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Shedding light on the chloroplast as a remote control of nuclear gene expression

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Plants rely on a sophisticated light sensing and signaling system that allows them to respond to environmental changes. Photosensory protein systems -phytochromes, cryptochromes, phototropins, and ultraviolet (UV)-B photoreceptors- have evolved to let plants monitor light conditions and regulate different levels of gene expression and developmental processes. However, even though photoreceptor proteins are best characterized and deeply studied, it is also known that chloroplasts are able to sense light conditions and communicate the variations to the nucleus that adjust its transcriptome to the changing environment. The redox state of components of the photosynthetic electron transport chain works as a sensor of photosynthetic activity and can affect nuclear gene expression by a retrograde signaling pathway. Recently, our groups showed that a retrograde signaling pathway can modulate the alternative splicing process, revealing a novel layer of gene expression control by chloroplast retrograde signaling.

Light and Plants

Plants utilize light to sustain their life. As sessile organisms, in order to grow and develop successfully, plants have evolved extremely plastic adaptation and survival strategies. In this sense, light is a crucial factor for 2 reasons: it is the source of energy and it represents a rich source of information about plant surroundings. Plant strategies rely on a sophisticated light sensing and signaling system able to react to changes in the quantity, quality and duration of this environmental cue.[1] Photosensory protein systems have evolved to allow plants to monitor light and to regulate developmental processes of plant cells in response to light variations.

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Photosensor proteins are the phytochromes, cryptochromes, phototropins, and UV-B photoreceptors, whereby phytochromes mainly perceive red and far-red light wavelengths, and blue/UV-A light is perceived by cryptochromes and phototropins. Light perception by these photoreceptors triggers many biological processes by affecting gene expression. Besides the light signaling pathways involving the canonical photoreceptor proteins, the chloroplast, the organelle that carries out photosynthesis, has evolved ways to communicate to the nucleus. By using different mechanisms known as retrograde signaling pathways, the chloroplast is able to modulate nuclear gene expression.

Global gene expression is rapidly altered in response to light changes. Accumulated data suggest that light regulation can occur at many stages of gene expression. Light regulates the chromatin state,[2] transcription factor action,[3,4] translation,[5] and protein stability.[6] Among the multitude of steps that give rise to mature messenger mRNAs (mRNAs) and proteins, alternative splicing is a booster of transcript diversity, increasing the number of differential transcripts and protein isoforms a cell can produce from a single gene. In *Arabidopsis*, around 61% of multi-exonic genes encode pre-mRNAs that are alternatively spliced under normal growth conditions,[7] and light seems to drive alternative splicing regulation of several genes in plants as revealed by recent publications.[8,9] For example, Wu and colleagues[8] have shown that photoreceptor pathways regulate alternative splicing genome-wide in the moss *Physcomitrella patens*. More recently, we have demonstrated that chloroplasts are able to regulate nuclear alternative splicing in response to changes in the redox state of the photosynthetic electron transport components.[9] Here we summarize the results of the latest reports linking light to gene expression and alternative splicing modulation in plants.

Light Signals and Photoreceptor Proteins

Probably, the most dramatic process controlled by light in plants is photomorphogenesis. This includes all the developmental changes that take place during the first encounter of a growing seedling with light. When seedlings grow in darkness they are etiolated (yellowish, with closed cotyledons and long hypocotyls). Once exposed to light, they open their cotyledons and become photosynthetically competent and green, and hypocotyl elongation stops.[10] Light is perceived by distinct families of

photoreceptors that absorb, interpret, and transduce light-derived signals via distinct intracellular signaling pathways to generate a wide range of responses. Cryptochromes and phytochromes, which can localize in the nucleus, are involved in the control of light-regulated nuclear gene expression that ultimately leads to adaptive changes at the cellular and organismic levels.[3]

By the end of the 1990s, plant biologists had identified more than 100 individual genes whose expression is regulated by light via photoreceptor systems.[11,12] However, the dramatic developmental transitions during complex processes like seed germination and plant photomorphogenesis suggest that a much larger number of genes are involved in light control of plant development.[13] Consequently, enhanced by the advance of genome-wide technologies, it was shown that 20% of *Arabidopsis* and rice genomes are responsive to white light,[14] and this value rises to about 33% when tested using a customized microarray with ~9000 *Arabidopsis* expressed sequence tags (ESTs).[15]

The activation of photoreceptor proteins significantly affects transcription through signal transduction pathways and direct effects on transcription factors. Transcriptional regulation, post-translational modification and degradation of transcription factors are all important in the light-regulated control of development.[1] Light-mediated transcriptional control involves also chromatin remodeling. For instance, one of the cryptochromes (CRY2) associates with chromatin[16] and a phytochrome interacting factor (PIF3) associates with a histone deacetylase.[17] Moreover, photoreceptor proteins are also able to modulate alternative splicing. Recent report on *P. patens*[8] showed that alternative splicing is rapidly fine-tuned by light to modulate gene expression and reorganize metabolic processes in a way that might be dependent on red-light photoreceptors.

Even though the role of photoreceptor proteins in gene expression modulation by light is better understood, there are alternative ways for plants to sense light conditions and adjust their transcriptomes in response to these changes.

Retrograde Signals

Chloroplasts were once free living photosynthetic bacteria, and their gradual conversion to organelles has been accompanied by a dramatic reduction in genome size as a consequence of either loss or transfer of most of the endosymbiont genes to the nucleus. The right function of the plastid and the location of genes encoding chloroplast proteins in 2 different cellular compartments fosters coordination in the expression of the 2 different genomes, explaining why mechanisms ensuring fluid communication have evolved.[18,19] Signaling between chloroplasts and the nucleus is bidirectional.[20] Anterograde signaling involves flow of information from the nucleus to the organelle. In contrast, in retrograde signaling, information is transmitted from chloroplasts to the nucleus.[21] Retrograde signaling is important to inform the nucleus about the developmental and also the functional state of the chloroplast.[20,21]

Retrograde signaling defects that have been well-characterized include *g*enome *un*coupled (*gun*) mutants.[22] In these mutants, communication between chloroplasts and the nucleus is disrupted. Two main signaling pathways are affected in the *gun* mutants, both of them acting in the tetrapyrrole biosynthetic pathway. Despite this genetic evidence, the nature of the signal itself is still not well-understood.[21] Mg-protoporphyrin IX, a tetrapyrrole pathway intermediate, has been proposed as a retrograde signal.[23,24] However, recent studies have shown that the effect on nuclear gene expression in *gun* mutants is not due to the accumulation of this metabolite but, most likely, to perturbation of the tetrapyrrole biosynthetic pathway that may alter the redox state of the plastid, which would, in turn, act as a retrograde signal.[25]

Reactive oxygen species, which are byproducts of several organellar processes, can also modulate nuclear gene expression.[26] Seedlings grown in the light and treated with norflurazon (an inhibitor of carotenoid biosynthesis) show an increase in singlet oxygen ($^1O_2$) production and photo-oxidative stress in the chloroplasts. Concomitantly, expression of $^1O_2$-responsive marker genes increases in these seedlings,[27] suggesting that reactive oxygen species can act as retrograde signals. Recently, other examples of retrograde signaling molecules have been proposed. For instance, in the SAL1-PAP retrograde pathway, a phosphonucleotide that accumulates in response to drought and high light stress inside chloroplasts and mitochondria, was proposed to move from the chloroplast to the nucleus and to alter nuclear gene expression by affecting RNA metabolism.[28] Another example is related to a chloroplast envelope-bound plant homeodomain transcription factor that is activated by proteolytic cleavage and would be able to transmit multiple retrograde signals from the chloroplast to the nucleus.[29] Although several retrograde events have been reported to date, it has been proposed that a single metabolite may not always be enough to act as a retrograde signal. In contrast, a variety of metabolites (a metabolite signature) could generate a "signal" that does not require any further components than those already known.[21]

Photosynthesis plays a role in retrograde signaling. The redox state of the plastoquinone (PQ) pool, that transfers electrons from Photosystem II to the cytochrome b6f complex, works as a sensor of photosynthetic activity. The redox state of the PQ pool was suggested to modulate the expression of 2 cytosolic ascorbate peroxidase during excess light.[30] Interestingly, this mechanism of regulation through the PQ pool is also important under normal physiological conditions like in light and darkness fluctuations that happen during day and night transitions, as has been reported for the Lhcb locus and its transcriptional regulation.[31] Recently, our groups showed that the redox state of the PQ pool can also modulate alternative splicing, describing a novel level of gene expression regulation through retrograde signaling.[9]

Chloroplast and Nuclear Alternative Splicing

As pointed out, there is evidence that the chloroplast communicates its energy status to the nucleus. When considering the strategies used by the 2 organelles to mutually regulate gene expression a problem emerges: the chloroplast is an organelle of prokaryotic origin, without neither spliceosomes nor alternative splicing, whereas the nucleus possesses a genome that makes extensive use of alternative splicing,[7] giving rise to different mRNA variants, leading to proteins with different functions or

to the regulation of total levels of the protein expressed.[32-36] This might prompt the chloroplast to "communicate its needs" in a "language" that the nucleus "understands" to specify the appropriate mRNA isoforms or those to be favored or down-regulated in different light conditions. We were recently able to show that the chloroplast can, in fact, regulate nuclear alternative splicing. Among the analyzed alternative splicing events in our study, those for the genes encoding the Ser/Arg-rich (SR) proteins At-RS31 and At-SR30, and the splicing factor At-U2AF65, are the most affected.[9] In particular, alternative splicing events in *At-RS31* involve the intron at the conserved position in the first RNA recognition motif of this SR protein. These events are highly conserved from green single-celled algae to angiosperms implicating an ancient regulatory function.[37] We determined that alternative splicing of *At-RS31* is modulated by the chloroplast resulting in changes of *mRNA1* isoform levels.[9] This is the only *At-RS31* splice variant that is translated into the protein.[37] The other 2 transcript isoforms of *At-RS31* are *mRNA2*, that is actively degraded by nonsense-mediated mRNA decay (NMD),[36,38] and *mRNA3*, that is being accumulated in the nucleus.[9,38] Alternative splicing of *At-RS31* is affected in a way that *mRNA3* isoform is relatively more abundant in low light intensities and in dark, likely reducing At-RS31 protein levels in these conditions.[9] Similar alternative splicing patterns to those of dark treated seedlings are observed when DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) -a drug that blocks photosynthetic electron transport from Photosystem II (PSII) to plastoquinone, generating an increase in the oxidation of the PQ pool– is added under normal light conditions, indicating that a functional chloroplast with an active photosynthetic electron transport chain is needed to generate the *At-RS31* alternative splicing response to light.[9] Furthermore, by the use of DBMIB (2,5-Dibromo-3-methyl-6-isopropyl-p-benzoquinone) -that blocks electron transport downstream of the PQ pool, keeping it reduced- we observed an enhancement in the effect of light: upon DBMIB treatment, lower light intensities modulate *At-RS31* alternative splicing as higher light intensities do. Interestingly, this drug also showed effects in dark-incubated seedlings, arguing for a direct role as a quinone analog. Altogether, these results suggest the redox state of the PQ pool –the next electron transport component downstream of PSII- to be the main candidate to be linked to nuclear alternative splicing regulation.[9,39]

Retrograde signaling can occur between chloroplast (and mitochondria) and the nucleus inside the same cell. Interestingly, our data revealed as well the existence of a chloroplast-derived light triggered signal that is able to travel through the plant. This signal can be the same that acts in the leaves (at the intracellular level) or be a different one, but it is able to move from leaves to roots affecting the alternative splicing pattern of *At-RS31* in the nuclei of root cells (see **Fig. 1**).[9,39]

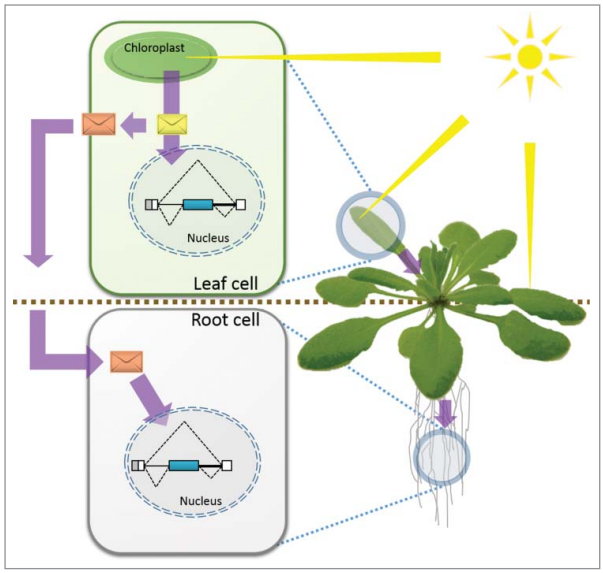

Figure 1. Plants use chloroplasts as light sensors that generate signals able to fine-tune nuclear gene expression. Light perceived in the chloroplast, the photosynthetically specialized organelle in the plant cell, triggers a signal that reaches the nucleus and affects alternative splicing, one important step in gene expression regulation able to generate several messages and proteins from a single gene. The light induced signal, or a derived one, is able to travel through the plant to non-photosynthetic tissue (i.e.: roots) affecting the alternative splicing there.

Perspectives

Despite all the advances in the understanding of retrograde signaling pathways, we are far from fully understanding the way they work and even farther from the comprehension of the interactions they might have with other cellular signaling mechanisms. Future research in this field might solve these questions if we are able to determine the components involved in these retrograde light signaling pathways and the nature of the signal(s). In particular, in the emerging field of alternative splicing regulation by retrograde signaling it would be fascinating to identify the nature of the mobile retrograde signal that affects the alternative splicing process in the roots[9] and also to determine whether mitochondria are able to modulate alternative splicing in a similar manner as chloroplasts. Finally, besides light variations, chloroplasts are also able to integrate information related to temperature, availability of CO_2, water and nutrients, plus information about their own developmental stage,[40] which turns them into very sensitive and smart remote controls for the regulation of nuclear gene expression at different levels and with long distance effects, since some of the retrograde signals are mobile and can communicate environmental fluctuations through the whole plant.[9,41,42]

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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