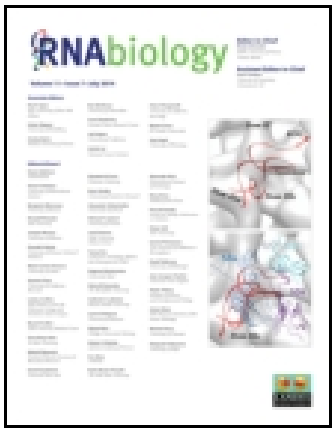

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Let there be light: Regulation of gene expression in plants

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Let there be light: Regulation of gene expression in plants

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Abbreviations: mRNA, messenger RNA; Pol II, RNA polymerase II; DBMIB, 2,5-dibromo-3-methyl-6-isopropyl-benzoquinone; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; PS, photosystem; PQ, plastoquinone; ROS, reactive oxygen species

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Gene expression regulation relies on a variety of molecular mechanisms affecting different steps of a messenger RNA (mRNA) life: transcription, processing, splicing, alternative splicing, transport, translation, storage and decay. Light induces massive reprogramming of gene expression in plants. Differences in alternative splicing patterns in response to environmental stimuli suggest that alternative splicing plays an important role in plant adaptation to changing life conditions. In a recent publication, our laboratories showed that light regulates alternative splicing of a subset of *Arabidopsis* genes encoding proteins involved in RNA processing by chloroplast retrograde signals. The light effect on alternative splicing is also observed in roots when the communication with the photosynthetic tissues is not interrupted, suggesting that a signaling molecule travels through the plant. These results point at alternative splicing regulation by retrograde signals as an important mechanism for plant adaptation to their environment.

The Life of a mRNA in Plants

The birth of mRNA molecules in plants does not differ much from that of other eukaryotes. Transcription from a DNA template is carried out by RNA polymerase II (Pol II) to form the precursor mRNA (pre-mRNA) molecule. The pre-mRNA undergoes 5' end capping, splicing and 3' end cleavage and polyadenylation, processes that have been shown to be coupled to transcription.[1]

Splicing is performed by the spliceosome, a ribonucleoprotein machinery that recognizes splice sites consisting of consensus sequences: strong splice sites are more adjusted to the consensus, and therefore more efficiently recognized compared to weak splice sites. Competition between strong and weak splice sites along the nascent pre-mRNA leads to alternative splicing.[2] Transcriptome diversity is increased by alternative splicing since it allows a single gene to produce 2 or more mature mRNA variants that are similar but not identical, expanding the coding capacity of eukaryotic genomes.[2,3] Alternative splicing can also regulate mRNA levels through degradation of specific alternative splicing isoforms by nonsense-mediated mRNA decay, introducing a quality control mechanism.[4] Once in the cytoplasm, translatable mature mRNA is also subjected to different pathways of degradation. Each of these processes from transcription to degradation can be regulated, thus allowing multiple layers of gene expression regulation.

Transcription and Alternative Splicing

Alternative splicing regulation is mostly performed by splicing factors that recognize *cis*-acting elements present in the RNA molecule, known as splicing enhancers or silencers. However, many different approaches, both *in vivo* and *in vitro*, have revealed another layer of regulation that involves a mechanistic coupling between transcription and splicing machineries.[5] Accumulated evidence indicates that pre-mRNA splicing occurs,[6] or is committed to occur, co-transcriptionally. This means that the actual splicing reactions take place, or that the factors

needed for splicing are recruited to the pre-mRNA target sequences, before RNA Pol II has reached the end of the gene and while the transcript is still associated to chromatin.[7,8] Chromatin structure, nucleosome positioning, post-translational histone modifications and the existence of adaptor complexes between the chromatin and splicing machineries can regulate alternative splicing through its coupling with transcription.[7] Changes in RNA Pol II elongation rate can also modulate alternative splicing: in most cases slow RNA Pol II elongation leads to higher inclusion of alternative exons;[9] however, it has also been reported that slow elongation can cause exon skipping.[10]

Alternative Splicing in Plants

Approximately 60% of *Arabidopsis* genes produce different transcript isoforms due to alternative splicing.[11] This percentage is lower than that of mammalian cells (95% in multiexonic genes),[12] but still high enough to consider alternative splicing as a main contributor to expanding the repertoire of transcripts and proteins in plants.[13]

The frequency of different alternative splicing events in plants has been deeply studied. Intron retention is the most prominent event in plants, whereas cassette exons are the most common alternative splicing event in animals. However, the alternative splicing landscape is more complex since multiple splicing events may occur in the same transcript, raising the question of a possible coordination between them.[11]

Different cell types, tissues, developmental stages and environmental conditions show differences in the presence and abundance of splicing factors that contribute to modulate alternative splicing patterns.[11] Widespread changes in the patterns of splicing mRNA isoforms in response to stress and developmental cues suggest an important role for alternative splicing in plant development and environmental responses.[3] Alternative splicing is important for photosynthesis, flowering, defense responses and the circadian clock.[13]

Several abiotic stresses can regulate alternative splicing, such as high or low temperature, drought, salt stress or light.[14] Global changes in alternative splicing were found under salt stress, which involve about 49% of all intron-containing genes. Among them, most genes that showed significant changes were associated with specific functional pathways, such as stress response and RNA splicing.[15] Light/dark conditions affect alternative splicing of a subset of *Arabidopsis* genes preferentially encoding proteins involved in RNA processing. The alternative splicing of *AtRS31*, which encodes a serine/arginine-rich splicing factor, changes in different light conditions through a mechanism that involves the chloroplast (see below).[16]

Altogether, conspicuous and widespread differences in alternative splicing patterns in response to environmental stimuli suggest that alternative splicing plays important roles in plant adaptation to changing life conditions.

Nuclear Gene Expression Regulation by Light: the Role of Retrograde Signals

One key strategy for plants to adapt to challenges imposed by stress conditions and to cope with the changing environment is the fine tuning of gene expression in response to those changes.[17,18] As briefly described before, gene expression regulation can rely on a wide variety of molecular mechanisms affecting different steps of the mRNA life like transcription, processing, splicing, alternative splicing, transport, translation, storage and decay.[19] Light is one of the most important environmental cues for almost all living organisms and it is also the source of energy for plants.[20] It is therefore not surprising that plants have adopted the ability to sense multiple parameters of light signals, including light quantity (fluence), quality (wavelength), direction and duration.[21] Light signals are perceived through different families of photoreceptor proteins. Red and far-red lights are sensed by phytochromes. Blue and ultraviolet (UV)-A wavelengths are sensed by cryptochromes, phototropins, and members of the Zeitlupe family in *Arabidopsis*, whereas UV-B is perceived by the UVR8 photoreceptor. Light perception by these photoreceptors triggers many biological processes, including gene expression regulation by signal transduction or by nuclear relocalization of light-activated photoreceptors.[22-24]

Besides photoreceptor proteins, once a green seedling is established, chloroplasts play a key role in sensing light fluctuations and in the communication of these changes to the nucleus by retrograde signaling pathways.[25,26] Two different modes can be established for retrograde signaling. First, there is a chloroplast *biogenic* control of nuclear genes during early plastidial development, triggered by signals related to the photosystems and pigment biogenesis, and, secondly, there is a chloroplast *operational* control associated with signals induced by the function of mature chloroplast to regulate plant responses to varying light conditions.[27-30] Most of the operational retrograde signals are dependent on the quantity and/or quality of light. Changes in light quality might lead to preferential excitation of one of the photosystems (PS), leading to redox changes in intersystem electron carriers, particularly the plastoquinone (PQ) pool and the cytochrome b6f complex, whereas high light reduces the whole electron transfer chain and causes accumulation of reducing equivalents in the stroma as well as the production of reactive oxygen species (ROS).[31,32] Redox signals from photosynthetic electron transport components have been shown to control the expression of genes in the chloroplast genome at both the transcriptional and translational levels, as well as the expression of nuclear genes mainly at the transcriptional level.[33] The redox state of the PQ pool in particular has been strongly suggested as a prominent candidate for the origin of chloroplast redox signals. This has been demonstrated by using the photosynthetic electron transfer inhibitors 2,5-dibromo-3-methyl-6-isopropyl-benzoquinone (DBMIB) and 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) and by modulating the redox state of the PQ pool by light that predominantly excites either PSII or PSI reducing or oxidizing the PQ pool, respectively.[32,34] Interestingly, changes in temperature, light conditions, CO_2 availability and nutrients

impact on the photosynthesis efficiency, changing the photosynthetic electron flux and the redox state of the components involved in it.[35] Therefore, signals arising from the photosynthetic electron transport chain components (i.e.: PQ pool) will be integrating diverse environmental cues to regulate gene expression in order to fine tune plant responses.[36] While the transmission pathway followed by the redox signals remains still elusive, evidence for the effects of these signals on nuclear gene expression including the regulation of transcription, stability and translational efficiency is continuously growing.[34,37,38] Other signals, not directly derived from the redox state of the components of the photosynthetic electron transport chain have been reported. Among these, ROS -continuously produced during photosynthesis by partial reduction of oxygen molecules or energy transfer to them- were shown to work as signaling molecules affecting nuclear gene expression.[39-43]

Finally, to add more complexity to this scenario, it is interesting to point out that different light signals are connected with signals from other pathways and both, light receptor proteins and chloroplast derived signals, interact in the same network and contribute to the control of plant responses and development.[44-46]

Regulation of Alternative Splicing by Light: a Novel Role for Retrograde Signals

Light induces massive reprogramming of the plant transcriptome. Up to one third of the transcriptome can be regulated by light in *Arabidopsis* and similar results were obtained in other plant species.[47,48] Noticeably, many of the genes affected by light conditions encode transcription factors or proteins with DNA binding domains.[49] Besides the transcriptional effects, chromatin modifications are tightly regulated by light.[50] As an example, acetylation of lysine 9 in histone 3 (H3K9ac), a mark that positively correlates with active transcription, is enriched in light regulated genes, in a light intensity-dependent manner.[51] Alternative splicing is also under light control. Pioneer work of Mikio Nishimura, performed in pumpkin in the 90's, showed that light regulates alternative splicing patterns of the transcripts coding for a hydroxypyruvate reductase and an ascorbate peroxidase, determining different subcellular localizations of the protein products.[52,53] More recently it was shown that alternative splicing regulation of circadian clock-related genes in *Arabidopsis* is important for the proper functioning of the biological clock,[54,55] and that light is affecting the alternative splicing of splicing factor coding genes.[56,57] It was also shown that an *Arabidopsis* mutant for a gene that codes for an ortholog of the human potential splicing factor SR140 fails in phytochrome B responses.[58] Furthermore, a recent publication reveals that light-regulated alternative splicing is important in shaping transcriptome responses to light in the moss *Physcomitrella patens*.[59] The authors proposed that alternative splicing is rapidly fine-tuned by light in this system and these responses are misregulated in *P. patens* mutants defective in red light sensing phytochromes. In summary, plant responses to light also include alternative splicing regulation, and the photoreceptor proteins might be key players in this scene[59]

In a recent publication, our laboratories showed that light regulates alternative splicing of a subset of *Arabidopsis* genes encoding proteins involved in RNA processing by chloroplast retrograde signals. Earlier evidence had shown that the mRNA for a negative regulator of tetrapyrrole biosynthesis of *Chlamydomonas reinhardtii*, the product of a FLU-like gene, undergoes alternative splicing whose pattern is controlled by light and plastid signals.[60] Using the alternative splicing of *At-RS31*, a gene encoding a serine arginine-rich splicing factor[61] as a model, we showed that light modulates the relative amounts of its mRNA isoforms in a way that the protein coding isoform (*mRNA1*) is more abundant in light. The participation of phytochrome and cryptochrome photosensory pathways was ruled out for the regulation of this event by light/dark transitions. Changes in *At-RS31* alternative splicing occur in seedlings both under prolonged light/dark regimes and under natural short day (8:16 hr light:dark) photoperiod conditions but not in long day photoperiods. Photosynthetically active different light qualities produce similar effects than white light, in a light intensity-dependent manner. The light signaling pathway does not involve the circadian clock since the light/dark effect on splicing is still observed in several clock mutants. Since photoreceptor proteins are not involved in this regulatory mechanism we tested whether the chloroplast, which is able to sense and to communicate light signals to the nucleus, was triggering the alternative splicing changes in response to light. Consequently, drugs that disrupt chloroplast function like DCMU and DBMIB abolish the splicing responses to light showing the involvement of the organelle in the pathway. Both DCMU and DBMIB inhibit the overall electron transport chain, but whereas DCMU increases the oxidized PQ pool by blocking the electron transfer from the PSII to PQ, DBMIB keeps the PQ pool reduced by preventing the electron transfer to cytochrome b6f. DCMU duplicates the effect of darkness but DBMIB mimics the light effect on *At-RS31*, revealing that the reduced PQ pool upregulated by light initiates the retrograde signaling pathway. The nature of the retrograde signal is4 still unknown, however. Interestingly, we showed that alternative splicing regulation of *At-RS31* by light would be important for plant survival when facing suboptimal light conditions. Furthermore, the light effect on *At-RS31* alternative splicing is also observed in roots when the communication with the photosynthetic tissues is not interrupted, suggesting that a signaling molecule travels through the plant.[16] These results pointed at alternative splicing regulation by retrograde signals as an important mechanism for plants to adapt to the environment. Effort must be made to identify the signal that travels from the chloroplast to the nucleus as well as the nature of the molecule that communicates the light effect to the roots.

Perspectives: Searching for the Signal(s)

In the next years effort has to be done to clarify how much of the genome is regulated at the level of alternative splicing

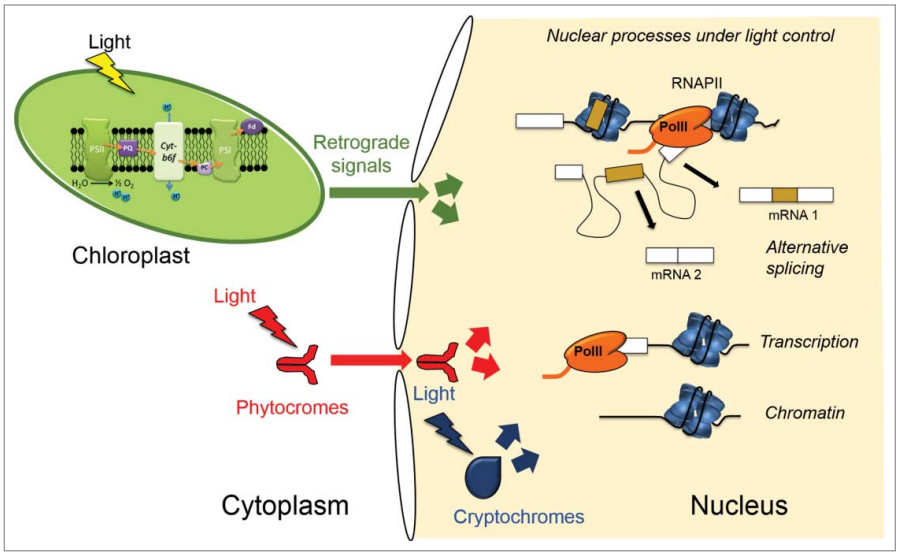

Figure 1. Scheme of light triggered signals affecting different aspects of nuclear gene expression. Photoreceptor proteins like phytochromes and cryptochromes absorb specific light wavelengths and transduce these signals into chromatin, transcriptional and post-transcriptional changes (see text for further details). The chloroplast is also able to act as a light sensor. Chloroplast derived retrograde signals, longer known for transcriptional regulation, are also able to regulate alternative splicing decisions in the nucleus.

in response to light by the different pathways, the role of photoreceptor proteins, plastid signals, and the possible interactions between them.

The chloroplast and the sensitivity of the photosynthetic mechanisms make this organelle ideal for the integration of different signals,[33] not only from the environment, but also derived from the different tissues, developmental and nutritional states of plants. Besides the chloroplast retrograde signals derived from the redox state of the photosynthetic electron transport chain components, and those related to ROS, other retrograde signals related to chloroplast biogenesis have been studied:[25,28] tetrapyrroles,[30] those linked to thioredoxins,[62,63] and other mechanisms.[64,65] Sugars produced by photosynthesis, besides being the main source of biochemical energy, are also sensed as signals in the plant cell.[66,67] The interaction of chloroplast signals with retrograde signals generated in mitochondria deserves further investigation.[68] We are just starting to understand the way in which the different pieces work together: which genes are regulated, which processes are affected (i.e., chromatin, transcription, splicing, translation), and the possible connections and cross regulations of the different layers (**Fig. 1**).

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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