Photochemistry and Photobiology, 2017, 93: 656–665

Invited Review

Casting Away the Shadows: Elucidating the Role of Light-mediated Posttranscriptional Control in Plants†

Carlos E. Hernando, Carolina Garcia and Julieta L. Mateos*

Fundación Instituto Leloir, IIBBA-CONICET, Buenos Aires, Argentina

Received 3 November 2016, accepted 15 February 2017, DOI: 10.1111/php.12762

ABSTRACT

Light signals trigger precise changes in gene expression networks that activate distinctive developmental programs in plants. The transcriptome is shaped at different stages, both by the regulation of gene expression and also by posttranscriptional mechanisms that alter the sequence or abundance of the transcripts generated. Posttranscriptional mechanisms have attracted much interest in recent years with the advent of high-throughput technologies and bioinformatics tools. One such posttranscriptional process, alternative splicing, increases proteome diversity without increasing gene number by changing the function of individual proteins, while another, miRNA-mediated gene silencing, fine-tunes the amount of mRNA produced. The manner in which plants make use of these two crucial posttranscriptional mechanisms to respond to light and adapt to their environment is the focus of active research. In this review, we summarize the current knowledge of light-mediated posttranscriptional control in *Arabidopsis thaliana* and focus on the biological impact of the various posttranscriptional processes. We also discuss a potential cross talk between the alternative splicing and miRNA pathways, highlighting the complexity of light responsiveness.

INTRODUCTION

Plants are sessile organisms and have consequently evolved a remarkable plasticity to alter their growth and development in response to environmental cues. Despite the myriad of environmental stimuli perceived by plants, light has perhaps the greatest impact throughout the entire life cycle. At least five major photoreceptor families are responsible for light perception: the phytochromes that absorb in the red/far-red spectrum; the blue/ultraviolet-A-responsive cryptochromes, including phototropins and members of the Zeitlupe family; and the ultraviolet-B-absorbing photoreceptors, such as UVR8 (1–3). These photoreceptors modulate complex organ-specific responses to light over multiple developmental stages, from seed germination and photomorphogenesis to other processes later in the life cycle, such as shade avoidance, flowering and senescence.

Beneath these light-dependent plant responses lie a complex network that orchestrates transcriptional, posttranscriptional, translational, posttranslational and metabolic regulatory mechanisms. Early research attempted to decipher these networks using both classical and reverse genetic approaches, mostly in the model plant *Arabidopsis thaliana*, to identify genes that, when mutated, resulted in aberrant photomorphogenic phenotypes. These pioneering discoveries yielded many *Arabidopsis* transcriptional regulators involved in light signaling, primarily transcription factors belonging to the B-box zinc-finger (BBX), basic helix-loop-helix (bHLH) and basic region/leucine zipper motif (bZIP) families (4). With the advent of genomewide technologies, transcriptome profiling experiments using microarrays have identified vast numbers of genes with altered expression patterns following light treatments in wild-type *Arabidopsis* and different photomorphogenic mutants; however, these gene expression data only offer partial insights into light-regulated transcriptome adjustments. This kind of information represents the steady state of transcripts, a snapshot summarizing multiple layers of gene regulation that integrates the effects of posttranscriptional mechanisms, such as selective mRNA degradation mediated by small regulatory RNAs or alternative splicing (AS), the pre-mRNA processing mechanism whereby one gene encodes several differently spliced transcripts.

Once transcription has been initiated, the nascent pre-mRNA undergoes a series of processing steps to generate a mature mRNA (5). During maturation, the exons of the mRNA may be joined in many different ways through AS at a variety of splicing sites. In addition to mRNA processing, noncoding RNAs (ncRNAs) such as microRNAs (miRNAs), small interfering RNAs (siRNAs) and long ncRNAs are known to be major regulators of gene expression in plants. In *Arabidopsis*, miRNAs and siRNAs can regulate the abundance and/or translation of their target mRNAs, playing key roles in almost all growth and developmental stages (6,7). Despite some findings suggesting that light regulates AS and the expression of specific miRNAs (8–10), it was not until the arrival of RT-PCR-based AS-specific panels and tiling arrays that sets of light-regulated AS events were identified (11–13). The development of high-throughput sequencing technologies and more robust data processing tools are beginning to unveil the intricate interactions between light, AS and miRNAs and their role in adjusting plant growth and development. We are currently witnessing a

*Corresponding author email: jmateos@leloir.org.ar (Julieta Lisa Mateos)

†This article is a part of the Special Issue dedicated to Dr. Wolfgang Gärtner on the occasion of his 65th birthday. Dr. Gärtner helped me to cast the shadows away on my first steps into plant biochemistry (Julieta Mateos).

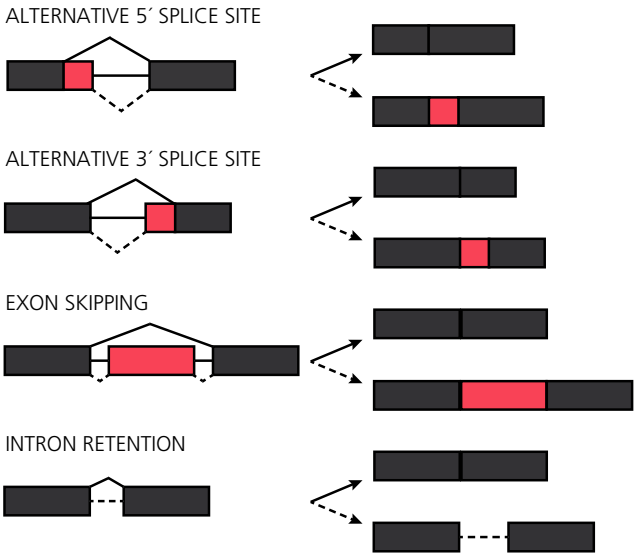


Figure 1. Types of alternative splicing events. Gray boxes: exons; pink boxes: alternative exons; lines: introns; solid arrow: constitutive spliced mRNA; broken arrow: alternative spliced mRNA.

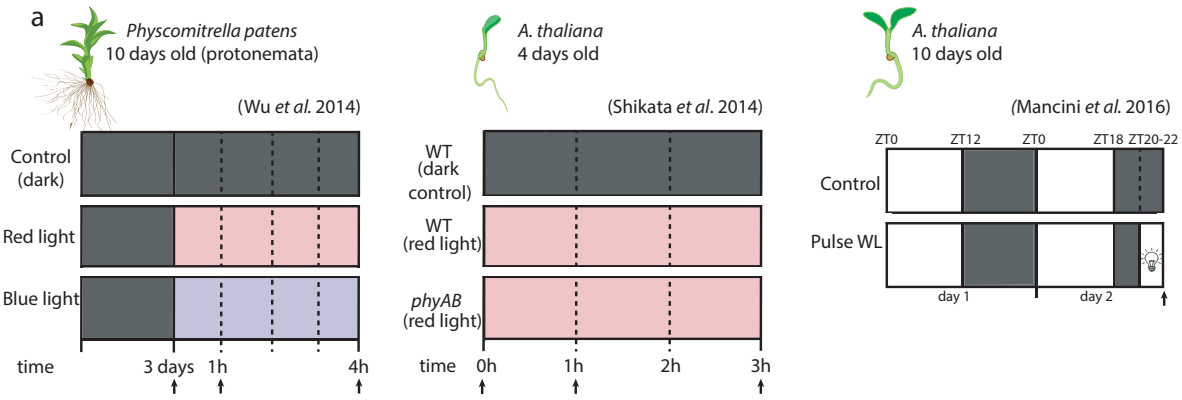
paradigm shift in the way we look at light-regulated growth and development, expanding the view from a simple signaling pathway with few components to mechanistic insights into the organization of a complex multilayer network at the whole-organism level (14–16).

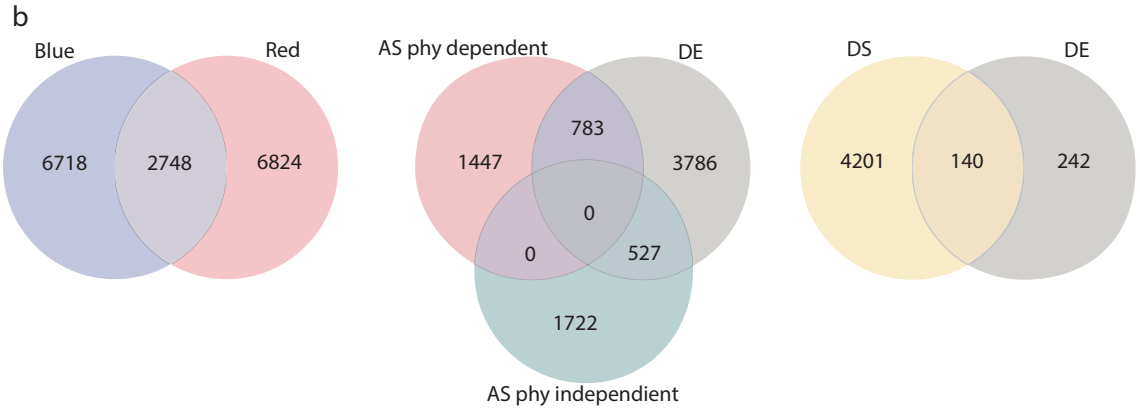
In this review, we describe how our understanding of light-regulated posttranscriptional mechanisms has begun to expand in recent years through the introduction of new technologies in the field of transcriptomics. Particularly, we will focus on the regulatory role of light in two essential posttranscriptional processes, AS and miRNA processing. Moreover, we present novel insights on this topic from our meta-analysis of all available data.

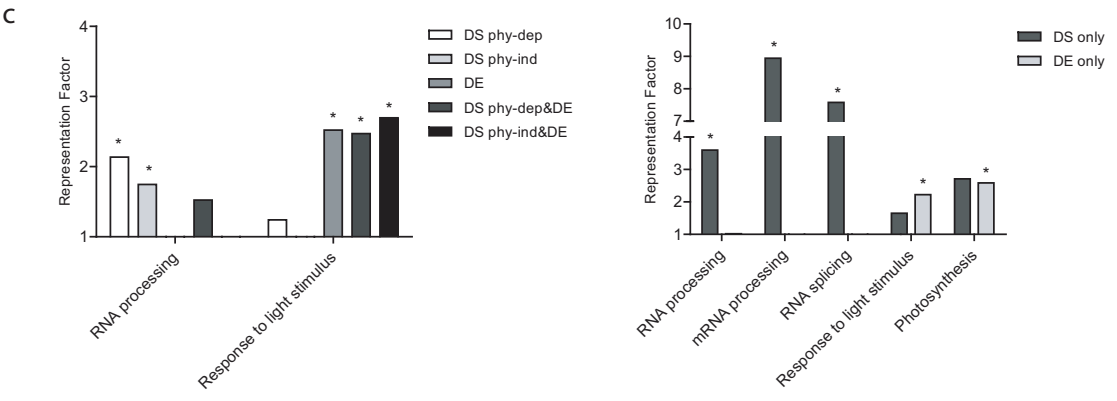
Light-mediated regulation of AS

During transcription, pre-mRNAs undergo processing to give rise to mature mRNAs. First, the pre-mRNA receives a 7-methylguanosine cap at its 5′ end to protect the molecule against degradation, and then, it is subjected to splicing to remove the introns, sequences that will not appear in mature mRNA (17,18). The splicing process is catalyzed by the "spliceosome," a dynamic complex consisting of five small nuclear ribonucleoproteins particles (snRNPs; U1, U2, U4, U5 and U6) and a variety of auxiliary proteins (19). During this cleavage and rejoining of the RNA, the spliceosome assembles on exon–intron boundary sequences known as 5′ donor splice sites (5′SS) and 3′ donor splice sites (3′SS), while the auxiliary RNA-binding proteins allow or inhibit the recruitment of the spliceosome to neighboring splice sites by recognizing other sequence motifs present in the pre-mRNA (17,18). Not all splicing sites are used constitutively; exons may be combined in many different ways through AS. The use of alternative 5′ and 3′ splicing sites causes that variable portions of introns to be removed and variable portions of exons to remain in the mRNA (Fig. 1). Exon skipping (ES) involves the removal of an exon together with their flanking introns (Fig. 1). Finally, intron retention (IR) gives place to the inclusion of an intron in the mature mRNA, being this the most frequent AS event reported in plants (Fig. 1) (20). Variability in the splicing pattern of a single pre-mRNA generates proteins harboring different domain combinations; thus, AS considerably increases the coding capacity of a genome (17). Likewise, AS can generate aberrant isoforms that are targets for RNA degradation. The retention of introns alters the open reading frame, which can result in a premature termination codon (PTC). Many PTCs are recognized by the nonsense-mediated decay (NMD) mechanism that leads to the degradation of the transcripts (21,22), establishing a connection between transcript level regulation and AS (23).

All previously mentioned posttranscriptional processing steps are subject to regulation and have been extensively studied in plants (24,25); nevertheless, our current understanding of the role of light-guided posttranscriptional mechanisms is limited to specific examples. The first light-regulated AS event was described for the *HYDROXYPYRUVATE REDUCTASE* gene in pumpkin in 1999 (8), and it was not until 2014 that high-throughput sequencing technologies were employed to address this issue on a genomewide scale (14). Wu *et al.* analyzed transcriptome changes during a 1- or 4-h exposure to red or blue light in the moss *Physcomitrella patens* (Fig. 2a), investigating the AS response at these wavelengths and addressing the existence of putative light-dependent mechanisms controlling splicing. The authors reported thousands of IR events occurring specifically in response to either blue (6718 IR events) or red (6824 IR events) light. Of all differentially spliced IR events observed in the experiments, 2748 were in common to both wavelengths (Fig. 2b), representing $\sim$29% of all events observed in the red- or blue-light conditions. By performing a Gene Ontology (GO) term analysis using the top 1000 events regulated either by red or blue light, we found a significant enrichment of terms related to RNA translation. Many of the blue-light-regulated IR events involved genes encoding proteins related to photosynthesis, implying that blue light immediately regulates photosynthetic activity by splicing transcripts required for this process. Neither splicing-related nor light-signaling genes appeared to be enriched in our analysis; however, the authors validated several IR events for a hand-picked subset of transcripts belonging to these processes. To explore this issue further, we performed a new meta-analysis of these data. Based on gene lists provided by the authors, we found that splicing-related genes represent around 1% of the genes with altered IR under red or blue light exclusively, as well as the shared IR events ($P < 8.075e\text{-}10$). On the other hand, light-signaling-related genes comprised less than 0.7% of the statistically significant IR events in all of these data sets ($P < 5.204e\text{-}09$) (Fig. 2d). This evidence supports the conclusions made by Wu *et al.* that light regulates the AS of several splicing factors, suggesting that AS could be a mechanism to regulate downstream transcripts such as those involved in photomorphogenesis. Additionally, the authors analyzed previous RNA-seq data from a mutant defective in phytochrome chromophore biosynthesis (26) together with data from a set of phytochrome knockout mutants to identify whether these photoreceptors mediate red-light-regulated AS. The red-light-induced AS observed in wild-type plants was reduced in this series of mutants, indicating that phytochromes participate in splicing regulation. Remarkably, Wu *et al.* showed that more than 70% of the top 1000 IR events upregulated by 1 h of either red- or blue-light illumination displayed no change in gene expression, revealing that light-activated IR is not associated with transcriptional activity. Interestingly, a repetitive GAA *cis*-element







d

Ligth	Splicing related genes	Light signaling related genes
Red	1,2%	0,58%
Blue	1,1%	0,66%
Red & Blue	1%	0,79%

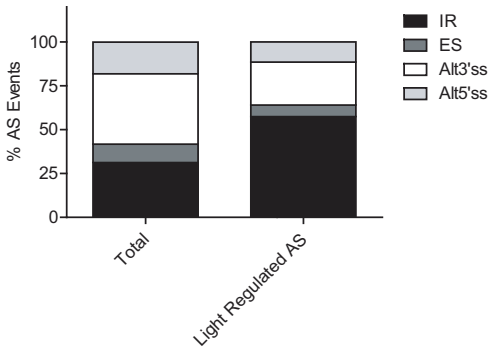


Figure 2. Genomewide studies of light-regulated alternative splicing (AS) in plants. (a) Scheme of the experimental designs used in (14–16). Arrows indicate when samples were taken. (b) Analysis of the genomewide transcriptome analysis. From left to right: statistically significant intron retention events affected by red and/or blue light in *Physcomitrella patens* (14); phytochrome-dependent AS events, phytochrome-independent AS events and differentially expressed genes (DEs) reported by Shikata *et al.* (15); genes regulated by light at the AS level (DS genes) and genes differentially affected by light at the expression level (DE genes) reported by Mancini *et al.* (16). (c) Functional analysis of alternatively spliced and differentially expressed transcripts. Left: GO-term enrichment analysis of the data extracted from Shikata *et al.* Right: GO-term enrichment analysis of the data extracted from Mancini *et al.* In the last two data sets, the representation factors were determined as in (62). * indicates a statistically significant overrepresentation, assessed using a hypergeometric test ($P \leq 0.05$). (d) Percentage of genes related to splicing and light signaling (according to (14)) among the statistically significant intron retention events affected by light. For this analysis, we used the *Physcomitrella* genome annotation version 1.6 and the best *Arabidopsis* hit according to this annotation version, all provided as supplementary information by the author. We considered a gene related to splicing or light signaling when its best *Arabidopsis* hit displayed a GO annotation related to these processes in the TAIR10 *Arabidopsis* genome annotation. (d) Relative frequencies of different AS types for all detected AS events by Mancini *et al.*, and these data were reported as a supplementary table by the authors. Total expressed: relative frequencies of AS events expressed in Arabidopsis. Light-regulated AS: relative frequencies of AS events among the light-regulated AS events. Alt3′ss and Alt5′ss: alternative acceptor and donor splicing sites, respectively; ES: exon skipping; IR: intron retention.

was enriched at both the 5′SS and 3′SS of retained introns in red- and blue-light-responsive AS events, suggesting that this GAA motif is an exonic splicing regulator that functions in light-regulated IR.

In the same year that Wu *et al.* employed RNA-seq technology to analyze light-regulated AS in *Physcomitrella patens*, Shikata *et al.* used similar resources to address light-mediated AS during photomorphogenesis in *Arabidopsis* (15). They identified genes with phytochrome-dependent AS changes by performing a genomewide transcriptome profiling on a series of time courses of four-day-old wild-type and *phyAphyB* double-mutant (*phyAB*) etiolated seedlings exposed to continuous red light for 1 or 3 h (Fig. 2a). After 1 h of light treatment, 1505 transcripts exhibited phytochrome-mediated AS, whereas 1678 genes were differentially expressed, with only 187 transcripts moderated by both processes. The 3-h treatment revealed 1116 and 4382 transcripts with phytochrome-dependent AS and differential expression, respectively, with 396 transcripts affected by both regulatory processes. These observations suggest that AS regulation is as important as transcriptional regulation in early phytochrome-mediated light signaling, while after 3 h of treatment, differential expression of transcripts increased considerably to become the dominant process. To further characterize the phytochrome-responsive transcripts, the authors performed a GO analysis on different subsets of genes. After 1 h of red-light treatment, GO terms related to RNA splicing were significantly enriched among transcripts that exhibited phytochrome-dependent AS alone, while genes showing phytochrome-dependent differential expression were enriched in categories associated with light signaling. Of the genes that presented only phytochrome-dependent AS changes, 58 were splicing-related genes, such as serine/arginine-rich (SR) proteins, the U1 small nuclear ribonucleoprotein and the U2 auxiliary factor 65a. The authors reported that the phytochrome-mediated regulation of the splicing-related genes after 3 h of red-light treatment was achieved more at the expression level than the AS level. Furthermore, the GO terms linked to photosynthesis and plastid/chloroplast function were enriched in the phytochrome-mediated AS gene subset after 3 h of treatment, suggesting that this process is also involved in light-induced chloroplast differentiation during seedling de-etiolation. Besides these observations, Shikata *et al.* mentioned a set of red-responsive but phytochrome-independent AS alterations in both treatments. To address the biological significance of these genes, we performed a new meta-analysis of these data and found that the number of differentially spliced AS events regulated via the phytochromes (2230) was similar to the number of events affected in a phytochrome-independent manner (2249). The latter involves several pathways such as blue-light and UV-light photoreceptors as well as photoreceptor-independent pathways, therefore attributing 50% of the response only to phyA and phyB (Fig. 2b). Similar to the authors' analysis, we performed a GO-term assessment of the data and found a significant enrichment of RNA processing-related transcripts among genes exhibiting phytochrome-dependent and phytochrome-independent AS (Fig. 2c). Furthermore, we showed that light-stimulus-related transcripts (e.g. light signaling and photosynthesis) were enriched among the differentially expressed genes. The same observation was made for those transcripts that experienced both differential expression and light-regulated AS in a phytochrome-dependent or phytochrome-independent manner (Fig. 2c). Our findings reinforce the concept that a significant number of transcripts with light-modulated AS encode splicing-related proteins and that the genes that exhibit light-regulated AS in addition to differential expression are mainly related to light-signaling pathways and photosynthetic processes. Shikata *et al.* also addressed the physiological relevance of phytochrome-mediated AS by comparing the effect of overexpressing two alternatively spliced isoforms of the light-signaling gene *SPA1-RELATED 3* (*SPA3*) with plants overexpressing the functional full-length isoform in wild-type *Arabidopsis*. Transgenic plants carrying the alternatively spliced isoforms of *SPA3* observed under red light displayed a short hypocotyl phenotype and resembled *spa3* knockout mutants, demonstrating that the proteins encoded by these isoforms have a dominant-negative effect on the endogenous *SPA3*. Finally, Shikata *et al.* investigated the role of phyA and phyB in the control of AS in the SR gene transcripts *ARGININE/SERINE-RICH SPLICING FACTOR 31* (*RS31*) and *SERINE-RICH PROTEIN SPLICING FACTOR 34B* (*SR34b*), analyzing their splicing under different red/far-red treatments and in the phytochrome knockout mutants *phyA, phyB* and the double null *phyAB*. They showed that red-light-induced alterations in the splicing of *RS31* were suppressed by a subsequent pulse of far-red light, indicating that defects on this AS event are also affected by the most distinguishing feature of typical phytochrome-mediated responses: red/far-red reversibility. By contrast, *SR34b* did not show clear red-/far-red-light reversibility. Despite this, both *RS31* and *SR34b* displayed red-light-induced AS changes in the *phyAB* double mutant (15).

Another genomewide transcriptome profiling study assessing the light regulation of AS was performed in 2016 by Mancini *et al.* (16). Here, the authors sought to expand our understanding of AS in light-grown plants from a few reported examples to the whole transcriptome, and to identify additional possible posttranscriptional mechanisms involved in regulating circadian clock

function and/or the floral transition. To achieve this, these workers used a 2-h pulse of light given in the middle of the night to *Arabidopsis* plants entrained to a 12-h light:12-h dark photoperiod (Fig. 2a). An interesting aspect of this work was the bioinformatics methodology employed to detect AS events from the RNA-seq data; multiexonic genes were partitioned into features defined as "bins," corresponding to exonic regions (exon-bins), intronic regions (intron-bins) and AS regions (AS-bins). First, the differentially spliced AS-bins between treatments were determined with an approach similar to the differential expression analysis. The selection of differentially spliced AS-bins was then restricted to those bins for which the differential AS analysis was supported by changes in the number of splice junctions. This approach makes it possible to compute the splicing metrics PSI (percent spliced-in) and PIR (percent intron retention) (27,28), a bioinformatics improvement that increases the statistical strength of AS event detection. The authors identified a total of 382 genes with AS events regulated by the light pulse treatment, as well as 4341 genes whose mRNA levels significantly changed. Interestingly, less than half of the genes that displayed an altered AS pattern under light showed alterations at the total mRNA level, further indicating that light affects AS through mechanisms distinct from those by which it affects gene expression. From the different type of AS events, IR were emerging as the most frequent in response to light (16) (Fig. 2d). Interestingly, light promoted intron retention of some genes, whereas it enhanced intron exclusion in others (16), indicating that light regulates AS rather than affecting splicing in general. Furthermore, a GO-term analysis showed that categories associated with RNA processing were significantly enriched among transcripts with light-regulated AS patterns, but not among the genes whose mRNA levels alone were affected. To fully appreciate the significance of these data and to contrast them with findings in *Physcomitrella*, we performed a similar meta-analysis of the RNA-seq data from Mancini *et al.* As reported by the authors, GO terms related to RNA processing were enriched in AS events, particularly in the categories of mRNA processing and RNA splicing. Also, the genes that were differentially expressed in the light treatment were enriched in light-stimulus-related GO categories (Fig. 2c). Interestingly, Mancini *et al.* reported that, among the genes showing light-regulated AS events, several encode SR proteins and heterogeneous nuclear ribonucleoproteins (hnRNPs) that are known to modulate the recruitment of spliceosomal snRNPs to donor and acceptor splicing sites (18). In addition, the authors evaluated the effect of white light on the AS of *SERINE-RICH PROTEIN SPLICING FACTOR 30* (*SR30*) in light-grown wild-type, *phyAB* and *cryptochrome 1 cryptochrome 2* (*cry1cry2*) double-mutant plants. They found that light had a similar effect on the AS of *SR30* in the wild type and in the *phyAB* and *cry1cry2* mutants, suggesting that a significant part of the light effect may be modulated by an intermediate molecule generated during photosynthesis, rather than by these photoreceptors. Furthermore, the authors reported that the strong effect of a 2-h red-light pulse on the AS of *SR30* was not impaired in the quintuple mutant *phyABCDE*. This is in concordance with the observation of Shikata *et al.*, who found that approximately 43.6% of all AS events regulated by red light were independent of phyA and phyB. In addition to studying the role of *trans*-acting factors, Mancini *et al.* also looked for *cis*-sequences that might play a role in light-induced AS. They screened the flanking regions of the exon–intron boundaries for potential *cis*-regulatory sequences involved in mediating the light effects on AS, particularly focusing on 232 introns that showed differential retention in response to the light pulse (14). In contrast to the findings of Wu *et al.*, no enriched motifs were found near the 5′SS and 3′SS (16).

So far, we have reviewed and analyzed the available data regarding light-regulated genomewide transcriptome changes in plants. All three studies showed that light induces rapid changes in the AS of splicing-related genes in light-grown plants or etiolated seedlings, suggesting that light regulates AS patterns mostly through its effect on splicing factors themselves. The data presented by Shikata *et al.* suggest that this phenomenon occurs during the early stages of signal transduction, and that possibly the large changes observed in differential gene expression are a result of early signal amplification. This indicates that light-regulated AS of splicing factors may also control the function of light-signaling-related genes and/or other transcripts. Although the reports we reviewed emphasize the fact that photoreceptors play an important role in controlling AS in plants, it is clear that a significant part of the light effect does not appear to operate through traditional photoreceptor pathways. This highlights the relevance of a retrograde signaling circuit connecting photosynthetic activity in the chloroplast to the regulation of AS in the nucleus (29); however, little is known about this circuit. Despite the progress made in this field, important questions remain unanswered, such as how light modulates AS and how light triggers the initial steps that result in AS.

MiRNA posttranscriptional regulation contributes to light responses

Small RNAs are involved in many stages of plant development and several small RNA pathways in plants contribute to plasticity and adaptation. MiRNAs are a predominant class of small RNAs involved in posttranscriptional gene regulation by reducing the levels of their target genes. Many targets for miRNAs encode transcription factors (30); thus, reducing the expression of their encoding genes affects their downstream targets as well, causing a major transcriptomic change in the cell.

Few studies at a genomewide level describe how miRNAs respond to and transmit light signals in plants (14–16,31), and none have examined the biological relevance of light-mediated miRNA regulation. Transcriptome profiling experiments with microarrays or, most recently, RNA-seq revealed several miRNA genes that were differentially expressed following a variety of light treatments in *Arabidopsis* seedlings. For instance, a pulse of white light in the middle of the night induced the expression of miR398b, miR398c, miR163, miR157c and *HUA ENHANCER 1* (*HEN1*), an enzyme participating in miRNA biogenesis, while the same treatment repressed miR408, miR834a and miR822a (16). Similarly, red light applied to four-day-old etiolated seedlings altered the expression of miR163, miR156c, miR157c, miR169 l and miR824a (15). By contrast, two-week-old plants exposed to UV light had diminished miR160, miR165, miR167 and miR939 levels (32) (Fig. 3). Based on these observations, it is clear that miRNA transcripts respond to specific wavelengths rather than to light more generally.

At least two papers have addressed the role of light-responsive miRNAs in early plant development in detail. Light induces

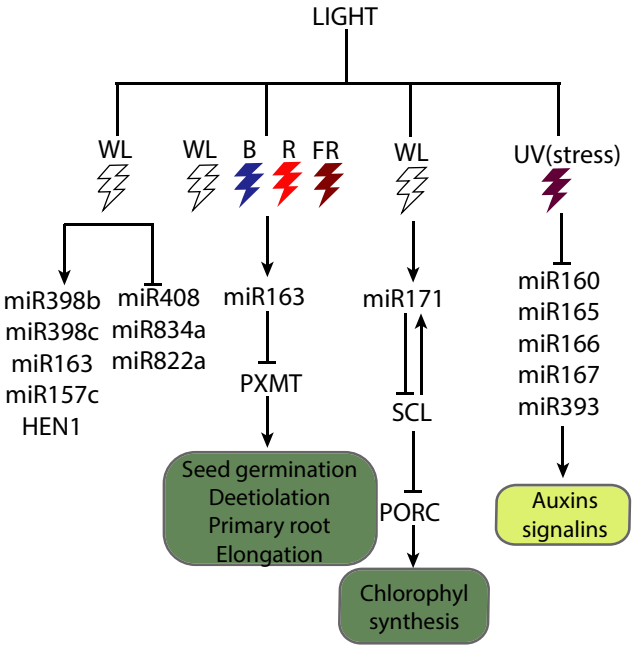


Figure 3. State of the art of light-regulated miRNAs. Here we summarize the current knowledge of light-regulated miRNAs and proteins related to miRNA biosynthesis. Biological processes in which each miRNA set acts (green) or is believed to act (yellow) are shown. WL: white light, B: blue light, R: red light, FR: far-red light, UV: ultraviolet light. Arrows and bar-headed lines indicate transcriptional activation and transcriptional repression, respectively.

the expression of *MIR171*, which targets transcripts encoding scarecrow-like proteins (SCL6/22/27) that negatively regulate chlorophyll biosynthesis in *Arabidopsis* (33) (Fig. 3). It was recently shown that SCL27 binds to the promoter of *PROTOCHLOROPHYLLIDE OXIDOREDUCTASE C* (*PORC*), which encodes a key enzyme in chlorophyll biosynthesis. Plants overexpressing *MIR171c* resemble *scl6scl22scl27* triple mutants, with higher levels of *PORC* transcripts and, concomitantly, higher chlorophyll contents. Additionally, SCL27 binds to *MIR171,* activating its expression in a regulatory feedback loop (34). On the other hand, DELLA proteins upregulate the expression of *POR* genes (35) and promote chlorophyll biosynthesis (34) by acting via the SCLs; the interaction between the DELLA protein REPRESSOR OF GA (RGA) and SCL27 decreases the capacity of SCL27 to bind to DNA promoters. Light therefore triggers two parallel modes of releasing the inhibition on *PORC* to increase chlorophyll biosynthesis: promoting DELLAs to reduce the SCL's capacity to decrease *PORC* expression, and activating miR171 to clear SCL transcripts. In the second report, Chung *et al.* described the role of light-inducible miR163 in seed germination and primary root elongation (36). The expression pattern of miR163 and its target *PARAXANTHINE METHYLTRANSFERASE 1* (*PXMT1*) are inversely correlated and are regulated by a variety of light wavelengths during seedling de-etiolation (Fig. 3). The authors showed that miR163 mediates seedling root growth through downregulating *PXMT1* and found that seeds of the *miR163* knockout mutant have delayed germination (36). Altogether, the results of this study suggest that miR163 functions in the early stages of growth, from seed germination to seedling root growth, by light-induced targeting of *PXMT1*.

Mechanisms of miRNA regulation by light

MiRNA genes are generated from endogenous loci, and their resemblance to protein-coding genes means their transcript abundance is in part guided by the same rules (37), for example, the existence of *cis*-elements in their promoters that respond to environmental and endogenous stimuli. In addition to transcriptional control, miRNA production involves their excision from the stem loop of a fold-back precursor; hence, mature miRNA levels could also be adjusted by modulating their biogenesis. During processing, an imperfect double-stranded RNA (dsRNA) structure is recognized by the miRNA processing machinery and processed to release a ~21-nucleotide small RNA. In plants, all miRNA-generating events take place in the nucleus (38), while mature miRNA acts in the cytoplasm of the cell. The ribonuclease III DICER-LIKE 1 (DCL1) is assisted by accessory proteins to produce two staggered cuts in the dsRNA precursor that release the miRNA/miRNA* duplex (39,40). The HYPONASTIC LEAVES 1 (HYL1) (41,42) and SERRATE (SE) proteins (43,44) assist miRNA processing (45,46) by improving the efficiency and precision of DCL1 cleavages (47). Other regulators have been lately identified such as *C-TERMINAL DOMAIN PHOSPHATASE-LIKE 1 (CPL1)/FIERY2 (FRY2),* which participates in the dephosphorylation of HYL1 needed for optimal HYL1 activity (48). Later, the miRNA/miRNA* molecule is methylated by the action of HEN1 (49) to stabilize the duplex and prevent its degradation (50–52). To complete miRNA maturation, the duplex is exported to the cytoplasm (53) and loaded into the RNA-induced silencing complex, and the miRNA* is degraded. Once in the silencing complex, the single-stranded mature miRNA binds to ARGONAUTE 1 (AGO1) and is ready to scan for its messenger targets to regulate gene expression.

Light may regulate the expression or maturation of miRNAs. Motifs known to confer light responsiveness have been described in upstream regions of a subset of miRNA genes (32,54), suggesting that miRNA levels react to different light signals and help to attenuate the expression of their light-responsive target genes. Moreover, LONG HYPOCOTYL 5 (HY5), a bZIP transcription factor and positive regulator of plant photomorphogenesis, mediates gene transcription indirectly, partially by targeting miRNAs. Genomewide mapping of HY5-binding sites showed that miR156d, miR172b, miR402, miR408, miR775, miR858, miR869 and miR1888 bind directly to this protein (13), and that 21 targets of those miRNAs were upregulated in the *hy5* knockout mutant (13,55), implying that those target genes could be repressed by HY5 via the activation of specific miRNAs. HY5 also binds to the promoters of clock genes such as *CIRCADIAN CLOCK-ASSOCIATED 1, LATE ELONGATED HYPOCOTYL, TIME OF CAB EXPRESSION 1* and *EARLY FLOWERING 4*, but the binding of HY5 alone is not sufficient to maintain proper circadian rhythms (55). Thus, either through *cis*-elements on promoters or through HY5 induction, light controls miRNA abundance and therefore this posttranscriptional process could participate in repressing or at least fine-tuning the expression amplitude of genes in the plant's response to light.

Regulating miRNA biogenesis could hypothetically be another way of controlling their levels. Interestingly, several mutants of genes involved in almost each step of miRNA biogenesis mentioned above show hypersensitivity to light in *Arabidopsis* (10,56), suggesting that light regulates miRNA biogenesis.

Several alleles of the *ago1* mutant have an exaggerated response to light (10), and furthermore, light regulatory pathways mediated by phyA are upregulated in *ago1*, demonstrating that deregulating the phyA pathway might account for part of the altered light response. The exact mechanism and the specific miRNAs involved remain to be clarified, but the phenotypic analysis of the *ago1* mutant suggests that miRNAs might act as negative regulators of light-signaling pathways (10). Mutations in *HYL1*, *HASTY* and *HEN1* cause *Arabidopsis* to have shorter hypocotyls than the wild type under both dark and light conditions, a phenotype that is dependent on the fluence of white light (56). This hypersensitivity to light implicates HYL1, HASTY and HEN1 as negative regulators in the de-etiolation process, although only the production of HEN1 was induced by light (56). Light-mediated induction of *HEN1* is dependent on the photoreceptors phyA, phyB, cry1 and cry2, and on HY5 and HY5 HOMOLOG (HYH), all of which are involved in photomorphogenic behaviors. The increased levels of HEN1 in seedlings lead to an increase of miR157d and miR319. Tsai *et al.* showed that miR157d targets HY5 transcript (56), forming a negative feedback loop between HY5 and HEN1 during photomorphogenesis. This suggests an interesting example of a mechanism for light-mediated RNA biogenesis in photomorphogenesis.

CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) is an E3 ligase involved in photomorphogenesis that promotes the degradation of light-regulated transcription factors and photoreceptors. COP1 represents another mechanistic link between light signaling and miRNA biogenesis, because the absence of COP1 impairs the accumulation of miRNAs. COP1 is believed to stabilize HYL1 by protecting it from degradation by an unknown protease in a light-dependent manner (57). This observation is surprising, as COP1 is associated with the proteolytic decay of proteins rather than their stabilization; therefore, the mechanism by which COP1 contributes to protein stabilization remains to be described.

These observations highlight the role of light in modulating the posttranscriptional mechanisms of gene expression, which allow plants to adapt to changing light environments.

Integrating the AS and miRNA pathway in response to light

So far, we have reviewed that two of the most important gene posttranscriptional mechanisms, namely AS and the miRNA regulatory pathway, respond to light, which is considered to be the most important environmental cue for plants. It would be intriguing to establish whether there is cross talk between these processes. Using data from the transcriptome studies described in this review, we searched for miRNAs or genes involved in their biogenesis that undergo AS in response to light. In *Physcomitrella patens,* most of the factors involved in miRNA processing undergo AS under light (14). Upon treatment with red or blue-light pulses, IR events are induced in *SE, HEN1, CPL1* and *DCL1* in *Physcomitrella* (Fig. 4a). Intriguingly, a certain light wavelength specificity was observed; only red light affects the AS of *DAWDLE* (*DDL*) thought to stabilize miRNA primary transcripts (58,59), while blue light affects *HYL1* splicing, but red light has no effect on *HYL1* (Fig. 4a). Also, blue and red light can generate different isoforms of the same gene; for example, we observed that in *HEN1,* the second intron is retained after a red pulse, while blue light caused the retention of intron 7. Both treatments result in a nonfunctional HEN1 protein, as one disrupts the methyltransferase domain and the other generates a truncated protein containing only the RNA-binding domain. Furthermore, red light induces an alternative donor

a

miRNA-related genes that undergo AS under light treatments:

Red light	Blue light
DCL1	*DCL1*
SE	*SE*
HEN1	*HEN1*
CPL1	*CPL1*
DDL	*HYL1*

b

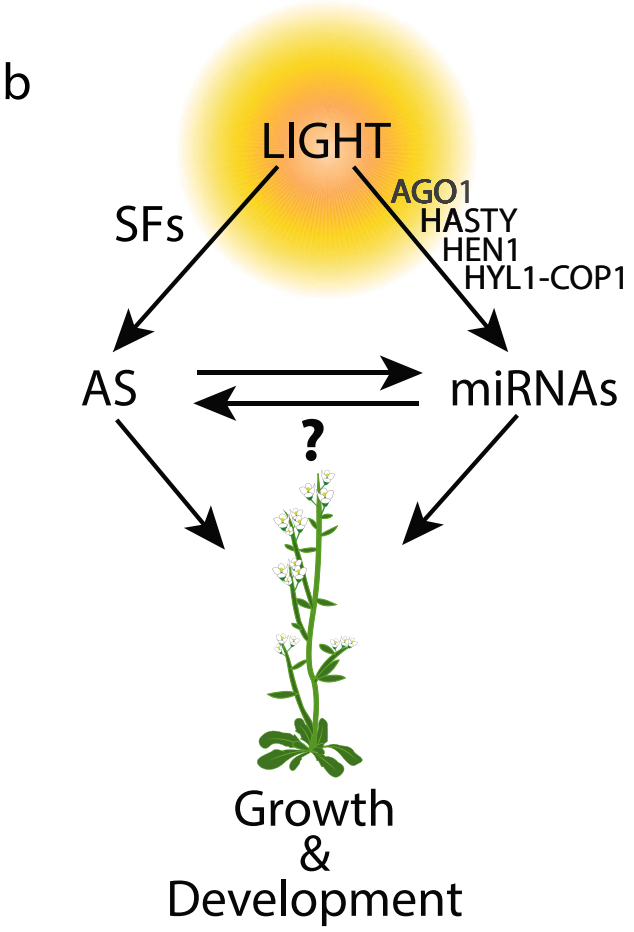


Figure 4. Insights into light-mediated posttranscriptional regulation in plants. (a) Transcripts whose alternative splicing (AS) pattern is affected by light in *Physcomitrella patens*. (b) Diagram depicting the role of light-mediated posttranscriptional control of plant growth and development through AS and miRNAs. The genes displayed here are likely to link light signaling with the regulation of both AS and miRNA synthesis. The question mark represents the putative cross talk between AS and miRNA biosynthesis and/or function.

splice site event in *DCL1,* whereas blue light results in an alternative acceptor splice site in the transcript.

Developing a systematic bioinformatics search of the *Arabidopsis* transcriptome, Yang *et al.* revealed that at least 12% of high-confidence miRNA binding sites were affected by AS, as different isoforms of a gene diverge at the miRNA recognition sequence (60). In particular, AS observed in *DCL1*, *TAS1* and *SPL4* abolished the capacity of miRNAs to bind to them, as the binding sites disappear in their alternative isoforms. The biological relevance of AS in *SPL4* was underscored using transgenic plants bearing isoforms with or without the miRNA binding site, which resulted in two distinguishable phenotypes (60).

Perhaps the strongest association between AS and the miRNA pathway in response to light is exemplified by COP1 protein. COP1 is an interesting protein linked not only to light-induced miRNA biogenesis (57) but also to AS. The AS form of HYH lacks a COP1-interacting motif and is therefore more resistant to selective protein degradation mediated by COP1 (61).

CONCLUSIONS AND PERSPECTIVES

Light is a major environmental cue that modulates plant growth and development. Here we described how two important post-transcriptional mechanisms that shape the transcriptome are affected by light treatments; miRNA transcription and biogenesis are tightly regulated by light, while light treatments affect the splicing of hundreds of genes (Fig. 4b). Besides, our meta-analysis of previously reported experiments suggests that light regulates the levels of miRNAs by affecting the AS of the genes that participate in their biogenesis (Fig. 4b); however, the possibility that different isoforms have a different biological impact remains to be evaluated. Also, AS of the miRNA binding site is a plausible mechanism to lessen miRNA-based gene expression (Fig. 4b) (60), although whether this affects light-responsive genes remains unknown. The opposing mechanism, that is whether miRNAs regulate AS, was not investigated. The possibility that light participates in this likely cross talk between AS and miRNA-mediated gene regulation to shape gene expression, and ultimately plant responses to light, is an exciting topic and remains to be addressed.

Acknowledgements—CEH was supported by the Fundación Bunge y Born Postdoctoral Fellowship. CG was supported by a CONICET Postdoctoral Fellowship, and JLM was supported by CONINCET. This work has been supported in part by grants to JLM from ANPCyT and the Max-Planck Partner Group. We apologize to colleagues whose work has not been included in this review due to space constraints.

REFERENCES

1. Jenkins, G. I. (2014) The UV-B photoreceptor UVR8: From structure to physiology. *Plant Cell* **26**, 21–37.
2. Kami, C., S. Lorrain, P. Hornitschek and C. Fankhauser (2010) Light-regulated plant growth and development. *Curr. Top. Dev. Biol.* **91**, 29–66.
3. Moglich, A., X. Yang, R. A. Ayers and K. Moffat (2010) Structure and function of plant photoreceptors. *Annu. Rev. Plant Biol.* **61**, 21–47.
4. Wu, S. H. (2014) Gene expression regulation in photomorphogenesis from the perspective of the central dogma. *Annu. Rev. Plant Biol.* **65**, 311–333.
5. Darnell Jr, J. E. (2013) Reflections on the history of pre-mRNA processing and highlights of current knowledge: A unified picture. *RNA* **19**, 443–460.
6. Brodersen, P. and O. Voinnet (2006) The diversity of RNA silencing pathways in plants. *Trends Genet.* **22**, 268–280.
7. Mallory, A. C. and H. Vaucheret (2006) Functions of microRNAs and related small RNAs in plants. *Nat. Genet.* **38**(Suppl), S31–S36.
8. Mano, S., M. Hayashi and M. Nishimura (1999) Light regulates alternative splicing of hydroxypyruvate reductase in pumpkin. *Plant J.* **17**, 309–320.
9. Mano, S., M. Hayashi and M. Nishimura (2000) A leaf-peroxisomal protein, hydroxypyruvate reductase, is produced by light-regulated alternative splicing. *Cell Biochem. Biophys.* **32**, 147–154.
10. Sorin, C., J. D. Bussell, I. Camus, K. Ljung, M. Kowalczyk, G. Geiss, H. McKhann, C. Garcion, H. Vaucheret, G. Sandberg and C. Bellini. (2005) Auxin and light control of adventitious rooting in Arabidopsis require ARGONAUTE1. *Plant Cell* **17**, 1343–1359.
11. Simpson, C. G., J. Fuller, M. Maronova, M. Kalyna, D. Davidson, J. McNicol, A. Barta and J. W. Brown. (2008) Monitoring changes in alternative precursor messenger RNA splicing in multiple gene transcripts. *Plant J.* **53**, 1035–1048.
12. Jung, K.-H., L. E. Bartley, P. Cao, P. E. Canlas and P. C. Ronald (2009) Analysis of alternatively spliced rice transcripts using microarray data. *Rice* **2**, 44–55.
13. Zhang, H., H. He, X. Wang, X. Wang, X. Yang, L. Li and X. W. Deng. (2011) Genome-wide mapping of the HY5-mediated gene networks in Arabidopsis that involve both transcriptional and post-transcriptional regulation. *Plant J.* **65**, 346–358.
14. Wu, H. P., Y. S. Su, H. C. Chen, Y. R. Chen, C. C. Wu, W. D. Lin and S. L. Tu. (2014) Genome-wide analysis of light-regulated alternative splicing mediated by photoreceptors in Physcomitrella patens. *Genome Biol.* **15**, R10.
15. Shikata, H., K. Hanada, T. Ushijima, M. Nakashima, Y. Suzuki, T. Matsushita (2014) Phytochrome controls alternative splicing to mediate light responses in Arabidopsis. *Proc. Natl Acad. Sci. USA* **111**, 18781–18786.
16. Mancini, E., S. E. Sanchez, A. Romanowski, R. G. Schlaen, M. Sanchez-Lamas, P. D. Cerdán and M. J. Yanovsky (2016) Acute effects of light on alternative splicing in light-grown plants. *Photochem. Photobiol.* **92**, 126–133.
17. Reddy, A. S., Y. Marquez, M. Kalyna and A. Barta (2013) Complexity of the alternative splicing landscape in plants. *Plant Cell* **25**, 3657–3683.
18. Kornblihtt, A. R., I. E. Schor, M. Alló, G. Dujardin, E. Petrillo, M. J. Muñoz (2013) Alternative splicing: A pivotal step between eukaryotic transcription and translation. *Nat. Rev. Mol. Cell Biol.* **14**, 153–165.
19. Wahl, M. C., C. L. Will and R. Luhrmann (2009) The spliceosome: Design principles of a dynamic RNP machine. *Cell* **136**, 701–718.
20. Marquez, Y., J. W. Brown, C. Simpson, A. Barta and M. Kalyna (2012) Transcriptome survey reveals increased complexity of the alternative splicing landscape in Arabidopsis. *Genome Res.* **22**, 1184–1195.
21. Arciga-Reyes, L., L. Wootton, M. Kieffer and B. Davies (2006) UPF1 is required for nonsense-mediated mRNA decay (NMD) and RNAi in Arabidopsis. *Plant J.* **47**, 480–489.
22. Isken, O. and L. E. Maquat (2008) The multiple lives of NMD factors: Balancing roles in gene and genome regulation. *Nat. Rev. Genet.* **9**, 699–712.
23. Nicholson, P. and O. Muhlemann (2010) Cutting the nonsense: The degradation of PTC-containing mRNAs. *Biochem. Soc. Trans.* **38**, 1615–1620.
24. Gallie, D. R. (1993) Posttranscriptional regulation of gene expression in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **44**, 77–105.
25. Floris, M., H. Mahgoub, E. Lanet, C. Robaglia and B. Menand (2009) Post-transcriptional regulation of gene expression in plants during abiotic stress. *Int. J. Mol. Sci.* **10**, 3168–3185.
26. Chen, Y. R., Y. S. Su and S. L. Tu (2012) Distinct phytochrome actions in nonvascular plants revealed by targeted inactivation of phytobilin biosynthesis. *Proc. Natl Acad. Sci. USA* **109**, 8310–8315.
27. Pervouchine, D. D., D. G. Knowles and R. Guigo (2013) Intron-centric estimation of alternative splicing from RNA-seq data. *Bioinformatics* **29**, 273–274.
28. Braunschweig, U., N. L. Barbosa-Morais, Q. Pan, E. N. Nachman, B. Alipanahi, T. Gonatopoulos-Pournatzis, B. Frey, M. Irimia and B. J. Blencowe. (2014) Widespread intron retention in mammals functionally tunes transcriptomes. *Genome Res.* **24**, 1774–1786.

29. Petrillo, E., M. A. Godoy Herz, A. Fuchs, D. Reifer, J. Fuller, M. J. Yanovsky, C. Simpson, J. W. Brown, A. Barta, M. Kalyna and A. R. Kornblihtt. (2014) A chloroplast retrograde signal regulates nuclear alternative splicing. *Science* **344**, 427–430.
30. Bartel, D. P. (2004) MicroRNAs: Genomics, biogenesis, mechanism, and function. *Cell* **116**, 281–297.
31. Wang, H., P. J. Chung, J. Liu, I. C. Jang, M. J. Kean, J. Xu and N. H. Chua. (2014) Genome-wide identification of long noncoding natural antisense transcripts and their responses to light in Arabidopsis. *Genome Res.* **24**, 444–453.
32. Zhou, X., G. Wang and W. Zhang (2007) UV-B responsive microRNA genes in Arabidopsis thaliana. *Mol. Syst. Biol.* **3**, 103.
33. Wang, L., Y. X. Mai, Y. C. Zhang, Q. Luo and H. Q. Yang (2010) MicroRNA171c-targeted SCL6-II, SCL6-III, and SCL6-IV genes regulate shoot branching in Arabidopsis. *Mol Plant* **3**, 794–806.
34. Ma, Z., X. Hu, W. Cai, W. Huang, X. Zhou, Q. Luo, H. Yang, J. Wang and J. Huang. (2014) Arabidopsis miR171-targeted scarecrow-like proteins bind to GT cis-elements and mediate gibberellin-regulated chlorophyll biosynthesis under light conditions. *PLoS Genet.* **10**, e1004519.
35. Cheminant, S., M. Wild, F. Bouvier, S. Pelletier, J. P. Renou, M. Erhardt, S. Hayes, M. J. Terry, P. Genschik and P. Achard. (2011) DELLAs regulate chlorophyll and carotenoid biosynthesis to prevent photooxidative damage during seedling deetiolation in Arabidopsis. *Plant Cell* **23**, 1849–1860.
36. Chung, P. J., B. S. Park, H. Wang, J. Liu, I. C. Jang, N. H. Chua (2016) Light-inducible MiR163 targets PXMT1 transcripts to promote seed germination and primary root elongation in Arabidopsis. *Plant Physiol.* **170**, 1772–1782.
37. Allen, E., Z. Xie, A. M. Gustafson, G. H. Sung, J. W. Spatafora, J. C. Carrington (2004) Evolution of microRNA genes by inverted duplication of target gene sequences in Arabidopsis thaliana. *Nat. Genet.* **36**, 1282–1290.
38. Papp, I., M. F. Mette, W. Aufsatz, L. Daxinger, S. E. Schauer, A. Ray, der van Winden J., M. Matzke and A. J. Matzke. (2003) Evidence for nuclear processing of plant micro RNA and short interfering RNA precursors. *Plant Physiol.* **132**, 1382–1390.
39. Park, W., J. Li, R. Song, J. Messing and X. Chen (2002) CARPEL FACTORY, a Dicer homolog, and HEN1, a novel protein, act in microRNA metabolism in Arabidopsis thaliana. *Curr. Biol.* **12**, 1484–1495.
40. Reinhart, B. J., E. G. Weinstein, M. W. Rhoades, B. Bartel and D. P. Bartel (2002) MicroRNAs in plants. *Genes Dev.* **16**, 1616–1626.
41. Han, M. H., S. Goud, L. Song and N. Fedoroff (2004) The Arabidopsis double-stranded RNA-binding protein HYL1 plays a role in microRNA-mediated gene regulation. *Proc. Natl Acad. Sci. USA* **101**, 1093–1098.
42. Vazquez, F., V. Gasciolli, P. Crete and H. Vaucheret (2004) The nuclear dsRNA binding protein HYL1 is required for microRNA accumulation and plant development, but not posttranscriptional transgene silencing. *Curr. Biol.* **14**, 346–351.
43. Lobbes, D., G. Rallapalli, D. D. Schmidt, C. Martin and J. Clarke (2006) SERRATE: A new player on the plant microRNA scene. *EMBO Rep.* **7**, 1052–1058.
44. Yang, L., Z. Liu, F. Lu, A. Dong and H. Huang (2006) SERRATE is a novel nuclear regulator in primary microRNA processing in Arabidopsis. *Plant J.* **47**, 841–850.
45. Kurihara, Y., Y. Takashi and Y. Watanabe (2006) The interaction between DCL1 and HYL1 is important for efficient and precise processing of pri-miRNA in plant microRNA biogenesis. *RNA* **12**, 206–212.
46. Kurihara, Y. and Y. Watanabe (2004) Arabidopsis micro-RNA biogenesis through Dicer-like 1 protein functions. *Proc. Natl Acad. Sci. USA* **101**, 12753–12758.
47. Dong, Z., M. H. Han and N. Fedoroff (2008) The RNA-binding proteins HYL1 and SE promote accurate in vitro processing of pri-miRNA by DCL1. *Proc. Natl Acad. Sci. USA* **105**, 9970–9975.
48. Manavella, P. A., J. Hagmann, F. Ott, S. Laubinger, M. Franz, *et al.* (2012) Fast-forward genetics identifies plant CPL phosphatases as regulators of miRNA processing factor HYL1. *Cell* **151**, 859–870.
49. Huang, Y., L. Ji, Q. Huang, D. G. Vassylyev, X. Chen, J. B. Ma. (2009) Structural insights into mechanisms of the small RNA methyltransferase HEN1. *Nature* **461**, 823–827.
50. Boutet, S., F. Vazquez, J. Liu, C. Béclin, M. Fagard, A. Gratias, J. B. Morel, P. Crété, X. Chen and H. Vaucheret. (2003) Arabidopsis HEN1: A genetic link between endogenous miRNA controlling development and siRNA controlling transgene silencing and virus resistance. *Curr. Biol.* **13**, 843–848.
51. Li, J., Z. Yang, B. Yu, J. Liu and X. Chen (2005) Methylation protects miRNAs and siRNAs from a 3′-end uridylation activity in Arabidopsis. *Curr. Biol.* **15**, 1501–1507.
52. Yu, B., Z. Yang, J. Li, S. Minakhina, M. Yang, R. W. Padgett, R. Steward and X. Chen. (2005) Methylation as a crucial step in plant microRNA biogenesis. *Science* **307**, 932–935.
53. Park, M. Y., G. Wu, A. Gonzalez-Sulser, H. Vaucheret and R. S. Poethig (2005) Nuclear processing and export of microRNAs in Arabidopsis. *Proc. Natl Acad. Sci. USA* **102**, 3691–3696.
54. Sire, C., A. B. Moreno, M. Garcia-Chapa, J. J. Lopez-Moya and B. San Segundo (2009) Diurnal oscillation in the accumulation of Arabidopsis microRNAs, miR167, miR168, miR171 and miR398. *FEBS Lett.* **583**, 1039–1044.
55. Lee, J., K. He, V. Stolc, H. Lee, P. Figueroa, Y. Gao, W. Tongprasit, H. Zhao, I. Lee and X. W. Deng. (2007) Analysis of transcription factor HY5 genomic binding sites revealed its hierarchical role in light regulation of development. *Plant Cell* **19**, 731–749.
56. Tsai, H. L., Y. H. Li, W. P. Hsieh, M. C. Lin, J. H. Ahn, S. H. Wu (2014) HUA ENHANCER1 is involved in posttranscriptional regulation of positive and negative regulators in Arabidopsis photomorphogenesis. *Plant Cell* **26**, 2858–2872.
57. Cho, S. K., S. Ben Chaabane, P. Shah, C. P. Poulsen and S. W. Yang (2014) COP1 E3 ligase protects HYL1 to retain microRNA biogenesis. *Nat. Commun.* **5**, 5867.
58. Morris, E. R., D. Chevalier and J. C. Walker (2006) DAWDLE, a forkhead-associated domain gene, regulates multiple aspects of plant development. *Plant Physiol.* **141**, 932–941.
59. Yu, B., L. Bi, B. Zheng, L. Ji, D. Chevalier, M. Agarwal, V. Ramachandran, W. Li, T. Lagrange, J. C. Walker and X. Chen. (2008) The FHA domain proteins DAWDLE in Arabidopsis and SNIP1 in humans act in small RNA biogenesis. *Proc. Natl Acad. Sci. USA* **105**, 10073–10078.
60. Yang, X., H. Zhang and L. Li (2012) Alternative mRNA processing increases the complexity of microRNA-based gene regulation in Arabidopsis. *Plant J.* **70**, 421–431.
61. Sibout, R., P. Sukumar, C. Hettiarachchi, M. Holm, G. K. Muday, C. S. Hardtke (2006) Opposite root growth phenotypes of hy5 versus hy5 hyh mutants correlate with increased constitutive auxin signaling. *PLoS Genet.* **2**, e202.
62. Hernando, C. E., S. E. Sanchez, E. Mancini and M. J. Yanovsky (2015) Genome wide comparative analysis of the effects of PRMT5 and PRMT4/CARM1 arginine methyltransferases on the Arabidopsis thaliana transcriptome. *BMC Genom.* **16**, 192.

AUTHOR BIOGRAPHIES

Carlos E. Hernando obtained a B.S. in Biotechnology followed by a Ph.D. in Molecular Biology from the San Martin National University, Argentina, under the direction of Dr. Marcelo Yanovsky. He is currently a Teaching Assistant in Plant Biotechnology at the San Martin National University and a postdoctoral fellow at the Leloir Institute in Buenos Aires, Argentina, under the direction of Dr. Marcelo Yanovsky. His research focuses on the role of posttranscriptional regulation in plant growth and development.

Carolina Garcia obtained a B.S. in Biology at the National University of Cordoba, Argentina, followed by a Ph.D. in Molecular Biology from the University of Buenos Aires, Argentina, under the direction of Dr. Gustavo E. Svlever. She is currently a postdoctoral fellow at Leloir Institute in Buenos Aires under the direction of Dr. Marcelo Yanovsky and Dr. Julieta Mateos. Her research focuses on the molecular mechanisms involved in flowering.

Julieta L. Mateos obtained a B.S. in Biotechnology at the University of Quilmes, Argentina, followed by a Ph.D. in Plant Molecular Biology from the University of Buenos Aires, Argentina, under the direction of Dr. Jorge Casal and Prof. Dr. Silvia E. Braslavsky. She was a postdoctoral fellow at the Institute of Molecular and Cell Biology of Rosario, Argentina, in the laboratory of Dr. Javier Palatnik, studying the mechanisms underlying miRNA biogenesis. Later she worked as a senior postdoc at the Max-Planck Institute for Plant Breeding Research in Cologne, Germany, in Prof. George Coupland's group and became a Humboldt Fellow. She is currently a member of the National Scientific and Technical Research Council (CONICET) at the Leloir Institute in Buenos Aires, and was recently appointed as head of a Max-Planck-Partner Group. Now she is engaged in research into the transcriptional and posttranscriptional regulation of plant development.