Chapter 8
Epigenetics of Light Signaling During Plant Development

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Abstract Light controls plant growth and development by directly impacting gene expression, physiology, and metabolism. For 20 years it has been known that light also targets epigenetic mechanisms to control different outputs. This research field is still at a relatively young stage, given its complexity and overall limitation to the plant model Arabidopsis. This chapter highlights major knowledge of the epigenetics of light signaling in Arabidopsis. Different developmental stages are discussed, including germination and early seedling development, control of the circadian clock and flowering, as well as hormone crosstalk and stress responses, and finally environmental memory. While most of the knowledge has been built up based on a laboratory plant model, studies on plants with commercial value are emerging. These studies show that some mechanisms using light signaling and epigenetic remodeling are conserved between different plant species, but other mechanisms show species specificity. The increasing availability of tools to study crops may allow the development of novel solutions for crop improvement by targeting epigenetic factors with light. This is of particular relevance in the future of agriculture, which will undoubtedly include indoor farming and the usage of artificial light.

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8.1 Introduction

Light is a broad regulator of plant growth and development. It impacts gene expression, metabolism, physiology, and morphology with tissue- and developmental stage-specific activity. Wavelengths from ultraviolet (UV) to far-red regions contribute to this regulatory control with independent, overlapping, synergistic, or antagonistic actions.

Light activity over plant growth is facilitated by photoreceptors, mediators between light perception and activation of internal light responses. It is known, although with still limited information, that different light receptors target epigenetic reprogramming, including chromatin condensation, histone modifications, and expression of noncoding RNAs (Fisher and Franklin 2011; van Zanten et al. 2012; Wang et al. 2014a; Perrella and Kaiserli 2016). Distinct light signaling pathways may also target similar epigenetic mechanisms but with light-specific effects (Guo et al. 2008). This feature may provide an additional level of plasticity to plants to allow for a more efficient response to light cues and changing light quality conditions. In addition, epigenetic remodeling provides a tool for the integration of light with additional environmental cues and internal signals, which is key for optimal plant growth and survival (Nicotra et al. 2010; Johansson et al. 2014; Legris et al. 2016; Xiao et al. 2017).

Known plant photoreceptors include the UV receptor UVR8, cryptochromes (cry), phototropins, LOV-domain sensors, and phytochromes (phy) (Folta and Carvalho 2015). Phytochromes are mostly responsive to red and far-red light, but also have roles in absorbing blue/near UV light. Cryptochromes, phototropins, and LOV-domain sensors are the main responders to blue light, while cryptochromes also interfere with green light absorption. Additional sensors, including a green light sensor, await identification.

Phytochromes play major roles during development, from the control of photosynthesis, to seed germination, flowering establishment, and shade avoidance responses. *Arabidopsis thaliana* (Arabidopsis) contains five phytochromes (phyA-E) with different sensitivities to light intensity, and distinct and overlapping activities during development. These molecules are synthesized in a biologically inactive, red-light absorbing, Pr, form. Upon red light perception Pr is converted into the biologically active, far-red light absorbing, Pfr (Pham et al. 2018). The photoreversibility of phy allows for a rapid response to fluctuating environmental conditions. An initial response upon phy activation involves the control of expression and activity of several transcription factors that then initiate specific signaling cascades controlled at the transcriptional and posttranscriptional levels. In addition, phy also mediates red and far-red light responses via epigenetic remodeling. PhyA activation, for example, is followed by an enrichment in acetylation of H3K9/14 (histone H3 lysine 9/14) and H3K27, as well as trimethylation of H3K4 at phyA-controlled transcription sites (Jang et al. 2011). Additional histone modifications have been reported, including increased H3K27me3 and decreased H3K27ac upon phyA repression. PhyB regulates nucleus size and heterochromatin condensation levels,

with obvious expected impacts on gene expression (van Zanten et al. 2010a, b; Snoek et al. 2017). This regulation may be achieved through controlled activity of the HISTONE DEACETYLASE6 (HDA6), which acts in cooperation with METHYLTRANSFERASE 1 (MET1) (Tessadori et al. 2009; To et al. 2011; Snoek et al. 2017).

Cryptochromes are additional regulators of photosynthesis and play roles during seed germination, flowering, and control of stomatal opening. Arabidopsis contains two cry, cry1 and cry2. Cry are activated upon blue/UV-A sensing through phosphorylation, which activates internal cascades involving transcriptional and post-transcriptional regulation. Cry also mediate light responses through epigenetic regulation. Similarly to phyB, cry2 regulates reversible chromatin compaction in response to low light, a function that is under control of phyB (van Zanten et al. 2010b). A target of cry2 may be a chromatin protein complex responsible for chromatin compaction, and that may include HDA6.

Knowledge on the effects of light on epigenetics during plant development is at a young stage. It has been poorly explored in other plants besides Arabidopsis. In this chapter we will focus on this model species, and on relevant examples that have connected light with plant epigenetics at different stages of plant development and during stress responses. We will go beyond the broad examples depicted in the introduction to describe known mechanisms in more detail. We will make an emphasis on the possibilities that further advancements in the field may allow extrapolation to other species, in particular to crop plants with commercial value, with possible benefits on plant quality and yield.

8.2   Plant Development

8.2.1   Seed Germination and Early Seedling Development

Seed germination and early seedling development are controlled by internal and external cues, including light and phytohormones. Light triggers seed germination, inhibits hypocotyl growth, and promotes chloroplast differentiation and initiation of photosynthesis. Two important hormones at this stage with antagonistic activities are abscisic acid (ABA) and gibberellic acid (GA) (Fig. 8.1a). ABA is a positive regulator of dormancy, whereas GA promotes plant growth and development (Koornneef et al. 2002). Light-activated phyB triggers a decrease in ABA and an increase in GA levels, resulting in the promotion of seed germination (Mazzella et al. 2005; Seo et al. 2008). PhyB-mediated changes in ABA and GA result from profound shifts at transcriptional levels in the two pathways. A transcription factor central in this process, which is degraded upon phyB light activation, is the basic helix-loop-helix PHYTOCHROME INTERACTING FACTOR 3-LIKE5 (PIL5). PIL5 is a phy-interacting protein that acts as a negative regulator of seed germination and inhibition of hypocotyl elongation (Oh et al. 2004). PIL5 activates ABA
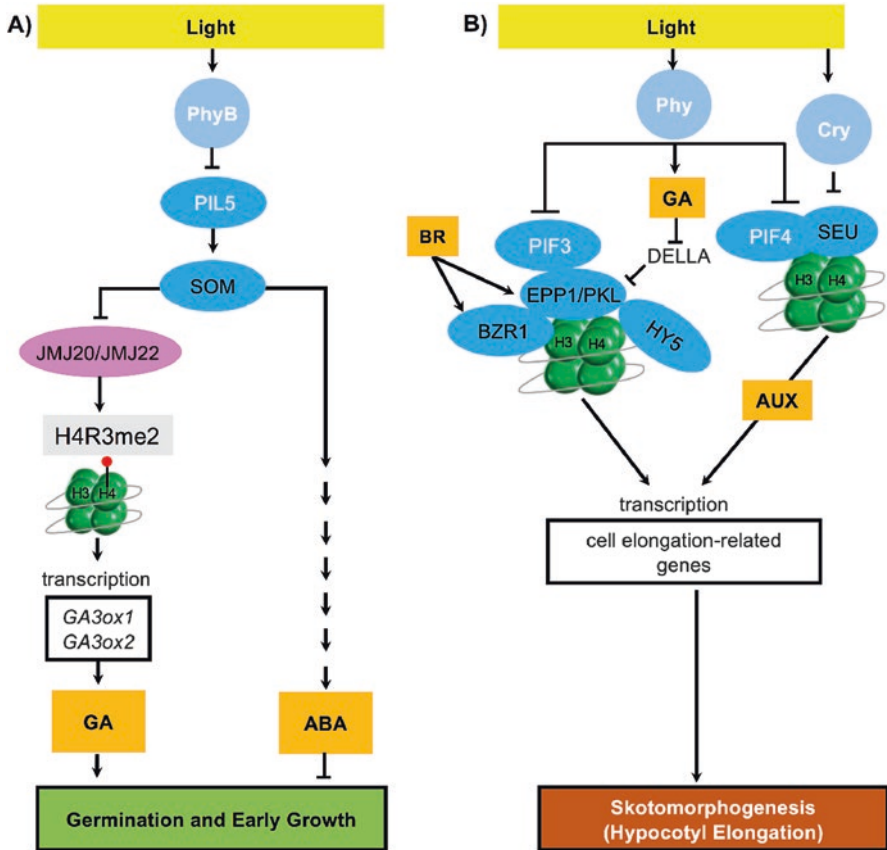
Fig. 8.1 Connecting light and hormone signaling with epigenetics during seed germination and hypocotyl growth. (**a**) PhyB is activated by light and triggers PIL5 degradation, releasing the repression of SOM on histone arginine demethylases, JMJ20 and JMJ22, which remove R3me2s on H4 in the chromatin region of GA genes (*GA3ox1* and *GA3ox2*), activating their transcription. The increase in GA promotes germination and early growth. In the absence of light, PIL5 activates ABA biosynthesis through SOM, and inhibits germination. (**b**) Light represses hypocotyl elongation by repressing PIF and other factors. In the dark, PIF3 acts together with EPP1/PKL and BZR1 to repress trimethylation of H3 of cell elongation-related genes. PIF4 interacts with SEU, blocking H3K4me3 methylation of auxin biosynthesis-related genes, interfering in this way with cell elongation. GA, gibberellic acid; ABA, abscisic acid; BR, brassinosteroids; AUX, auxins; H3-H4, Histones

biosynthesis and inhibits GA biosynthesis, partly through the positive modulation of SOMNUS (SOM), a nucleus-localized CCCH-type zinc finger protein (Fig. 8.1a) (Kim et al. 2008). SOM directly represses the histone arginine demethylases JUMONJI DOMAIN-CONTAINING PROTEIN 20 and 22 (JMJ20 and JMJ22). Upon light-induced derepression, JMJ20 and JMJ22 remove repressive symmetric histone H4 arginine 3 dimethylation (H4R3me2s) in the chromatin region of two GA metabolic genes, *GA3ox1* and *GA3ox2*, promoting an increase in bioactive GA,

and seed germination and early growth (Fig. 8.1a) (Cho et al. 2012). The regulatory effect of H4R3me2s on the expression of GA genes waits further clarification. The activity of histone arginine demethylase by Jumonji domain-containing proteins has been characterized in humans, highlighting the transferability of epigenetic studies and mechanisms between different organisms (Neff 2012).

Other hormones besides GA and ABA act on the crosstalk of light signaling and epigenetics during early plant growth. One known example is the signaling of brassinosteroids (BRs) via ENHANCED PHOTOMORPHOGENIC 1/PICKLE (EPP1/PKL), an ATP-dependent chromatin-remodeling factor of the chromodomain/helicase/DNA binding family (Fig. 8.1b). EPP1/PKL interacts with PHYTOCHROME INTERACTING FACTOR 3 (PIF3) and BRASSINAZOLE RESISTANT1 (BZR1) to promote hypocotyl growth by repressing trimethylation of H3K27 of cell elongation-related genes (Fig. 8.1b) (Zhang et al. 2008, 2012, 2014). DELLA proteins, negative regulators of the GA pathway, physically interact with PKL to repress its activity. PKL also regulates DNA methylation at *loci* targeted by RNA-directed DNA methylation (Yang et al. 2017). PIF4, in turn, interacts with the transcriptional regulator SEUSS (SEU) to regulate light, temperature, and auxin (AUX) signaling (Fig. 8.1b). Mutations in *SEU* affect H3K4me3 methylation at the AUX biosynthetic genes *INDOLE-3-ACETIC ACID INDUCIBLE 9* and *19* (*IAA9* and *IAA19*), interfering with proper cell elongation (Huai et al. 2018). Additionally, while PIF4 is part of the red/far-red light signaling pathway, SEU also responds to blue light, suggesting its extensive regulatory effect on epigenetics in response to changing light conditions.

Additional relevant examples of histone modifications include other specific trimethylation events and acetylation/deacetylation on a number of different genes and genomic regions, such as non-transposable element genes, intergenic regions, and transposable elements (Bertrand et al. 2005; Benhamed et al. 2006; Guo et al. 2008; Charron et al. 2009). For instance, the inhibition of light-induced seed germination mediated by PIF1 is partly achieved by increased levels of H3K36me3 at *PIF1* under the control of the H3K4 and H3K36 methyltransferase EARLY FLOWERING IN SHORT DAYS (EFS) (Lee et al. 2014). The HISTONE DEACETYLASE 15 (HDA15) is another interesting case study. HDA15 acts as a negative regulator of light-induced germination and photosynthesis establishment, but as a positive regulator of light repression of hypocotyl growth (Liu et al. 2013; Tang et al. 2017; Gu et al. 2017). In the dark, HDA15 interacts with PIF1 to lower histone H3 acetylation levels in genes involved in seed germination. Upon phyB activation, PIF1 is repressed and HDA15 activity on germination-related genes is dismissed. HDA15 also interacts with PIF3 to repress genes involved in chlorophyll biosynthesis and photosynthesis in dark-grown seedlings. Similarly to PIF1, PIF3 is repressed upon light exposure, ending HDA15 repressive activity, and allowing expression of target genes. In contrast, HDA15 acts as a positive regulator of light responses in the repression of hypocotyl elongation. In the hypocotyl, HDA15 interacts in a light-dependent manner with four NUCLEAR FACTOR-YC homologs (NF-YCs), NF-YC1, NF-YC3, NF-YC4, and NF-YC9, to decrease levels of histone H4 acetylation at the chromatin of positive regulators of hypocotyl elongation.

Under darkness, the NF-YC-HDAC15 complex is dismissed, increasing the levels of H4 acetylation at target genes and promoting hypocotyl growth. These three examples clearly suggest that the factors interacting with HDA15 define its biological role. Tissue- and developmental-specific interactions are therefore key to determine the output seen in terms of epigenetic reprogramming in response to light, even during this small developmental window of early plant growth.

A factor that may allow for hormone crosstalk during light responses is the Elongator complex. Elongator promotes RNA polymerase II-mediated transcript elongation through epigenetic modifications, including histone acetylation and DNA demethylation. Elongator complex was recently identified as a positive regulator of photomorphogenesis, and seems like an excellent candidate as integrator of light, hormones, and epigenetic reprogramming not only during early seedling establishment but also at various stages of plant development (Woloszynska et al. 2018a, b). Additional regulators integrate light responses and chromatin remodeling during early plant development, allowing for a massive rapid transcriptomic reprogramming, crucial for the transition to germination and photomorphogenesis. A critical challenge in research remains building detailed molecular networks that describe these regulatory mechanisms with direct targets of light signaling pathways and of chromatin-remodeling factors. While individual studies targeting specific molecules provide useful information, additional comprehensive studies are needed. Large-scale approaches may be a part of the solution, as seen with recent results obtained from RNA-sequencing, small RNA-sequencing, DNA methylation-sequencing (Methyl-seq or bisulfite sequencing), histone monoubiquitination profiling, and studies of nuclear architecture organization (Bourbousse et al. 2012, 2015; Narsai et al. 2017; Kawakatsu et al. 2017). Thousands of *loci* show dynamic changes at the epigenomic, transcriptomic, and alternative splicing pattern levels during the transition from a dormant seed stage to an active vegetative growth stage under the presence of light. Abundance of various small RNAs (sRNAs) populations, including microRNAs (miRNAs) and small interfering RNAs (siRNAs), correlates with this developmental transition. Modifications in specific siRNAs associate, for instance, with an extensive DNA demethylation towards the end of seed germination/early seedling development. Active changes in miRNAs are related to the control of gene expression by inhibition of translation or degradation of target transcripts. Changes in histone monoubiquitination and heterochromatin reorganization allow for rapid control over transcription. Challenging studies will be to identify individual molecular players in these pathways, and to add to the very few that have already been pinpointed, such as CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and DE-ETIOLATED 1 (DET1). COP1 and DET1 are required to maintain a decondensed state of heterochromatin in the dark, ensuring repression of genes needed for the transition to light growth. ELONGATED HYPOCOTYL 5 (HY5) is a master regulator of light signaling and a positive regulator of the transition to photomorphogenesis that also impacts light-regulated chromatin organization. For example, HY5 acts with EPP1/PKL to repress trimethyl H3K27 at target *loci* and regulate hypocotyl cell elongation (Fig. 8.1b) (Jing et al. 2013). HY5 also regulates expression of several miRNAs that in turn control the

transcript accumulation of different target genes (Zhang et al. 2011). Furthermore, *HY5* expression is in turn partly regulated via histone acetylation (Charron et al. 2009).

During germination and early seedling establishment, light acts together with other external cues, such as water uptake (imbibition), temperature, and nutrients, to regulate plant development. Light-specific epigenetic mechanisms may therefore be difficult to discern. Nevertheless, integrated analyses between different processes that regulate gene expression are essential to acquire more information on the role of light over epigenetics during early plant growth and the establishment of photosynthesis.

8.2.2   Circadian Clock

The circadian clock is an oscillator system synchronized approximately to a 24-h period that regulates rhythmicity of different developmental processes. From cyanobacteria to plants or humans, circadian clocks ensure more robust predictions and anticipated responses to environmental conditions, which contributes to higher fitness (Bell-Pedersen et al. 2005). Synchronization in plants is controlled externally by light and temperature, and these environmental inputs connect to internal interlocked regulatory feedback loops (Harmer 2009; Cui et al. 2014). Three chief loops exist in Arabidopsis: morning, central, and evening. The morning loop is initiated with the activity of the Myb transcription factors CIRCADIAN CLOCK-ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY), which induce expression of *PSEUDO-RESPONSE REGULATOR 7* and *9* (*PRR7* and *PRR9*), and the resultant products in turn repress *CCA1* and *LHY*. The central loop uses CCA1 and LHY to repress expression of the evening-phase gene *TIMING OF CAB EXPRESSION 1 (TOC1)*. The evening loop includes TOC1 to suppress accumulation of CCA1/LHY, and the activity of GIGANTEA (GI), EARLY FLOWERING 3 and 4 (ELF3 and ELF4), and LUX ARRHYTHMO (LUX). Each loop contains regulatory elements that act at the transcriptional, posttranscriptional, and posttranslational levels. These regulatory checkpoints have been reviewed extensively, therefore we will focus on the impact of light at the epigenetic level.

Chromatin remodeling is one of the mechanisms that allows the circadian clock to be connected to light signals, including photoperiod, and light intensity and quality (Stratmann and Más 2008; Barneche et al. 2014). Altered levels of histone acetylation, methylation, phosphorylation, and ubiquitination are associated with diurnal changes in expression of core clock and other genes, although the mechanisms governing these histone modifications require further clarification (Song and Noh 2012; Himanen et al. 2012; Malapeira et al. 2012; Barneche et al. 2014; Baerenfaller et al. 2016). The regulation of circadian clock through day-length is in turn important for additional developmental responses regulated by the circadian clock, allowing their indirect connection to photoperiod.

The 24 h-rhythmic histone acetylation at the *TOC1* promoter is under the control of various factors (activators and repressors) (Perales and Más 2007; Farinas and Mas 2011). At dawn, CCA1 represses *TOC1* by binding to its promoter and preventing acetylation, while during the day this binding decreases and is counteracted by factors that induce H3 acetylation, such as REVEILLE 8/LHY-CCA1-LIKE 5 (RVE8/LCL5). This allows *TOC1* to reach a peak of expression at dusk. During the night, histone deacetylases function to promote a *TOC1* promoter hypoacetylated state. It was recently shown that TOC1 interacts with PIF3 to repress its activity as a transcription factor (Soy et al. 2016). This finding establishes an important link between the circadian clock core components and the phytochrome photosensory pathway. One factor that may be recruited by CCA1 and LHY, to negatively regulate *TOC1* and other gene targets such as *GI*, is DET1, which binds to the non-acetylated tail of histone H2B (Benvenuto et al. 2002; Lau et al. 2011). Histone acetylation also seems to be necessary for differential expression of additional clock elements, such as *CCA1*, *LHY*, *PRR7*, *PRR9*, and *LUX* (Song and Noh 2012; Hemmes et al. 2012; Malapeira et al. 2012; Wang et al. 2013).

Proper H3K4 trimethylation at *LHY*, *TOC1*, and *CCA1* is essential for their accurate expression and functioning. H3K4me3 at the promoter of these genes might be mediated by the histone methyltransferase SET DOMAIN GROUP 2/ARABIDOPSIS TRITHORAX RELATED 3 (SDG2/ATXR3). Another epigenetic marker related to the expression of these clock genes is H3K36me2. In terms of the activity of histone demethylases, a reported example includes JUMONJI DOMAIN CONTAINING 5/30 (JMJD5/JMJ30) and its regulatory role over the pace of the circadian clock (Jones et al. 2010; Lu et al. 2011). *JMJD5*/*JMJ30* expression has a peak at dusk and is negatively regulated by direct binding of CCA1 and LHY to its promoter. In turn, JMJD5/JMJ30 acts in a feedback loop to control *CCA1* and *LHY* expression.

In the past 10 years, several reports have contributed to increase knowledge on the mechanisms that link epigenetics to light and the circadian clock. Further studies should focus not only on transcriptional regulation but also on regulation at posttranscriptional levels. For instance, the PROTEIN ARGININE METHYL TRANSFERASE 5 (PRMT5), which performs methylation on histones and Sm spliceosomal proteins, controls alternative splicing of *PRR7* and *PRR9* (Sanchez et al. 2010). Alternative splicing of *PRR7* and *PRR9* also requires the activity of the SKI-INTERACTING PROTEIN (SKIP) splicing factor (Wang et al. 2012; Cui et al. 2017), and disruption of *SKIP* affects the clock length. This splicing factor also regulates alternative splicing of salt stress-responsive genes, highlighting the possible crosstalk of different signaling pathways under the control of light (Feng et al. 2015). Such crosstalk is in fact addressed in further detail in Sects. 8.3, 8.4, and 8.5 of this chapter.

8.2.3 Flowering

Flowering ensures proper crop yield when fruits and/or seeds are harvested, and its correct timing maximizes yield and quality. It represents a fundamental transition during plant development from a vegetative to a reproductive stage, which ultimately relies on epigenetic regulation. Similarly to the previous sections, we will focus on the impact of light on these adjustments. Flowering is particularly sensitive to light quality and quantity, especially in plants that are photoperiod sensitive. Arabidopsis is a long-day plant, which means it flowers when exposed to long days and short nights, upon reaching adequate developmental maturity. Light, together with additional environmental factors, is perceived by plants, and along with endogenous cues, activates internal pathways that initiate flowering. Floral integrators, such as the florigen FLOWERING LOCUS T (FT) and SUPPRESSOR OF OVEREXPRESSION OF CO 1 (SOC1), trigger the transition of the meristematic vegetative apex to a meristematic floral meristem. Immediately upstream of floral integrators, additional essential players communicate environmental cues to downstream pathways. These include the transcription factors FLOWERING LOCUS C (FLC) and CONSTANS (CO) (Blümel et al. 2015).

CO is the main responder to long day inputs. It is stabilized by cry2 and phyA during late afternoons and by the circadian clock to rhythmically induce *FT* expression under long days (Fig. 8.2) (Shrestha et al. 2014). CO directly binds to the *FT* promoter and also affects histone modifiers at the *FT locus* to regulate its expression (Fig. 8.2) (Wenkel et al. 2006; Gu et al. 2013; Wang et al. 2014b). For instance, CO physically interacts with MORF RELATED GENE 1 and 2 (MRG1 and MRG2), which bind to H3K4me3 and H3K36me3 at the *FT locus* to more robustly activate its expression (Fig. 8.2) (Xu et al. 2014; Bu et al. 2014). MRG1/2 also interact with the histone H4-specific acetyltransferases HAM and HAM2 to regulate histone acetylation at the *FT* promoter and 5′ region, which results in its high expression (Fig. 8.2). Moreover, CO associates at the *FT* distal promoter with NUCLEAR FACTOR-Y (NF-Y) transcription factors (Cao et al. 2014). NF-Y subunit C counteracts levels of H3K27me3 at the *FT* chromatin by interacting with and attenuating CURLY LEAF (CLF), a histone methyltransferase part of the Polycomb Repressive Complex 2, PRC2 (Liu et al. 2018). A CO-NF-Y complex additionally recruits the H3K27 demethylase RELATIVE OF EARLY FLOWERING 6 (REF6) to the chromatin of *SOC1* to reduce repressive H3K27me3 levels and induce flowering (Fig. 8.2) (Hou et al. 2014). The circadian clock also induces *FT* independently of CO: *GI* regulates processing of the microRNA miR172, which in turns upregulates *FT* (Jung et al. 2007).

At dusk, CO affects acetylation and methylation, repressing *FT* expression in order to prevent early flowering and ensure optimal flowering time (Gu et al. 2013; Wang et al. 2014b). For example, CO recruits the AFR-HDAC complex that includes two relatives of the yeast SAP30, SAP30 FUNCTION-RELATED 1 (AFR1) and AFR2. CO seems to enable recruitment of AFR-HDAC to *FT* by making *FT* chromatin accessible to the transcription factor AGAMOUS-LIKE 18 (AGL18), which

Fig. 8.2 Connecting flowering with epigenetics and the circadian clock, under long days. PhyA, cry2, and the circadian clock are involved in the stability of CO. During late afternoons, CO binds the *FT* gene promoter and affects histone modifiers at the *FT* locus to regulate its expression. In addition, the CO-NF-Y complex recruits REF6 to the chromatin of *SOC1* to induce flowering. GA-mediated degradation of DELLAs enhances NF-Y binding to the *SOC1* promoter and recruitment of REF6 to promote flowering. Histone modifiers: H4-specific acetyltransferases HAM and HAM2; histone methyltransferase CLF; and demethylase REF6. PROM, promoter; CDS, coding-sequence
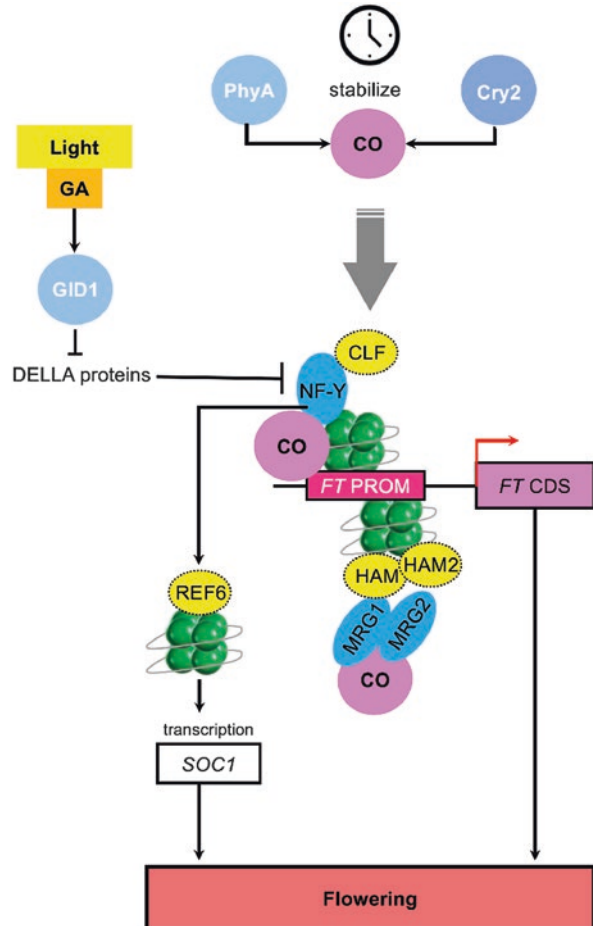
then brings the complex to the *FT* chromatin (Gu et al. 2013). These examples are not exhaustive and show that distinct epigenetic mechanisms regulate *FT* in response to light. Current knowledge is not complete and further research is needed.

Both cry2 and phyB control transient chromatin compaction that regulates transition to flowering (Tessadori et al. 2007, 2009). Blue light-activated cry2 triggers a large-scale chromatin reorganization that includes decondensation of heterochromatic chromocenters and the chromatin of gene-rich regions (Tessadori et al. 2007). This process does not rely on CO, indicating that photoreceptors and CO may act together or independently on epigenetic modifications to regulate flowering in response to light. Comparing Arabidopsis accessions with different origins has allowed the identification of polymorphisms in *PHYB* and in the histone modifier *HISTONE DEACETYLASE 6* (*HDA6*) (Tessadori et al. 2009). These polymorphisms correlate with different levels of light-mediated chromatin remodeling. Chromatin

plasticity in response to light seems therefore to be associated with the plant capacity for environmental acclimation.

Under short days a CO-independent pathway ensures that plants do not transition to flowering. The histone deacetylase HDA9 maintains the transcription factor *AGAMOUS-LIKE 19* (*AGL19*) repressed by acting on H3K9 and H3K27 at this *locus* (Kim et al. 2013). AGL19 is a well-known inducer of the prolonged cold exposure pathway (vernalization) that also promotes flowering in Arabidopsis. The histone methyltransferase CLF is also known to act in the autonomous (developmental) pathway (Liu et al. 2018). These observations highlight the overlap of epigenetic regulatory mechanisms between different pathways that control flowering. The crosstalk of different pathways ensures proper flowering synchronization to different environmental cues.

8.3   Hormone Crosstalk

Plant hormones such as GAs, auxin (AUX), cytokinins (CKs), and brassinosteroids (BRs) control essential developmental processes and are essential for proper growth (Depuydt and Hardtke 2011). GAs promote cell elongation and are essential for seed germination, stem elongation, and floral development. CKs regulate cell proliferation, while AUX and BRs may be involved in both processes as well as in cell elongation. These hormones may share overlapping mechanisms and have synergistic or antagonistic activities. Hormonal action, from synthesis to sensing and signaling, often depends on epigenetic modifications to ensure rapid and effective biochemical responses. Described mechanisms include histone modification, chromatin remodeling, DNA methylation, and action of sRNAs (Yamamuro et al. 2016). Hormonal activity is well known to be linked to light cues (Lau and Deng 2010). We will focus here on examples of this crosstalk at the epigenetic level with an emphasis on hormonal action during plant development. Activity of stress-related hormones will be discussed in Sect. 8.4.

DELLA proteins are central components of the GA pathway. As negative regulators of GA, DELLAs repress GA-induced growth. DELLA proteins are degraded upon binding to the GA receptor GA INSENSITIVE DWARF 1 (GID1) in a GA-dependent manner, allowing the activation of GA-mediated responses (Fig. 8.2). DELLAs also interfere with light signaling and are stabilized, for example, during light repression of hypocotyl elongation (Achard et al. 2007). DELLAs block transcriptional activity of the negative regulators of photomorphogenesis PIF3 and PIF4 by binding to their DNA-recognition sites, and by promoting their degradation through the ubiquitin-proteasome system (Cao et al. 2005; Feng et al. 2008; de Lucas et al. 2008; Li et al. 2016). This mechanism allows the integration of GA and light cues in order to optimize plant growth under changing environmental conditions. During the floral transition NF-Y factors interact with CO in the photoperiod pathway and with DELLAs to regulate *SOC1* expression (Fig. 8.2) (Hou et al. 2014). GA-mediated degradation of DELLAs enhances NF-Y binding to the *SOC1*

promoter and recruitment of REF6, accelerating the transition to flowering initiated by long days. The flexibility in terms of the possible combinations of multiple NF-Y subunits with distinct properties and *trans*-acting partners may enhance plastic responses to shifts in external cues.

Under low ratios of red to far-red light, shade intolerant plants, including Arabidopsis, undergo a series of responses known as the shade avoidance syndrome (SAS). Green light sensing is also important to trigger SAS (Zhang and Folta 2012). Typical SAS signs include stem elongation, leaf hyponasty, and reduced branching (Yang and Li 2017). In natural environments, SAS helps plants escaping from neighbors in dense vegetation in order to maximize access to sunlight. In agricultural contexts, prolonged shading can severely affect crop yield. It is well known that SAS requires changes in gene expression, and is mediated by localized transport and fluxes of auxin that induce cell division at particular spots. Other hormones may also be involved, such as GAs, BRs, CKs, ethylene, ABA, strigolactone, salicylic acid (SA), and jasmonic acid (JA). The modulation of the auxin pathway is initiated by pools of phytochrome in equilibrium under low ratios of red to far-red light, as well as by signaling from the UV-receptor UVR8 and cryptochromes. Under shade conditions, photoreceptors stabilize PIF transcription factors, which in turn activate auxin biosynthesis, transport, and signaling (Hornitschek et al. 2012). PIF proteins are now emerging as recruiters of chromatin modulators under shade. PIF7 recruits MRG1/MRG2 that bind H3K3m3/H3K36me3 at the chromatin of shade responsive genes, and bring histone acetyltransferases (HATs) to nearby chromatin to induce histone acetylation and activate SAS-related gene expression (Peng et al. 2018).

A crosstalk between phytochrome, auxin, and JA signaling and chromatin remodeling has been established with the action of the cytoplasmic localized JA-conjugating enzyme FAR-RED INSENSITIVE 219/JASMONATE RESISTANCE 1 (FIN219/JAR1). FIN219/JAR1 acts synergistically with phyA to negatively regulate SAS, reducing *PIF5* expression and COP1 levels (Swain et al. 2017). In addition, FIN219/JAR1 accumulation is reduced under shade. The *fin219* mutant, an epiallele of *FIN29* with altered methylation patterns, is more sensitive to shade (Hsieh et al. 2000). While reduced *FIN219* levels as a result of the *fin219* mutation seem to be at the basis of altered SAS, it may be interesting to verify whether the altered methylation status itself interferes with hormonal signaling.

Light effects are not specific to aerial parts of plants, and studies on roots should be further explored. Far-red light detection in shoots, for example, reduces auxin signaling in cortex cells in roots and reduces lateral root outgrowth through activity of HY5 (van Gelderen et al. 2018). It is very likely that light-mediated epigenetic remodeling supports root development. Interestingly, the H3K27 methyltransferase CLF binds the chromatin of the auxin efflux carrier *PIN FORMED 1* (*PIN1*) and functions to reduce auxin maxima and regulate the establishment of lateral roots (Gu et al. 2014). CLF, as referred in Sect. 8.2.3, affects flowering in association with CO (Fig. 8.2). It may be of interest therefore to analyze effects of light on CLF activity in roots.

8.4 Stress Responses

As sessile organisms, plants have evolved complex mechanisms to cope with abiotic and biotic stress cues, which include the activity of hormones ABA, JA, SA, and ethylene, and the modulation of reactive oxygen species (ROS) (Verma et al. 2016). Reversible epigenetic modifications, at various plant developmental stages, integrate light and internal signals and allow for rapid responses to environmental stress, towards ensuring plant survival.

Light and ABA control guard cell dynamics and stomatal aperture, as well as water loss, which is particularly relevant under drought and high salinity. Exposure of plants to ABA and low light conditions induces expression of the linker H1.3 histone (Fig. 8.3) (Rutowicz et al. 2015). H1.3 controls DNA methylation under low light and drought conditions, together with other H1 variants, H1.1 and H1.2. Furthermore, *h1.3* mutant plants display reduced stomatal density and CO_2 assimilation rate, and are unable to trigger proper responses to drought. Finally, H1.3 activity in response to light does not depend on photoreceptors but on
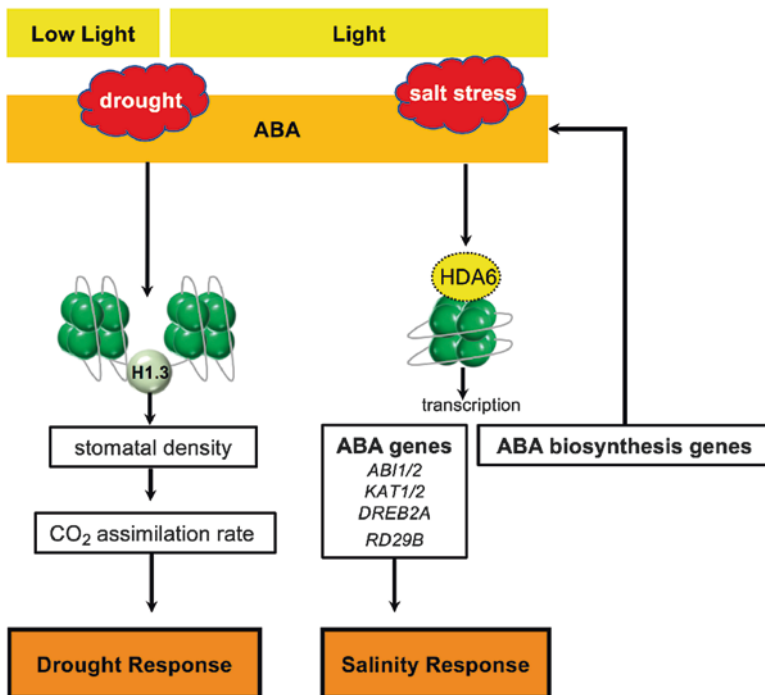

Fig. 8.3 Connecting hormones and stress signaling with epigenetics, an example with ABA. The response of plants to ABA and low light conditions induces the activity of the linker H1.3 histone. H1.3 controls DNA methylation during stomata development, which affects stomatal density and CO_2 assimilation rates and responses to drought stress. Salinity stress activates the ABA biosynthesis pathway through HDA6 and leads to increased ABA levels and ABA signaling

chloroplast-to-nucleus retrograde signaling. The epigenetic targets of H1.3 in the control of stomata opening under stress remain to be identified. Interestingly, histones of the H1.3-type subfamily are conserved in angiosperms but are absent in older plant lineages. This suggests that the mechanism using H1.3-ABA-light to control stomatal aperture, and possibly other biological functions using H1 histones, may have been important in the evolution of angiosperms, the largest group of plants. Additional epigenetic factors with roles in light responses and stomata regulation are yet to be found. An interesting candidate could be NF-YC9, given its activity in the ABA pathway and the regulation of stomatal aperture, and the roles of NF-Y members in chromatin remodeling (see Sect. 8.2.3) (Bi et al. 2017).

As referred in Sect. 8.2.3, the histone deacetylase HDA6 is a mediator of light-controlled chromatin compaction (Tessadori et al. 2009). Mutant plants in *HDA6* also display hypersensitivity to ABA and salt stress (Chen et al. 2010; Chen and Wu 2010). ABA and salt stress affect H3K4 trimethylation, H3K9 dimethylation, and H3 acetylation of several genes in the ABA pathway (Fig. 8.3). HDA6 is part of this regulatory process and may target ABA pathway genes, such as *ABI1/2*, *KAT1/2*, *DREB2A*, and *RD29B* (Fig. 8.3). Further studies are needed to connect the simultaneous response of HDA6, and of other histone deacetylases, to light and ABA. Light regulatory effects have in fact been identified in other histone deacetylases (HDAs), but more is known on the role of these factors in response to stress (Ueda et al. 2017). Arabidopsis contains 18 HDAs divided into three classes, and HDA6 is included in class I. HDA15, a HDA type II, mediates tolerance to salt stress, and its activity is regulated through subcellular compartmentalization by light-controlled protein shuttling between the cytoplasm and the nucleus (Alinsug et al. 2012). It seems that different families of HDAs show functional diversification and may act at an epistatic level to allow for nonselective histone deacetylases to acquire specificity upon particular environmental conditions.

Plant cells possess different mechanisms to cope with damaging UV light, which can include chromatin regulators. The UV RESISTANCE LOCUS 8 (UVR8) is a UV-B signaling component that helps in UV protection. UVR8 interacts with chromatin mainly via interaction with histone H2B in different genomic regions, including in the *HY5* promoter. UVR8 increases acetylation of K9 and K14 of histone H3 at UV-responsive *loci*, such as *EARLY LIGHT-INDUCIBLE PROTEIN 1* (*ELIP1*) (Cloix and Jenkins 2008; Velanis et al. 2016). UVR8-regulated chromatin modification also requires the activity of HY5. In addition, inhibiting activity of histone acetyltransferases prior to damage by UV-B reduces the capacity for DNA repair, highlighting the fundamental role of histone acetylation in plant survival under UV (Campi et al. 2012; Velanis et al. 2016). Known acetyltransferases with role in UV-B-induced damage repair and signaling include HAM1 and HAM2 of the MYST family, and HAG3 of the GNAT family (Fina and Casati 2015). On the other hand, the histone acetyltransferases HAC1 (HAC family) and HAF1 (HAF family) do not directly participate in damage repair but still have roles in signaling and plant responses to UV light (Fina et al. 2017). It may be possible that different families of histone modifiers have evolved specific functions to support plants in more efficient responses to UV stress conditions.

Synthesis of secondary metabolites, such as anthocyanins in the flavonoid pathway, provides a mechanism for protection under various stress conditions. UV and far-red light are well-known promoters of anthocyanin production, which is known to require epigenetic reprogramming. A study targeting the role of miRNAs in stress-induced anthocyanin biosynthesis identified miR858a as a positive regulator of this induction (Wang et al. 2016). miR858a inhibits translation of *ARABIDOPSIS MYB-LIKE 2* (*MYBL2*), a transcription factor functioning as a negative regulator of anthocyanin biosynthesis. The role of light is integrated via the activity of HY5, which activates *MIR858A* expression and represses *MYBL2* by binding to its promoter, as well as via histone demethylation and deacetylation.

8.5   Environmental Memory

A research field that is gaining relevance in the recent years is the study of epigenetic mechanisms that allow plants to keep track of past exposure to environmental conditions, and to transmit this memory to future generations (Baulcombe and Dean 2014; Buzas 2017; Lämke and Bäurle 2017; Bäurle 2018; He and Li 2018). Some authors divide plant memory into two parts: priming and memory. Priming refers to when a plant or a plant tissue is exposed to a particular environmental condition that triggers physiological conditions for its adaptation. Upon a later exposure (in a time window of hours or days) to the same environmental cue, this plant or tissue shows a more robust physiological response given its primed state, when compared to the first naïve organism. Plant memory describes the transmission of physiological priming from a primed plant or tissue to newly synthesized cells or tissues, not exposed to the priming condition, or to new generations.

Environmental memory has been described in response to various abiotic and biotic factors. There is growing evidence that epigenetics is a central regulator of plant memory. Various reports are emerging, and more studies are required, but it is becoming clear that this increasing knowledge may be useful for crop improvement. Climate change is associated not only with global warming but also with extreme and sudden shifts in environmental conditions. The latter may be in fact the major challenge to farmers. For proper yields, crops must be able to adjust growth to fluctuating weather. Targeting epigenetics mechanisms of plant memory in crop biotechnology may therefore be of high interest to plant producers in order to obtain plants that respond more rapidly to the environment and also are more resilient in their responses.

The most explored environmental conditions affecting plant memory include winter cold exposure and its effect over flowering (vernalization), and virus-induced silencing (Baulcombe and Dean 2014). In terms of light effects on plant memory, knowledge remains scarce, but a couple of studies have shown that light may impact epigenetic memory to a large extent. Excessive UV light is a stress signal that induces responses in plants such as the accumulation of secondary metabolites to protect cellular structures. Plants keep track of this primed state, as plants previously

exposed to UV show more robust responses to UV upon a second exposure (Müller-Xing et al. 2014). With the current depletion of stratospheric ozone, understanding the mechanisms of UV memory is of particular relevance. UV exposure is sensed and signaled by the UVR8 receptor, which activates downstream pathways that directly target, for example, *CHALCONE SYNTHASE* (*CHS*) in the flavonoid biosynthetic pathway (Müller-Xing et al. 2014). UV modulation of *CHS* requires epigenetic mechanisms, through at least increased histone acetylation (H3K9) at the *CHS locus* (Schenke et al. 2014). DNA damage repair pathways are also activated by UV, as a result of the UV damaging effect on DNA. This activation involves chromatin modifications and is linked to epigenetic memory (Molinier 2017). In another study analyzing plant responses to excessive white light, the authors failed to prove the hypothesis that altered DNA methylation patterns supported priming responses, including the synthesis and accumulation of photoprotective compounds (Ganguly et al. 2018). Nevertheless, it is still possible that other epigenetic mechanisms, such as histone modification, sustain priming to excessive white light. The histone acetyltransferase HAG1/GCN5 may be an interesting factor to analyze, given its described putative role in light-induced preparation of chromatin for priming inducible gene activation (Servet et al. 2010).

Drought and other stress conditions, such as exposure to high salt, low temperature, UV irradiation, heavy metals, phosphate starvation, and biotic cues, trigger proline accumulation (Szabados and Savouré 2010; Aleksza et al. 2017). The activation of proline synthesis is affected by light and phytohormones, such as ABA and BRs (Abrahám et al. 2003). Proline acts as an osmoprotectant that increases stress tolerance. Engineering of proline metabolism may bring interesting solutions to agriculture. Salinity-induced proline accumulation is memorable (Feng et al. 2016). This memory is dependent on light, is restricted to the shoot, and uses HY5 in the phyA pathway. Salt memory is based on the retention of increased H3K4me3 levels at Δ^1-*PYRROLINE-5-CARBOXYLATE SYNTHETASE 1* (*P5CS1*), which encodes the rate-limiting proline biosynthetic enzyme. HY5 binds to a C/A-box light responsive element at the *P5CS1* promoter and helps maintaining H3K4me3. There is still no evidence on how HY5 maintains H3K4me3 at *PCS1*. It may directly interact with H3K4 histone methyltransferases or demethylases or it may recruit the histone acetyltransferase HAT1/GCN5 to acetylate histones and activate light-responsive gene expression. It may also be of interest to assess whether modulating proline with light may target flowering quality, particularly in plants exposed to stress. This suggestion comes from the fact that proline is active during flower transition, male gametophyte, and seed development (Székely et al. 2008; Mattioli et al. 2009, 2012). In addition, FRIGIDA (FRI), which acts in the vernalization pathway upstream of FLC, increases *P5CS1* expression under drought (Chen et al. 2018).

Another guideline to be considered in future research for crop improvement may be to compare epigenetics of environmental memory, including of light memory, in wild and cultivated species. Specific mechanisms may be identified and provide novel solutions to obtain better crops.

8.6 Conclusions

Light regulates plant growth by directly impacting gene expression at various developmental stages and under different environmental conditions. Knowledge mostly obtained from Arabidopsis has shown that epigenetics is a fundamental tool in light signaling. Individual reports detailing specific molecular interactions have been helpful advancements and may also be complemented with parallel large-scale analysis.

Light and epigenetics in plants of agronomic importance have only just started being explored, and some similarities are often seen with the model Arabidopsis. The regulator of light responses HY5 has been identified in various plant species from green algae to flowering plants (Serrano-Bueno et al. 2017; Li et al. 2017). Given the master role of HY5 in light signaling and chromatin remodeling, it is an interesting target to further explore. Chromatin remodeling at the *FT locus* during the control of flowering is also conserved between Arabidopsis and other flowering species, including rice, soybean, and wheat (Blümel et al. 2015). Hormonal pathways display similarities as well between different plant species. Mechanisms that use histone modification also show similarities among organisms, from plants to yeast and humans. While we are at a point where some solid knowledge could be easily transferred to direct applications for crop growth, more studies are needed, particularly targeting specific crop species and possible exclusive gene expression regulatory mechanisms. Adaptation to distinct natural light environments, and different latitudes, may cause changes in light-mediated epigenetic responses that may then impact outputs measured as agronomic traits.

Indoor farming is likely a key solution for the future of agriculture. Usage of natural resources can be decreased, and large fields returned back to the wild. In the context of large urban areas, indoor farming may guarantee access to fresh and healthy produce by larger amounts of the population. Indoor crop growth facilitates a tighter control of environmental factors. Light environments, in particular, can be precisely controlled with the usage of light emitting diodes (LEDs). The large-scale commercialization of LEDs offers the possibility to effectively design light recipes to optimize crop growth and value. Near future breeding programs may consider including markers for light-responsive epigenetic remodeling.

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