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Light intensity-dependent retrograde signalling in higher plants

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ABSTRACT

Plants are able to acclimate to highly fluctuating light environment and evolved a short- and long-term light acclimatory responses, that are dependent on chloroplasts retrograde signalling. In this review we summarise recent evidences suggesting that the chloroplasts act as key sensors of light intensity changes in a wide range (low, high and excess light conditions) as well as sensors of darkness. They also participate in transduction and synchronisation of systemic retrograde signalling in response to differential light exposure of distinct leaves. Regulation of intra- and inter-cellular chloroplast retrograde signalling is dependent on the developmental and functional stage of the plastids. Therefore, it is discussed in following subsections: firstly, chloroplast biogenic control of nuclear genes, for example, signals related to photosystems and pigment biogenesis during early plastid development; secondly, signals in the mature chloroplast induced by changes in photosynthetic electron transport, reactive oxygen species, hormones and metabolite biosynthesis; thirdly, chloroplast signalling during leaf senescence. Moreover, with a help of meta-analysis of multiple microarray experiments, we showed that the expression of the same set of genes is regulated specifically in particular types of signals and types of light conditions. Furthermore, we also highlight the alternative scenarios of the chloroplast retrograde signals transduction and coordination linked to the role of photo-electrochemical signalling.

Introduction

Semiautonomous plastids originated from the engulfment of a free-living photosynthetic bacterium by a eukaryotic cell ca. 1.6 billion years ago (Biello, 2012). During the post-endosymbiotic evolution of chloroplasts most of the genes encoded by this bacterial ancestor were transferred to the host nuclear genome. The plastid genomes of current land plants encode only 60–200 proteins (Timmis et al., 2004; Bock, 2007; Eckardt, 2011), whereas the number of proteins in the chloroplast is estimated to be between 2000 and 4000 (Eckardt, 2011). Chloroplast multiprotein complexes, required to build up a fully functional chloroplast, are mosaics of subunits encoded and synthesised within the organelle itself (Rogalski et al., 2008a,b) as well as subunits encoded by genes in the nucleus, translated in the cytosol, and post-translationally imported into the chloroplasts (Bedard and Jarvis, 2005; Kleine et al., 2009). A total of 1750 different chloroplast proteins have been identified so far, and assigned to one or more of the three compartments: stroma (~344 proteins), thylakoids (~400), and envelope membranes (~400) (Ferro et al., 2010; Armbruster et al., 2010). The location of the genes encoding the chloroplast proteins in the different cellular compartments implies the existence of molecular and physiological mechanisms that coordinate the nuclear and plastid gene expression to maintain plastid and cellular functions under different developmental stages of the cell and various environmental conditions (Inaba, 2010). Signalling between chloroplasts and the nucleus is bidirectional.

In anterograde regulation, nuclear-encoded regulators are able to adjust the expression of nuclear-encoded genes and plastid-encoded genes for adequate plastid development and functioning within a particular cell type (Pesaresi et al., 2009; Kleine et al., 2009; Jung and Chory, 2010). For example, when a seedling first encounters light its plastids differentiate from proplastids or etioplasts to chloroplasts. Nuclear-encoded proteins are required for chloroplast DNA replication, transcription, translation and proper arrangement of photosynthetic machinery in developing thylakoid membranes (Jung and Chory, 2010). Anterograde pathway mutants that are defective in the import of nuclear-encoded proteins to the chloroplasts exhibit pale-green, albino or embryo-lethal phenotypes (Jarvis, 2008; Inaba and Schnell, 2008). Once chloroplast development is achieved, the activation of the plastid-encoded

Abbreviations: EEE, excess excitation energy; GSH and GSSH, reduced and oxidised glutathione forms; NPQ, nonphotochemical quenching; PCD, programmed cell death; PET, photosynthetic electron transport; PQ, plastoquinone; PSI and PSII, photosystems I and II; ROS, reactive oxygen species; SAA, systemic acquired acclimation; SAR, systemic acquired resistance.

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gene expression system is also regulated by the nucleus, at several levels: transcription of plastid DNA, transcript editing, maturation and processing, translation of plastid-encoded proteins, and post-translational events (Chatterjee et al., 1996; Kleine et al., 2009).

In retrograde signalling plastids activate signalling cascades that pass through the chloroplast envelope and the cytoplasm, enter the nucleus and finally regulate nuclear gene expression, mainly at the transcriptional level. The absence of functional chloroplasts, genetic defects in the plastid protein (e.g. the *ppi2-2* mutant), chemical (e.g. norflurazon, lincomycin) and physical (e.g. high light, low temperature) treatments can repress or deregulate the light-stimulated expression of nuclear-encoded genes, e.g. genes encoding the light-harvesting chlorophyll a/b binding protein (LHC) and Rubisco small subunit (RbcS) (Mochizuki et al., 2008; Jung and Chory, 2010; Pfannschmidt, 2010). The plastid-to nucleus retrograde signals are dependent on the developmental and functional stage of plastids. Firstly, chloroplast biogenic control of nuclear genes during early plastidial development engages the signals related to photosystems and pigment biogenesis. Secondly, chloroplast operational control of nuclear genes is associated with signals induced in the mature chloroplast to acclimate plants to fluctuating light conditions. Signals are originate from redox changes in the photosynthetic electron transport (PET) carriers, reactive oxygen species (ROS), ROS-induced processes and metabolite biosynthesis, e.g. sugars, salicylic acid, glutathione and from dissipation of absorbed light energy as a heat. Thirdly, chloroplast degradational control of nuclear genes during leaf senescence, involves signals mainly from degradation of Rubisco and remobilisation of reduced nitrogen to other parts of the plant (Pogson et al., 2008; Pfannschmidt, 2010). The retrograde signals can also be differentiated based on the place and time of their origin including: specific proteins and ROS that are able to direct nuclear gene induction/suppression and indirect signals, i.e. intermediates of carotenoid and tetrapyrrole biosynthesis, ROS-related processes, redox cascades in photosynthesis and metabolite pool changes (Kleine et al., 2009). The types of signals can also be distinguished according to distance scale, time and their target place of action: the short distance intracellular and long distance intercellular retrograde signalling can be considered (Karpiński and Szechyńska-Hebda, 2010; Szechyńska-Hebda et al., 2010; Karpiński et al., 2003).

According to current knowledge, recent developments and understanding in the field of plastid retrograde signalling, in this review we attempt to answer the following questions: What are the main sources and/or triggers of retrograde signals at different light intensities?, How are they dependent on the developmental stage of chloroplast? How do the signals pass the chloroplast envelope?, What redox retrograde signalling pathways interact with one another and what ROS scavenging enzymes are involved in this interaction in particular types of signals and types of light conditions? Moreover, we highlight the alternative scenarios of plastid–nucleus signal transduction linked to the role of the intra- and intercellular photo-electrochemical signalling and redox reactions induced by excess excitation energy (EEE).

Developmental- and light-intensity-dependent retrograde signalling

Plastids produce different signals at different stages of their development to optimise light harvesting and CO_2 fixation for growth within all developmental phases: from juvenile to vegetative and from vegetative to reproductive. On the other hand, light in natural environments constantly fluctuates. Changing cloudiness initiates both the high-light and the low-light signals in the time scale of minutes and hours, whereas the movements of leaves in the wind initiate even more frequent light changes. Acclimation strategies must concomitantly meet the challenges of light acclimation in the range from darkness to very high light in short- and long-term durations (Grieco et al., 2012). Therefore, chloroplast signals related to developmental requirements must be integrated with signals dependent on the actual light environment to match the current status of the plastids and to ensure the optimisation of cell/plant functioning.

Signals triggered by plastid biogenesis

In complete darkness, seedlings grow heterotrophically on seed reserves in the absence of chlorophyll and the functional chloroplasts, thus realising a developmental programme known as skotomorphogenesis. However, a substantial number of photosynthetic proteins are already present in the etioplasts, including ATPase, Rubisco, Cyt b_6f, NADPH:Pchlide oxidoreductase (POR) and individual subunits of the photosystems (Kanervo et al., 2008). Dark-grown seedlings also accumulate the chlorophyll precursor protochlorophyllide (Pchlide) (Mochizuki et al., 2010; Cheminant et al., 2011). Once the etiolated seedlings reach the light, the enzyme POR is photoactivated and catalyses the conversion of Pchlide to chlorophyllide, which is subsequently esterified to give chlorophyll (Cheminant et al., 2011). Moreover, a large number of additional photosynthetic proteins accumulate rapidly in 24 h and the seedlings undergo photomorphogenic development of chloroplasts.

Despite the fact that plastid biogenic regulation seems to be inseparable from light signals, recent findings suggest that the plastid-to-nucleus signalling that is related to their development and light-signalling can be independent or plastid signals can affect retrograde light signalling (Ruckle et al., 2012). The seedlings' shift from a very low light of 0.5 $\mu mol\, m^{-2}\, s^{-1}$ to a light intensity of 60 $\mu mol\, m^{-2}\, s^{-1}$ significantly changed the expression of 6424 genes. In seedlings treated and untreated with lincomycin (a light-independent inhibitor of chloroplast biogenesis), half of the light-regulated genes were also significantly regulated by the plastid, and 680 genes were significantly regulated only by the lincomycin treatment. Therefore, the integration of light and plastid signalling optimises chloroplast biogenesis and function by tailoring gene expression to both a particular degree of chloroplast function and the particular light environment. Forward genetic screens have identified several protein components of the biogenic control of plastid development and the light-dependent retrograde signalling pathways. One of them, GUN1 (*GENOMES UNCOUPLED1*), encodes a nucleic acid-binding, pentatricopeptide repeat (PPR) protein (Koussevitzky et al., 2007) acts inside the chloroplast as a switchboard of the signalling pathways: the tetrapyrrole intermediates (particularly Mg protochlorophyllide IX), chloroplast translation machinery (Koussevitzky et al., 2007; Cottage et al., 2010), and the redox state of PET (Inaba, 2010; Sun et al., 2011). Recently, the role of GUN1 in the mediation of plastid signals was strengthened by evidence of its association with impaired RNA editing (Koussevitzky et al., 2007; Kakizaki et al., 2012). A dysfunctional NAD(P)H dehydrogenase (NDH) complex was suggested to be mainly responsible for the direct generation of plastid signals originating from the deregulation in the cyclic electron transport around PSI and over-reduction in the stroma (Peng et al., 2011). Alternatively, the global impact on RNA editing, rather than impaired RNA editing of specific transcripts, may be important for plastid signalling. Next, plastid signals trigger a proteolytic cleavage of the envelope-bound plant homeodomain transcription factor PTM. Afterwards the N-terminal fragment of PTM is transmitted to the nucleus and activates the expression of the transcriptional regulator ABSCISIC ACID INSENSITIVE 4 (ABI4) to repress the transcription of the *LIGHT HARVESTING COMPLEX B* (*LHCB*) (Sun et al., 2011). Koussevitzky et al. (2007) suggested that ABI4 plays a central