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Genomic basis for light control of plant development

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ABSTRACT

Light is one of the key environmental signals regulating plant growth and development. Therefore, understanding the mechanisms by which light controls plant development has long been of great interest to plant biologists. Traditional genetic and molecular approaches have successfully identified key regulatory factors in light signaling, but recent genomic studies have revealed massive reprogramming of plant transcriptomes by light, identified binding sites across the entire genome of several pivotal transcription factors in light signaling, and discovered the involvement of epigenetic regulation in light-regulated gene expression. This review summarizes the key genomic work conducted in the last decade which provides new insights into light control of plant development.

INTRODUCTION

Light is one of the most important environmental factors that govern plant growth and development. In addition to being the primary energy source for plants, light also controls multiple developmental processes throughout the plant life cycle, including seed germination, seedling de-etiolation, phototropism, shade avoidance, circadian rhythms, and flowering time (Deng and Quail, 1999; Wang and Deng, 2003; Jiao et al., 2007; Li et al., 2011b). The phenotypic changes associated with seedling photomorphogenic development are among the most dramatic events mediated by light. Dark-grown seedlings undergo skotomorphogenesis (etiolation) and are characterized by long hypocotyls, closed cotyledons and apical hooks, and development of the proplastids into etioplasts. Light-grown seedlings undergo photomorphogenesis (de-etiolation) and are characterized by short hypocotyls, open and expanded cotyledons, and development of the proplastids into mature green chloroplasts.

Light signals are perceived by at least four distinct families of photoreceptors: phytochromes primarily absorb red (R) and far-red (FR) wavelengths (600–750 nm), cryptochromes and phototropins absorb blue (B) and ultraviolet-A (UV-A) (320–500 nm), and UV RESISTANCE LOCUS 8 (UVR8) has recently been shown to perceive UV-B (282–320 nm) (Rizzini et al., 2011). These photoreceptors absorb, interpret, and transduce light signals, via distinct intracellular signaling pathways to generate a wide range of responses, including modulating the expression of light-regulated nuclear genes, which ultimately leads to adaptive changes at the cellular and organismic levels.

Extensive progress has been made in the past two decades towards elucidating the molecular, cellular, and biochemical mechanisms underlying light perception and subsequent signal transduction (for reviews, see Jenkins, 2009; Yu et al., 2010; Pedmale et al., 2010; Li et al., 2011b). Traditional genetic and molecular approaches have been powerful at identifying various key regulators and their positions within these signaling cascades. However, genomic studies conducted in recent years have greatly expanded on these traditional approaches by providing an overall picture of the genome-wide changes that occur during photomorphogenesis. Here, we summarize the major advances in understanding photomorphogenesis at the genomic scale, and highlight

emerging insights into dynamic genomic (including epige-nomic) changes during seedling de-etiolation.

LIGHT-REGULATED GENE EXPRESSION IN PLANTS

By the mid-1990s, plant biologists had identified more than 100 individual genes whose expression is regulated by light using traditional approaches (Terzaghi and Cashmore, 1995; Fankhauser and Chory, 1997; Kuno and Furuya, 2000). However, the dramatic developmental transition during plant photomorphogenesis suggests that a much larger number of genes might be involved in light control of plant development. The entire field took a dramatic step forwards with the advent of microarray technology, first described by Dr. Schena and colleagues in 1995, which allowed light-regulated gene expression to be studied at increasingly larger scales, culminating in genome-wide analysis. Interestingly, in the original study Schena et al. used *Arabidopsis* transgenic plants over-expressing HAT4, a homeodomain transcription factor involved in the control of photomorphogenesis (Schena et al., 1995). From then on, plant biologists have progressed from studying individual genes to investigating genomic expression profiles (transcriptomes) in many plant processes, including photomorphogenesis. These whole-genome studies have added a new dimension to the understanding of light-regulated gene expression.

Development of techniques for analyzing light-regulated transcriptomes

The microarray used by Schena et al. only contained 45 cloned *Arabidopsis* cDNAs (Schena et al., 1995). Subsequent studies used arrays containing increasing numbers of genes. Early microarray-based studies of light-regulated gene expression were performed with arrays of 6000–8000 genes ("8K" arrays), representing ~25%–30% of the *Arabidopsis* genome (Ma et al., 2001, 2002; Tepperman et al., 2001, 2004; Wang et al., 2002). Later studies used the Affymetrix ATH1 arrays ("22K" arrays) (Monte et al., 2004; Tepperman et al., 2006) or Operon oligonucleotide arrays (Jiao et al., 2005; Ma et al., 2005), which provide close to full-genome coverage (>80%). However, microarrays are hybridization-based approaches. Although high-density or custom-made microarrays can be constructed, these approaches have several limitations, including high background levels owing to cross-hybridization, and the requirement for genomic sequence information (Wang et al., 2009; Ozsolak and Milos, 2011).

In recent years, the introduction of high-throughput next-generation sequencing technologies has revolutionized transcriptomics by allowing RNA analysis through massive cDNA sequencing (RNA-seq) (Wang et al., 2009; Ozsolak and Milos, 2011). RNA-seq has effectively eliminated several

challenges posed by microarray technologies, and achieved base-pair-level resolution and a much higher dynamic range of expression levels (Wang et al., 2009; Ozsolak and Milos, 2011). RNA-seq has been applied to yeast, Arabidopsis, mouse and human cells, and has already been used by plant biologists to investigate light regulation of plant transcriptomes (such as Zhang et al., 2011).

White light-regulated plant transcriptomes in *Arabidopsis* and rice

A landmark paper that demonstrated the massive extent of light-regulated gene expression in higher plants was published by Ma et al. in 2001. This study systematically investigated changes in gene expression during light-regulated *Arabidopsis* seedling development using an expressed sequence tag (EST)-based microarray. Of the 9216 ESTs (representing ~6120 unique genes) included in the array, one-third showed significant (two-fold or greater) differential expression between white light- and dark-grown seedlings, with 60% up-regulated and 40% down-regulated by light (Ma et al., 2001). Furthermore, different colors of light, even though they are perceived and transduced by distinct photoreceptors, largely affected the expression of the same fraction of the genome (Ma et al., 2001). Analysis of these light-regulated genes revealed more than 26 cellular pathways that were coordinately regulated by light (Ma et al., 2001).

Genetic screens for *Arabidopsis* mutants involved in light-regulated seedling development followed by biochemical analyses have identified a group of pleiotropic Constitutive Photomorphogenic/De-etiolated/Fusca (COP/DET/FUS) proteins that are central negative regulators of photomorphogenesis (Sullivan et al., 2003; Yi and Deng, 2005). Loss-of-function mutations of any of these COP/DET/FUS proteins caused a photomorphogenic seedling phenotype in darkness, characterized by open cotyledons and short hypocotyls, essentially mimicking light-grown wild-type seedlings (Deng et al., 1991, 1992; Wei and Deng, 1996). COP1, a conserved RING finger E3 ubiquitin ligase targeting specific proteins for degradation, is one of these proteins. Microarray analysis was performed to examine the genes controlled by COP1 in darkness. Consistent with the photomorphogenic phenotype of dark-grown *cop1* mutants, similar gene expression profiles were observed in wild-type seedlings grown in the light and multiple *cop1* mutant alleles grown in the dark (Ma et al., 2002). Genes regulated by COP1 in darkness were estimated to account for >20% of the *Arabidopsis* genome, thus suggesting that the majority of light-controlled genome expression can be achieved by the negative regulation of COP1 activity (Ma et al., 2002). Consistent with these findings, studies conducted in recent years demonstrated that COP1 targets several photomorphogenesis-promoting proteins for degradation, including elongated hypocotyl 5 (HY5; Osterlund

et al., 2000), HY5 homolog (HYH; Holm et al., 2002), long after far-red light 1 (LAF1; Seo et al., 2003), long hypocotyl in far-red 1 (HFR1; Duek et al., 2004; Jang et al., 2005; Yang et al., 2005), and the phytochromes (Seo et al., 2004; Jang et al., 2010).

The photomorphogenesis of monocot rice seedlings is promoted by FR, R and B light; consistent with this observation, phytochrome, cryptochrome, and phototropin genes were identified in rice (Kay et al., 1989; Dehesh et al., 1991; Basu et al., 2000; Kasahara et al., 2002; Matsumoto et al., 2003). A genomic study reported in 2005 systematically analyzed the changes in rice seedling transcriptomes during photomorphogenesis in comparison with *Arabidopsis*. As in *Arabidopsis*, light induces massive reprogramming of the rice transcriptome: at least 20% of rice genes are regulated by white light (Jiao et al., 2005). Organ-specific expression profiles during seedling photomorphogenesis indicate that light effects diverge significantly in separate organs. Global comparison of expression profiles between rice and *Arabidopsis* revealed a higher correlation of genomic expression patterns in continuous white light than in darkness, suggesting that the genomic expression profile of photomorphogenesis is more conserved than that of skotomorphogenesis (Jiao et al., 2005).

Phytochrome-regulated gene expression

In *Arabidopsis thaliana*, there are five phytochromes, designated phytochrome A (phyA) to phyE. phyA is light-labile whereas phyB–phyE are light-stable. phyA is the primary photoreceptor responsible for perceiving and mediating various responses to FR light (Dehesh et al., 1993; Nagatani et al., 1993; Parks and Quail, 1993; Whitelam et al., 1993). The first glimpse into the phyA transcriptional network was made by Tepperman et al. in 2001. Using oligonucleotide microarrays to measure global gene expression profiles in wild-type and *phyA* mutant seedlings, Tepperman et al. showed that 10% of the genes represented on the array were regulated by phyA in response to FR light. Strikingly, 44% of the genes responding to FR within 1 h were predicted to encode multiple classes of transcription factors (Tepperman et al., 2001). A later comparative transcriptomic study of various *Arabidopsis* mutants deficient in phyA signaling revealed new insights into the relationships of various genetically-identified phyA signaling loci in mediating FR light responses (Wang et al., 2002).

phyB is the predominant phytochrome regulating photomorphogenic responses in R light (Nagatani et al., 1991; Somers et al., 1991; Reed et al 1993). However, surprisingly, transcriptional profiles of etiolated *phyB* mutants subjected to R treatments did not differ dramatically from the wild-type controls (Ma et al., 2001; Tepperman et al., 2004), suggesting that one or more of the remaining phytochrome family members is predominantly responsible for perception and trans-

duction of R light. Subsequent studies showed that phyA plays a dominant role in regulating rapid gene expression responses to R light (Tepperman et al., 2006). These findings are consistent with the fact that the long hypocotyl and reduced cotyledon expansion phenotypes were enhanced in *phyA phyB* double mutants relative to *phyB* monogenic mutants in R light (Neff and Van Volkenburgh, 1994; Reed et al., 1994; Casal and Mazzella, 1998; Neff and Chory, 1998), revealing a role for phyA in responding to R light which is normally masked in the presence of phyB.

Cryptochrome-regulated gene expression

Arabidopsis has three cryptochrome (CRY) genes, *CRY1* to *CRY3*. CRY1 and CRY2 function primarily in the nucleus, whereas CRY3 probably acts in chloroplasts and mitochondria (Liu et al., 2011). Based on the results of several microarray-based genome expression profile analyses, B light changes the expression of around 5%–25% of *Arabidopsis* genes, depending on the test conditions; most of these changes are mediated by CRY1 and CRY2 (Ma et al., 2001; Wang et al., 2001; Folta et al., 2003; Ohgishi et al., 2004; Sellaro et al., 2009). The expression of many CRY-regulated genes is also regulated by other signaling pathways, such as phytochromes and phytohormones (Ma et al., 2001; Folta et al., 2003; Ohgishi et al., 2004; Sellaro et al., 2009), suggesting that CRY-dependent photomorphogenesis is integrated with extensive regulatory networks.

UV-B-regulated gene expression

UVR8 protein has been shown to specifically mediate UV-B responses (Brown et al., 2005; Favory et al., 2009; Jenkins, 2009), and recently been proven to be an UV-B photoreceptor (Rizzini et al., 2011). Transcriptomic analyses with maize (Casati and Walbot, 2003, 2004; Casati et al., 2006) and *Arabidopsis* (Brosché et al., 2002; Ulm et al., 2004; Brown et al., 2005; Kilian et al., 2007; Brown and Jenkins, 2008) have revealed a large number of genes involved in a wide range of cellular processes that are regulated by UV-B. It is interesting that different types of UV-B exposure regulate different sets of genes. High fluences of UV-B induce many genes normally expressed in defense, wound, or stress responses, whereas low fluences of UV-B stimulate a range of genes involved in UV protection or the amelioration of UV damage (Ulm et al., 2004; Ulm and Nagy, 2005; Brown and Jenkins, 2008; Jenkins, 2009).

Circadian clock-regulated gene expression

The circadian clock controls many metabolic, developmental and physiological processes in a time-of-day-specific manner in both plants and animals (McClung, 2008; Harmer, 2009; de

Montaigu et al., 2010). Light signals perceived and transduced by phytochromes and cryptochromes entrain the clock to the external light/dark cycles. Microarray technology has been extensively exploited to survey genome-wide circadian regulation of gene expression, and provided important insights into clock function (Harmer et al., 2000; Schaffer et al., 2001; Edwards et al., 2006; Covington and Harmer, 2007; Covington et al., 2008; Michael et al., 2008). Surprisingly, it has been shown that a large fraction of the plant transcriptome, as much as one-third of all expressed genes, is regulated by the circadian clock (Covington et al., 2008).

Several promoter motifs associated with phase-specific expression have been identified, including the morning element (ME) and the evening element (EE), which are over-represented in the promoters of morning- or evening-phased genes, respectively (Harmer et al., 2000; Harmer and Kay, 2005; Covington et al., 2008; Michael et al., 2008). EE is found in the promoters of approximately one-quarter of evening-phased genes and confers evening-phased expression on reporter genes (Harmer et al., 2000; Harmer and Kay, 2005; Covington et al., 2008; Michael et al., 2008). Consistent with this observation, circadian clock associated 1 (CCA1) and late elongated hypocotyl (LHY), two dawn-phased MYB-related transcription factors that are key components of the central oscillator, bind to the EE promoter sequences and lead to repression of evening-expressed genes (Alabadí et al., 2001; Harmer and Kay, 2005).

Role of transcription factors in light signaling

An important finding in transcriptomic analyses of photomorphogenesis is that transcription factor-encoding genes are highly enriched in genes that respond rapidly to light (early light-responsive genes), especially shortly after light exposure when light-stimulated photomorphogenesis is barely observable (Tepperman et al., 2001, 2004, 2006; Jiao et al., 2003; Ulm et al., 2004). For example, 44% (for FR light) and 25% (for R light) of functionally-classifiable genes responding within 1 h of FR or R light exposure encode transcription factors (Tepperman et al., 2001, 2004, 2006). A similar time-course study identified 64 transcription factor genes whose expression showed rapid responsiveness to B light (Jiao et al., 2003). In addition, of the 107 genes whose expression is regulated by low-level UV-B, > 30% of the genes with classifiable functions encode transcription factors (Ulm et al., 2004). The rapid responsiveness of these transcription factors indicates that they may represent a master set of transcriptional regulators that orchestrate the expression of the downstream target genes in the light-regulated transcriptional networks.

HY5, a constitutively-nuclear bZIP protein, is the first known and most extensively-studied transcription factor involved in promoting photomorphogenesis under a wide spectrum of wavelengths including FR, R, B, and UV-B

(Koornneef et al., 1980; Oyama, et al., 1997; Osterlund et al., 2000; Ulm et al., 2004). It was shown that the abundance of HY5 protein was directly correlated with the extent of photomorphogenic development (Osterlund et al., 2000). Thus, it is not surprising that HY5 may bind to more than 11,000 genes of *Arabidopsis* and detectably affect the expression of over 1100 genes (Zhang et al., 2011; see below). Most genes regulated by HY5 are also regulated by light, and about 20% of all light-regulated genes are regulated by HY5 (Ma et al., 2002).

Phytochrome-interacting factors (PIFs), a small subset of basic helix-loop-helix (bHLH) transcription factors, play central roles in phytochrome-mediated light signaling networks (Duek and Fankhauser, 2005; Castillon et al., 2007; Leivar and Quail, 2011). PIF3 is the founding member of the PIF subset, initially identified in a yeast two-hybrid screen for phyB-interacting proteins (Ni et al., 1998). The second member of the PIF family, PIF4, was isolated using a combination of genetic and reverse-genetic approaches (Huq and Quail, 2002). PIF1, PIF5, PIF6 and PIF7 were then identified by homology to PIF3 (Huq et al., 2004; Khanna et al., 2004; Oh et al., 2004; Leivar et al., 2008a). All PIF members contain a conserved motif in their N-termini, called the active phytochrome B-binding (APB) motif, which confers specific binding of PIFs to the biologically active Pfr form of phyB (Khanna et al., 2004; Duek and Fankhauser, 2005; Castillon et al., 2007; Leivar and Quail, 2011). By contrast, only two PIF proteins, PIF1 and PIF3, bind to the Pfr form of phyA (Ni et al., 1998; Huq et al., 2004). The recent finding that a quadruple PIF mutant, *pif1 pif3 pif4 pif5* (*pifq*), develops a *constitutively photomorphogenic* (*cop*)-like phenotype in darkness provides compelling evidence that the PIF proteins repress photomorphogenesis and promote skotomorphogenesis in etiolated seedlings (Leivar et al., 2008b; Shin et al., 2009; Quail, 2011). Consistent with this observation, microarray analysis showed that dark-grown *pifq* mutants had a gene expression pattern similar to that of wild-type plants grown in R light (Shin et al., 2009). A subset of genes were identified as potential direct targets of these bHLH transcription factors by comparing genes that rapidly responded to light in wild-type seedlings with those responding in the dark in *pifq* mutants (Leivar et al., 2009). Notably, genes encoding transcription factors were highly enriched among these genes, suggesting that they may be potential primary targets of PIF transcriptional regulation (Leivar et al., 2009).

GENOMIC BINDING SITES OF KEY TRANSCRIPTION FACTORS IN LIGHT SIGNALING

Chromatin immunoprecipitation (ChIP) is a well-established approach to investigate *in vivo* interactions between proteins and DNA. When ChIP is coupled with whole-genome DNA microarray (ChIP-chip) or high-throughput sequencing (ChIP-seq), transcription factor binding sites can be identified across

the entire genome. In this section, we will summarize the genome-wide binding site analyses of HY5, PIF1 (also known as phytochrome interacting factor 3-like 5 [PIL5]) and far-red elongated hypocotyl 3 (FHY3), three key transcription factors in light signaling.

HY5

Considering the pivotal role of HY5 in promoting photo-morphogenesis, it is of great importance to identify all of its target genes. An initial attempt was made in 2004 by generating an *Arabidopsis* promoter microarray, which includes about 3800 selected gene promoters amplified by PCR (Gao et al., 2004). A total of 42 promoter fragments were identified in this study which exhibited strong interaction with HY5 protein *in vitro* (Gao et al., 2004). With the development of the ChIP-chip technique and its successful application in yeast and mammalian systems (reviewed in Buck and Lieb, 2004), it became possible to identify *in vivo* binding sites of HY5 at the genomic scale. In one of the first genome-wide analyses of transcription factor binding sites in *Arabidopsis*, Lee and colleagues used ChIP-chip to identify 3894 *in vivo* HY5 binding sites in the *Arabidopsis* genome. They showed that HY5 preferentially binds to the promoter regions of its target genes, and that many of its targets were early light-responsive and transcription factor genes (Lee et al., 2007). Thus, these data support that HY5 is a high-order regulator of the transcriptional cascades involved in seedling photomorphogenesis.

A recent study by Zhang et al. (2011) re-profiled genome-wide HY5 binding sites with several improvements. First, wild-type *Arabidopsis* seedlings and affinity-purified antibody against endogenous HY5 protein were used by Zhang et al., whereas hemagglutinin (HA)-tagged HY5 transgenic lines and antibody for HA were used by Lee et al. (2007). This improvement may detect weak HY5 binding sites and reduce the risk of experimental artifacts associated with expressing an exogenous tagged protein. Second, Zhang et al. performed a genome-wide comparison of HY5 binding sites under continuous white light condition and light-to-dark transition. This analysis showed that HY5 binding to some target genes was regulated by light conditions, contradictory to the conclusion by Lee et al. that HY5 binding activity was not affected during the light-to-dark transition based on a small set of light-regulated genes. Finally, an *Arabidopsis* genome tiling array was used by Zhang et al., which covers approximately 97% of the genome and has a resolution 14 times higher than that used by Lee et al. Based on these improvements, Zhang et al. identified a total of 11,797 HY5 target genes, ~44% of all genes in the *Arabidopsis* genome. Comparison of HY5 target genes by ChIP-chip and HY5-regulated genes by RNA-seq revealed that HY5 regulated the expression of 1173 genes, either positively or negatively (Zhang et al., 2011). An unexpected discovery in this study was that HY5 directly regulates several microRNA

(miRNA) genes. Interestingly, over-expression of miR408, whose expression is regulated by HY5, leads to phenotypic changes opposite to those caused by the *hy5* mutation (Zhang et al., 2011).

PIF1

Despite the fact that PIFs have highly similar sequences and overall motif structures, they do not act redundantly, unlike many gene families. Instead, they have overlapping as well as distinct biological functions. PIF1 has been shown to function in inhibiting seed germination in darkness. None of the other PIFs seems to act redundantly with PIF1 in this process, as seeds of *pif1* single mutants, or any combinations of *pif* mutants containing the *pif1* mutation, germinate fully independent of light treatment (Oh et al., 2004; Shin et al., 2009). PIF1 exerts this function, at least in part, by regulating the expression of gibberellin (GA)- and abscisic acid (ABA)-biosynthetic and catabolic genes in the dark (Oh et al., 2004, 2006, 2007). In addition, PIF1 directly activates the expression of *RGA* and *GAI*, which encode two key DELLA proteins that function as repressors of GA signaling (Oh et al., 2007).

Recently, Oh et al. (2009) performed ChIP-chip analysis to identify 748 PIF1 binding sites in the *Arabidopsis* genome, most of which contain G-box elements (CACGTG). Comparison of ChIP-chip with microarray data indicates that PIF1 directly regulates the expression of 166 genes by binding to their promoters. Many of these genes encode transcriptional regulators involved in hormone signaling, while some encode enzymes involved in cell wall modification (Oh et al., 2009). These data indicate that PIF1 regulates seed germination not just by regulating ABA and GA signaling, but also by coordinating hormone signaling and modulating cell wall properties in imbibed seeds (Oh et al., 2009).

FHY3

FHY3 and its homolog far-red impaired response 1 (FAR1) were originally identified as phyA signaling components (Whitelam et al., 1993; Hudson et al., 1999; Wang and Deng, 2002). Recent studies showed that they are transposase-derived transcription factors directly activating the transcription of *FHY1* and *FHY1-like* (*FHL*), encoding two small plant-specific proteins required for nuclear accumulation of light-activated phyA (Hiltbrunner et al., 2005, 2006; Lin et al., 2007, 2008; Rausenberger et al., 2011). Thus, FHY3 and FAR1 indirectly control phyA nuclear accumulation and subsequent phyA responses. In addition to acting in phyA signaling, FHY3 and FAR1 were recently shown to function in the circadian clock by maintaining the rhythmic expression of *early flowering 4* (*ELF4*), a key player of the central oscillator of the *Arabidopsis* circadian clock (Li et al., 2011a). Therefore, identification of more FHY3 direct target genes and elucidation of new roles of FHY3 in plant development will contribute

to a better understanding of these transposase-derived transcription factors in plants.

A recent study by Ouyang et al. (2011) used ChIP-seq analysis to identify all FHY3 binding sites in the *Arabidopsis* genome. The data revealed 1559 and 1009 genes bound by FHY3 in darkness and FR light conditions, respectively, including the three previously-reported FHY3 target genes *FHY1*, *FHL* and *ELF4* (Ouyang et al., 2011). In addition, FHY3 also directly binds to two novel motifs in the 178-bp repeats of the *Arabidopsis* centromeric regions. Comparison of ChIP-seq and microarray data indicates that FHY3 quickly regulates the expression of 197 and 86 genes in darkness and FR, respectively, by directly binding to their promoters (Ouyang et al., 2011). Moreover, FHY3 also co-regulates a number of common target genes with PIF1 and HY5. An unexpected finding in this study is that FHY3 plays a role in regulating chloroplast division by directly activating the expression of *accumulation and replication of chloroplasts 5* (*ARC5*), a member of the dynamic GTPase family involved in chloroplast division (Ouyang et al., 2011). Therefore, genome-wide analysis of FHY3 target genes has led to the discovery of a novel function of FHY3 in *Arabidopsis* development which may be overlooked by traditional genetic or molecular approaches.

EPIGENETIC CONTROL OF LIGHT-REGULATED GENE EXPRESSION

In eukaryotes, chromatin structure and gene expression are regulated by several epigenetic mechanisms, including DNA methylation, histone modifications, and certain aspects of small-interfering RNA (siRNA) pathways (Henderson and Jacobsen, 2007; Zhang, 2008; He et al., 2011). Histone modifications provide a dynamic and reversible mechanism to regulate gene expression through changes in the chromatin state and the recruitment of protein complexes that regulate transcription (Berger, 2007). Evidence accumulated over the last decade demonstrates that histone modifications represent a layer of epigenetic control of light-regulated gene expression in photomorphogenesis.

Effects of histone modifications on the expression of light-responsive genes

Histone modifications are post-translational covalent modifications of histone proteins at their N-termini, among which, acetylation and methylation at lysine residues are the two most intensely studied epigenetic marks (He et al., 2011). Histone acetylation and methylation are established by histone acetyltransferases (HATs) and histone lysine methyltransferases (HKMTs), respectively, and removed by histone deacetylases (HDACs) and histone demethylases (HDMs), respectively (Liu et al., 2010; He et al., 2011). Recent studies have discovered both activating and repressive histone modifications correlated with gene activity. Histone lysine methylation can be associated with either gene activation or repression, whereas histone lysine acetylation is generally linked to gene activation (Berger, 2007; Liu et al., 2010; He et al., 2011). The intensity and combination of activating and repressive histone modifications dynamically regulate genome accessibility in plants (Berger, 2007; Pfluger and Wagner, 2007).

The pea (*Pisum sativum*) plastocyanin gene (*PetE*) is expressed only in photosynthetic tissues, and its transcription is activated by light (Chua et al., 2001). A 268-bp sequence in the *PetE* promoter functions as a general transcriptional enhancer, whereas histones H3 and H4 present on the enhancer are acetylated when the transcription of *PetE* is activated by light (Chua et al., 2001, 2003). Genetic studies of *Arabidopsis* mutants deficient in histone acetyltransferase (TAF1 and GCN5) and histone deacetylase (HD1) provided evidence for the importance of histone acetylation/deacetylation in light-activated expression of a number of genes (Bertrand et al., 2005; Benhamed et al., 2006). Subsequent genome-scale screening of target promoters bound by the *Arabidopsis* histone acetyltransferase GCN5 identified a large number of early light-responsive genes, many of which were also targeted by HY5 (Lee et al., 2007; Benhamed et al., 2008). It is thus possible that HY5 recruits GCN5 by protein interaction to acetylate histones on the target gene promoters and to activate light-responsive gene expression (Servet et al., 2010). These observations suggest that an overall histone acetylation homeostasis regulated by the antagonistic actions of HATs and HDACs is probably essential for light sensing and signal transduction in plants (Servet et al., 2010).

Dynamic landscapes of histone modifications in response to light

In 2008, Guo et al. analyzed the effects of light regulation on four selected histone modifications (H3K4me3, H3K9ac, H3K9me2, and H3K27me3) and the relationship of these histone modifications with the expression of representative light-regulated genes. It was shown that changes in H3K9ac in four representative genes in plants grown under different light conditions were an important component of light-regulated gene transcription during *Arabidopsis* seedling photomorphogenesis (Guo et al., 2008). However, a comprehensive genome-wide survey of histone modifications during photomorphogenesis is required to help understand the general regulatory role of histone modifications in light-regulated transcriptional networks.

A recent study by Charron et al. (2009) used ChIP-chip tiling array technology to examine the dynamic global changes of four selected histone modifications (H3K9ac, H3K9me3, H3K27ac, and H3K27me3) and their relationships with the alteration of gene activity in *Arabidopsis* seedlings undergoing photomorphogenesis. The genomic distribution of

these four histone modifications was significantly different before and after the seedlings were exposed to light, implying an adjustment of histone modification patterns in response to light (Charron et al., 2009). Interestingly, two transcription factor-encoding genes, *HY5* and *HYH*, exhibited a significantly higher level of the activating histone modification H3K9ac in seedlings undergoing photomorphogenesis relative to dark-grown seedlings (Charron et al., 2009), consistent with their increased transcription in response to light (Holm et al., 2002). Moreover, the putative downstream target genes of HY5 had higher levels of H3K9ac in light-grown than in dark-grown seedlings, suggesting the importance of this activating epigenetic mark in the regulation of light-responsive transcriptional networks. Further, genes acting in photosynthetic pathways were mostly modified by the activating epigenetic marks H3K9ac and H3K27ac in response to light, whereas H3K27ac and H3K27me3 potentially contributed to light regulation of GA metabolism (Charron et al., 2009). These observations revealed a combinatorial interplay between histone modifications and light-regulated gene expression, and delivered new insight into the chromatin-based regulation of photomorphogenesis.

Light-mediated chromatin modifications of the *Arabidopsis phyA* locus

All *phyA* genes that have been investigated so far, from both monocots and dicots, are highly expressed in etiolated seedlings and rapidly down-regulated by light (Quail, 1991; Cantón and Quail, 1999). This phenomenon has been known for more than two decades; however, the underlying mechanism remains elusive. Recently, a report by Jang et al. (2011) suggested that histone modifications of the *Arabidopsis phyA* locus are involved in this regulation. It was shown that *phyA* activation in the dark was accompanied by a significant enrichment of various activating histone marks in the *phyA* transcription and translation start sites, such as acetylation of histones H3 (K9/14 and K27) and H4 (K5, K8, K12, and K16) and methylation of histone H3 (K4me3). In contrast, upon light exposure, H3K27ac declined with a corresponding increase in the repressive H3K27me3 mark, and demethylation of H3K4me3 and deacetylation of H3K9/14 were also seen at these sites (Jang et al., 2011). Thus, the presence of these opposing marks around the *phyA* transcription/translation start sites may enable rapid activation and inactivation of *phyA* in response to changing light conditions. Notably, DNA methylation and small RNA pathways were not involved in light-mediated repression of *phyA* transcript levels (Jang et al., 2011). Next, it will be necessary to examine whether a similar mechanism also regulates *phyA* expression in monocots.

PERSPECTIVE

The last decade has seen dramatic progress in understand-ing the genomic basis for light control of plant development. It is well-established that light induces massive reprogramming of the plant transcriptome, and that transcription factors play important roles in the light-regulated transcriptional networks. However, only a few key transcription factors (such as HY5, PIF1 and FHY3) have been surveyed so far for their genome-wide binding sites. Additional studies are urgently required to systematically investigate the global binding sites of other key transcription factors in light signaling, such as PIF3 and other PIFs, LAF1, etc. Moreover, it is important to understand how these transcription factors co-regulate their common target genes, and how they interact with each other. These studies will help in filling the major gaps in our understanding of the structure and mechanisms of these transcriptional regulatory networks.

Microarray-based expression profiling studies have identified a large number of early light-responsive genes. However, reverse genetic studies are needed to examine their functional relevance to the light-controlled photomorphogenic responses. This functional profiling strategy has been utilized by several recent studies (Khanna et al., 2006; Sentandreu et al., 2011), whose results suggest that many of these early light-responsive genes have organ-specific effects, which might not be large enough to be detected by forward genetic screens. Organ-specific regulation of gene expression by light has been reported in *Arabidopsis* and rice (Jiao et al., 2005; Ma et al., 2005). Thus, identifying early light-responsive genes in specific organs combined with reverse genetic approaches will contribute to a greater understanding of how light induces distinct photomorphogenic responses in different organs.

In addition, growing evidence demonstrates that epigenetic regulation represents another layer of control for light-regulated gene expression in photomorphogenesis. However, to date, only histone modifications have been shown to mediate light control of gene expression. It will be of continuous interest to investigate whether other epigenetic mechanisms, such as DNA methylation and small RNA pathways, are also involved in light-regulated gene expression.

Finally, with the introduction of high-throughput sequencing technologies (such as RNA-seq and ChIP-seq) into the study of photomorphogenesis, there is no doubt that more accurate and dynamic changes in transcriptome, epigenome, and global binding sites of pivotal transcription factors in light signaling will be determined in future research. These studies will obviously shed more light on the mechanisms underlying light control of plant development.

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ABBREVIATIONS

ChIP, chromatin immunoprecipitation; COP, constitutive photo-morphogenic; CRY, cryptochrome; EST, expressed sequence tag; FHY, far-red elongated hypocotyl; HY, elongated hypocotyl; PHY, phytochrome; PIF, phytochrome-interacting factor

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