH, but not to the other Mg-chelatase subunits, CHLI, CHLD, and GUN4 (Du et al. 2012). *CHLH* and *GUN4* are major targets for light regulation during seedling de-etiolation (Stephenson and Terry 2008). Genetic studies showed that the *rtl1* mutant plants (a *chlh* allele) display ABA-insensitive phenotypes in stomatal movement. Interestingly, down-regulation of *CHLI* also confers ABA insensitivity in stomatal response, while up-regulation of *CHLI1* results in ABA hypersensitivity in seed germination (Du et al. 2012). The involvement of these chlorophyll biosynthesis and binding proteins in stomatal movement might coordinate internal development with external signals for optical air exchange and maximal photosynthesis.

13.4.4 Hydrotropic Response

Plant roots undergo hydrotropic growth in response to moisture gradient that helps plants acquire water and nutrients. ABA is involved in hydrotropism as the hydrotropic response was reduced in the ABA-deficient mutant *aba1* and ABA-responsive genes were induced upon hydro-treatment (Takahashi et al. 2002; Moriwaki et al. 2010). Recent study found that hydrotropism is less pronounced in dark-grown seedling than in light-grown seedling and pointing out that a light signal is required for the hydrotropic response (Moriwaki et al. 2012). A genetic study identified MIZUKUSSEI1 (MIZ1) as an essential factor for hydrotropism (Kobayashi et al. 2007). Blue light, but not red light, induces the localization of MIZ1-GFP fusion protein in the root tip. Light and ABA induce the expression of *MIZ1* (Moriwaki et al. 2012). *MIZ1* transcript level was down-regulated in the *phyAphyB* double and *hy5* mutants. Consistently, the hydrotropic curvature was reduced in these mutants compared to the wild type (Moriwaki et al. 2012). Thus, phyA and phyB photoreceptors and HY5 transcription factor play important roles in blue light-mediated induction of *MIZ1* and hydrotropism. Moreover, application of ABA to *hy5* restored its hydrotropic defect, whereas abamine SG (ABA synthesis inhibitor) treatment further reduced the hydrotropic response of *hy5* (Moriwaki et al. 2012).

13.5 Future Perspectives

The last decade has made promising progress in our understanding of the coregulation of light and ABA in plant developmental programs, especially in regulating seed germination. Although a number of signaling factors in the pathway were identified, the molecular and biochemical functions of some components are less well understood. Some of the known proteins belong to transcription factors and play roles through modulating gene expression. Other regulatory levels, including post-transcription, translation, post-translational modification, and epigenetic regulation, are likely involved as well. Furthermore, are there more components involved in the cross talk between light and ABA? If any, how do they function? Future studies using the combination of genetic and molecular approaches are deserved to answer these questions. Elucidating the model and underlying mechanism between light and ABA will certainly contribute to our better understanding of plants' adaptability and plasticity to changing environments and help to design stress-tolerant crops in agriculture.

Acknowledgments The work in the authors' laboratory was supported by grants from the National Natural Science Foundation of China (31170221, 31325002) and the Chinese Academy of Sciences.

References

Alabdi D, Blazquez MA. Molecular interactions between light and hormone signaling to control plant growth. Plant Mol Biol. 2009;69:409–17.

Ali-Rachedi S, Bouinot D, Wagner MH, Bonnet M, Sotta B, Grappin P, Jullien M. Changes in endogenous abscisic acid levels during dormancy release and maintenance of mature seeds: studies with the Cape VerdeIslands ecotype, the dormant model of Arabidopsis thaliana. Planta. 2004;219:479–88.

Bartholomew DM, Bartley GE, Scolnik PA. Abscisic acid control of rbcS and cab transcription in tomato leaves. Plant Physiol. 1991;96:291–6.

Borthwick HA, Hendricks SB, Parker MW, Toole EH, Toole VK. A reversible photoreaction controlling seed germination. Proc Natl Acad Sci USA. 1952;38:662–666.

Botto JF, Sanchez RA, Whitelam GC, Casal JJ. Phytochrome A mediates the promotion of seed germination by very low fluences of light and canopy shade light in Arabidopsis. Plant Physiol. 1996;110:439–44.

Bou-Torrent J, Roig-Villanova I, Martinez-Garcia JF. Light signaling: back to space. Trends Plant Sci. 2007;13:108–14.

Bu Q, Lv T, Shen H, Luong P, Wang J, Wang Z, Huang Z, Xiao L, Engineer C, Kim TH, Schroeder JI, Huq E. Regulation of drought tolerance by the F-box protein MAX2 in Arabidopsis. Plant Physiol. 2014;164:424–39.

Butler WL, Norris KH, Siegelman HW, Hendricks SB. Detection, assay, and preliminary purification of the pigment controlling photoresponsive development of plants. Proc Natl Acad Sci USA. 1959;45:1703–1708.

Casal JJ, Sanchez RA. Phytochromes and seed germination. Seed Sci Res. 1998;8:317–29.

Chang YC, Walling LL. Abscisic acid negatively regulates expression of chlorophyll a/b binding protein genes during soybean embryogeny. Plant Physiol. 1991;97:1260–4.

Charron JB, He H, Elling AA, Deng XW. Dynamic landscapes of four histone modifications during deetiolation in *Arabidopsis*. Plant Cell. 2009;21:3732–48.

Chen H, Zhang J, Neff MM, Hong SW, Zhang H, Deng XW, Xiong L. Integration of light and abscisic acid signaling during seed germination ans early seedling development. Proc Natl Acad Sci USA. 2008;105:4495–500.

Chen M, Chory J, Fankhauser C. Light signal transduction in higher plants. Annu Rev Genet. 2004;38:87–117.

Cho JN, Ryu JY, Jeong YM, Park J, Song JJ, Amasino RM, Noh B, Noh YS. Control of seed germination by light-induced histone arginine demethylation activity. Dev Cell. 2012;22:736–48.

Chory J. Light signal transduction: an infinite spectrum of possibilities. Plant J. 2010;61:982–91.

Christie JM. Phototropin blue-light receptors. Annu Rev Plant Biol. 2007;58:21–45.

Cutler SR, Rodriguez PL, Finkelstein RR, Abrams SR. Abscisic acid: emergence of a core signaling network. Annu Rev Plant Biol. 2010;61:651–79.

Demarsy E, Fankhauser C. Higher plants use LOV to perceive blue light. Curr Opin Plant Biol. 2009;12:69–74.

Du SY, Zhang XF, Lu Z, Xin Q, Wu Z, Jiang T, Lu Y, Wang XF, Zhang DP. Roles of the different components of magnesium chelatase in abscisic acid signal transduction. Plant Mol Biol. 2012;80:519–37.

Duque P, Chua NH. IMB1, a bromodomain protein induced during seed imbibition, regulates ABA- and phyA-mediated responses of germination in Arabidopsis. Plant J. 2003;35:787–99.

Finch-Savage WE, Leubner-Metzger G. Seed dormancy and the control of germination. New Phytol. 2006;171:501–23.

Finkelstein RR, Lynch TJ. The Arabidopsis abscisic acid response gene ABI5 encodes a basic leucine zipper transcription factor. Plant Cell. 2000;12:599–609.

Grappin P, Bouinot D, Sotta B, Miginiac E, Jullien M. Control of seed dormancy in *Nicotiana plumbaginifolia*: postimbibition abscisic acid synthesis imposes dormancy maintenance. Planta. 2000;210:279–85.

Hauser F, Waadt R, Schroeder JI. Evolution of abscisic acid synthesis and signaling mechanisms. Curr Biol. 2011;21:R346–355.

Heijde M, Ulm R. UV-B photoreceptor-mediated signalling in plants. Trends Plant Sci. 2012;17:230–7.

Henriques R, Jang IC, Chua NH. Regulated proteolysis in light-related signaling pathways. Curr Opin Plant Biol. 2009;12:49–56.

Hudson M, Ringli C, Boylan MT, Quail PH. The FAR1 locus encodes a novel nuclear protein specific to phytochrome A signaling. Genes Dev. 1999;13:2017–27.

Ito S, Song YH, Imaizumi T. LOV domain-containing F-box proteins: light-dependent protein degradation modules in Arabidopsis. Mol Plant. 2012;5:573–82.

Jiao Y, Lau OS, Deng XW. Light-regulated transcriptional networks in higher plants. Nat Rev Genet. 2007;8:217–30.

Johanningmeier U. Possible control of transcript levels by chlorophyll precursors in Chlamydomonas. Eur J Biochem. 1988;177:417–24.

Johanningmeier U, Howell SH. Regulation of light-harvesting chlorophyll-binding protein mRNA accumulation in Chlamydomonasreinhardtii. Possible involvement of chlorophyll synthesis precursors. J Biol Chem. 1984;259:13541–9.

Kahn A, Goss JA, Smith DE. Effect of gibberellin on germination of lettuce seeds. Science. 1957;125:645–6.

Kim DH, Yamaguchi S, Lim S, Oh E, Park J, Hanada A, Kamiya Y, Choi G. SOMNUS, a CCCH-type zinc finger protein in Arabidopsis, negatively regulates light-dependent seed germination downstream of PIL5. Plant Cell. 2008;20:1260–77.

Kinoshita T, Doi M, Suetsugu N, Kagawa T, Wada M, Shimazaki K. Phot1 and phot2 mediate blue light regulation of stomatal opening. Nature. 2001;414:656–660.

Kobayashi A, Takahashi A, Kakimoto Y, Miyazawa Y, Fujii N, Higashitani A, Takahashi H. A gene essential for hydrotropism. Proc Natl Acad Sci USA104. 2007;4724–4729.

Koornneef M, Bentsink L, Hilhorst H. Seed dormancy and germination. Curr Opin Plant Biol. 2002;5:33–6.

Kushiro T, Okamoto M, Nakabayashi K, Yamagishi K, Kitamura S, Asami T, Hirai N, Koshiba T, Kamiya Y, Nambara E. The Arabidopsis cytochrome P450 CYP707A encodes ABA 8'-hydroxylases: key enzymes in ABA catabolism. EMBO J. 2004;23:1647–56.

Lau OS, Deng XW. Plant Hormone signaling lightens up: integrators of light and hormone. Curr Opin Plant Biol. 2010;13:571–7.

Lau OS, Deng XW. Thephotomorphogenic repressors COP1 and DET1: 20 years later. Trends Plant Sci. 2012;17:584–93.

Lee J, He K, Stolc V, Lee H, Figueroa P, Gao Y, Tongprasit W, Zhao H, Lee I, Deng XW. Analysis of transcription factor HY5 genomic binding sites revealed its hierarchical role in light regulation of development. Plant Cell. 2007;19:731–49.

Lee KP, Piskurewicz U, Tureckova V, Carat S, Chappuis R, Strnad M, Fankhauser C, Lopez-Molina L. Spatially and genetically distinct control of seed germination by phytochromes A and B. Genes Dev. 2012;26:1984–96.

Lefebvre V, Helen N, Frey A, Sotta B, Seo M, Okamoto M, Nambara E, Marion-Poll A. Functional analysis of Arabidopsis NCED6 and NCED9 genes indicates that ABA synthesized in the endosperm is involved in the induction of seed dormancy. Plant J. 2006;45:309–91.

Leivar P, Monte E. PIFs: systems integrators in plant development. Plant Cell in press. 2014;26:56–78.

Leivar P, Monte E, Al-Sady B, Carle C, Storer A, Alonso JM, Ecker JR, Quail PH. The Arabidopsis phytochrome-interacting factor PIF7, together with PIF3 and PIF4, regulates responses to prolonged red light by modulating phyB levels. Plant Cell. 2008;20:337–52.

Leivar P, Quail PH. PIFs: pivotal components in a cellular signaling hub. Trends Plant Sci. 2011;16:19–28.

Lem S, Park J, Lee N, Jeong J, Toh S, Watanabe A, Kim J, Kang H, Kim DH, Kawakami N, Choi G. ABA-INSENSITIVE3, ABA-INSENSITIVE5, and DELLAs interact to activate the expression of SOMNUS and other high-temperature-inducible genes in imbibed seeds in Arabidopsis. Plant Cell. 2013;25:4863–78.

Li J, Li G, Wang H, Deng XW. Phytochrome signaling mechanisms. The Arabidopsis book e0148. 2011. doi:10.1199/tab.0148.

Lin R, Ding L, Casola C, Ripoll DR, Feschotte C, Wang H. Transposase-derived transcription factors regulate light signaling in *Arabidopsis*. Science. 2007;318:1302–5.

Liu R, Xu YH, Jiang SC, Lu K, Lu YF, Feng XJ, Wu Z, Liang S, Yu YT, Wang XF, Zhang DP. Light-harvesting chlorophyll a/b-binding proteins, positively involved in abscisic acid signaling, require a transcription repressor, WRKY40, to balance their fucntion. J Exp Bot. 2013;64:5443–56.

Mazzella MA, Arana MV, Staneloni RJ, Perelman S, Rodriguez Batiller MJ, Muschietti J, Cerdán PD, Chen K, Sánchez RA, Zhu T, Chory J, Casal JJ. Phytochrome control of the Arabidopsis transcriptome anticipates seedling exposure to light. Plant Cell. 2005;17:2507–16.

Moriwaki T, Miyazawa Y, Fujii N, Takahashi H. Light and abacisic acid signaling are integrated by MIZ1 gene expression and regulate hydrotropic response in roots of Arabidopsis thaliana. Plant, Cell Environ. 2012;35:1359–68.

Moriwaki T, Miyazawa Y, Takahashi H. Transcriptome analysis of gene expression during the hydrotropic response in Arabidopsis seedlings. Environ Exp Bot. 2010;69:148–57.

Nagatani A. Phytochrome: structural basis for its functions. Curr Opin Plant Biol. 2010;13:565–70.

Nambara E, Marion-Poll A. Abscisic acid biosynthesis and catabolism. Annu Rev Plant Biol. 2005;56:165–85.

Oh E, Kang H, Yamaguchi S, Park J, Lee D, Kamiya Y, Choi G. Genome-wide analysis of genes targeted by PHYTOCHROME INTERACTING FACTOR 3-LIKE5 during seed germination in Arabidopsis. Plant Cell. 2009;21:403–19.

Oh E, Kim J, Park E, Kim JI, Kang C, Choi G. PIL5, a phytochrome-interacting basic helix-loop-helix protein, is a key negative regulator of seed germination in Arabidopsis thaliana. Plant Cell. 2004;16:3045–58.

Oh E, Yamaguchi S, Hu J, Yusuke J, Jung B, Paik I, Lee HS, Sun TP, Kamiya Y, Choi G. PIL5, a phytochrome-interacting bHLH protein, regulates gibberellin responsiveness by binding directly to the GAI and RGA promoters in Arabidopsis seeds. Plant Cell. 2007;19:1192–208.

Oh E, Yamaguchi S, Kamiya Y, Bae G, Chung WI, Choi G. Light activates the degradation of PIL5 protein to promote seed germination through gibberellin in Arabidopsis. Plant J. 2006;47:124–39.

Osterlund MT, Hardtke CS, Wei N, Deng XW. Targeted destabilization of HY5 during light-regulated development of Arabidopsis. Nature. 2000;405:462–6.

Oyama T, Shimura Y, Okada K. The Arabidopsis HY5 gene encodes a bZIP protein that regulates stimulus-induced development of root and hypocotyl. Genes Dev. 1997;11:2983–95.

Park J, Lee N, Kim W, Lim S, Choi G. ABI3 and PIL5 collaboratively activate the expression of SOMNUS by directly binding to its promoter in imbibed Arabidopsis seeds. Plant Cell. 2011;23:1404–15.

Piskurewicz U, Turečková V, Lacombe E, Lopez-Molina L. Far-red light inhibits germination through DELLA-dependent stimulation of ABA synthesis and ABI3 activity. EMBO J. 2009;28:2259–71.

Sankhla N, Sankhla D. Reversal of (±)-abscisin II-induced inhibition of lettuce seed germination. Physiol Plant. 1968;21:190–5.

Sawada Y, Aoki M, Nakaminami K, Mitsuhashi W, Tatematsu K, Kushiro T, Koshiba T, Kamiya Y, Inoue Y, Nambara E, Toyomasu T. Phytochrome- and gibberellin-mediated regulation of abscisic acid metabolism during germination of photoblastic lettuce seeds. Plant Physiol. 2008;146:1386–96.

Seo M, Hanada A, Kuwahara A, Endo A, Okamoto M, Yamauchi Y, North H, Marion-Poll A, Sun TP, Koshiba T, Kamiya Y, Yamaguchi S, Nambara E. Regulation of hormone metabolism in Arabidopsis seeds: phytochrome regulation of abscisic acid metabolism and abscisic acid regulation of gibberellin metabolism. Plant J. 2006;48:354–66.

Seo M, Nambara E, Choi G, Yamaguchi S. Interaction of light and hormone signals in germination seeds. Plant Mol Biol. 2009;69:463–72.

Shen H, Luong P, Huq E. The F-box protein MAX2 functions as a positive regulator of photomorphogenesis in Arabidopsis. Plant Physiol. 2007;145:1471–83.

Shen H, Moon J, Huq E. PIF1 is regulated by light-mediated degradation through the ubiquitin-26S proteasome pathway to optimize photomorphogenesis of seedlings in Arabidopsis. Plant J. 2005;44:1023–35.

Shen H, Zhu L, Bu QY, Huq E. MAX2 affects multiple hormones to promote photomorphogenesis. Mol Plant. 2012;5:750–62.

Shen YY, Wang XF, Wu FQ, Du SY, Cao Z, Shang Y, Wang SL, Peng CC, Yu XC, Zhu SY, Fan RC, Xu YH, Zhang DP. The Mg-chelatase H subunit is an abscisic acid receptor. Nature. 2006;443:823–6.

Shi H, Zhong S, Mo X, Liu N, Nezames CD, Deng XW. HFR1 sequesters PIF1 to govern the transcriptional network underlying light-initiated seed germination in Arabidopsis. Plant Cell. 2013;25:3770–84.

Shinomura T. Phytochrome regulation of seed germination. J Plant Res. 1997;110:151–61.

Shinomura T, Nagatani A, Chory J, Furuya M. The induction of seed germination in Arabidopsis thaliana isregulated principally by Phytochrome B and secondarily byPhytochrome A. Plant Physiol. 1994;104:363–71.

Shinomura T, Nagatani A, Hanzawa H, Kubota M, Watanabe M, Furuya M. Action spectra for phytochrome A- and B-specific photoinduction of seed germination in Arabidopsis thaliana. Proc Natl Acad Sci USA. 1996;93:8129–33.

Staneloni RT, Rodriguez-Batiller MJ, Casal JJ. Abscisic acid, high-light, and oxidative stress down-regulate a photosynthetic gene via a promoter motif not involved in phytochrome-mediated transcriptional regulation. Mol Plant. 2008;1:75–83.

Stephenson PG, Terry MJ. Light signaling pathways regulating the Mg-chelatasebranchpoint of chlorophyll synthesis during de-etiolation in Arabidopsis thaliana. Photochem Photobiol Sci. 2008;7:1243–52.

Takahashi N, Goto N, Okada K, Takahashi H. Hydrotropism in abscisic acid, wavy, and gravitropic mutants of Arabidopsis thaliana. Planta. 2002;216:203–11.

Tanaka R, Tanaka A. Tetrapyrrole biosynthesis in higher plants. Annu Rev Plant Biol. 2007;58:321–46.

Tang WJ, Ji Q, Huang Y, Jiang Z, Bao M, Wang H, Lin R. FHY3 and FAR1 transcription factors integrate light and abscisic acid signaling in Arabidopsis. Plant Physiol. 2013;163:857–66.

Thompson AJ, Jackson AC, Parker RA, Morpeth DR, Burbidge A, Taylor IB. Abscisic acid biosynthesis in tomato: regulation of zeaxanthin epoxidase and 9-cisepoxycarotenoid dioxygenase mRNAs by light/dark cycles, water stress and abscisic acid. Plant Mol Biol. 2000;42:833–45.

Toyomasu T, Yamane H, Murofushi N, Inoue Y. Effects of exogenously applied gibberellin and red light on the endogenous levels of abscisic acid in photoblastic lettuce seeds. Plant Cell Physiol. 1994;35:127–9.

Voigt C, Oster U, Bornke F, Jahns P, Dietze KJ, Leister D, Kleine T. In-depth analysis of the distinctive effects of norflurazon implies that tetrapyrrole biosynthesis, organellar gene expression and ABA cooperate in the GUN-type of plastid signaling. Physiol Plant. 2010;138:503–19.

Wang H, Deng XW. *Arabidopsis* FHY3 defines a key phytochromeA signaling component directly interacting with its homologous partner FAR1. EMBO J. 2002;21:1339–49.

Warpeha KM, Upadhyay S, Yeh J, Adamiak J, Hawkins SI, Lapik YR, Anderson MB, Kaufman LS. The GCR1, GPA1, PRN1, NF-Y signal chain mediates both blue light ans abscisic acid responses in Arabidopsis. Plant Physiol. 2007;143:1590–600.

Weatherwax SC, Ong MS, Degenhardt J, Bray EA, Tobin EM. The interaction of light and abscisic acid in the regulation of plant gene expression. Plant Physiol. 1996;111:363–70.

Wu FQ, Xin Q, Cao Z, Liu ZQ, Du SY, Mei C, Zhao CX, Wang XF, Shang Y, Jiang T, Zhang XF, Yan L, Zhao R, Cui ZN, Liu R, Sun HL, Yang XL, Su Z, Zhang DP. The Mg-chelatase H subunit binds abscisic acid and functions in abscisic acid signaling: New evidence in Arabidopsis. Plant Physiol. 2009;150:1940–54.

Xu YH, Liu R, Yan L, Liu ZQ, Jiang SC, Shen YY, Wang XF, Zhang DP. Light-harvesting chlorophyll a/b-binding proteins are required for stomatal response to abacisic acid in Arabidopsis. J Exp Bot. 2012;63:1095–106.

Yu X, Liu H, Klejnot J, Lin C. The cryptochrome blue light receptors. The Arabidopsis book. 2010;8:e0135.