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Photosynthetic light reactions: integral to chloroplast retrograde signalling

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Chloroplast retrograde signalling is ultimately dependent on the function of the photosynthetic light reactions and not only guides the acclimation of the photosynthetic apparatus to changing environmental and metabolic cues, but has a much wider influence on the growth and development of plants. New information generated during the past few years about regulation of photosynthetic light reactions and identification of the underlying regulatory proteins has paved the way towards better understanding of the signalling molecules produced in chloroplasts upon changes in the environment. Likewise, the availability of various mutants lacking regulatory functions has made it possible to address the role of excitation energy distribution and electron flow in the thylakoid membrane in inducing the retrograde signals from chloroplasts to the nucleus. Such signalling molecules also induce and interact with hormonal signalling cascades to provide comprehensive information from chloroplasts to the nucleus.

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Introduction

Chloroplasts are sensitised to environmental changes, allowing them to protect the photosynthetic apparatus and maximise photosynthetic efficiency despite fluctuations in light, temperature and other potential stress factors. By extension, changes in photosynthetic machinery encode information about changes in prevailing environmental conditions. This makes the illuminated chloroplast an ideal signalling hub for regulating changes in nuclear gene expression (NGE) that are required for acclimation to the new environment. The importance of functional chloroplasts in retrograde signalling is well established, but the network of signalling components and mechanisms remains unestablished and widely debated. There are many different concepts that are currently considered to be the major components. Some examples include the plastoquinone (PQ) pool redox state as one of the oldest signalling models [1–3], which also has novel interpretations [4], as well as energy [5], metabolite [6] and sugar signalling [7], chlorophyll and carotenoid metabolism [8,9,10,11••,12], reactive oxygen [13,14], and others. Specific retrograde signalling pathways from chloroplasts to the nucleus have likewise been assigned under various environmental stress conditions (for example [15,16]), and integrated plastid signalling networks have been postulated [17,18].

We will not review these many processes and pathways, but instead we focus on the central role of photosynthetic light reactions in the instigation of chloroplast retrograde signalling networks in plants through environment- or metabolism-induced shifts in energy balance within the photosynthetic electron transfer chain (PETC). The energetic state of PETC reflects either the functional balance between photosystem II (PSII) and photosystem I (PSI), or the balance between the photosynthetic light reactions, which convert light to chemical energy, and the energy consumed by metabolism. Signalling based on sensing the energetic state of PETC provides a perfect mechanism to control growth, development and stress responses according to the energetic state of photosynthetic metabolism. The photosynthetic light reactions are, however, strictly and dynamically regulated to minimise the changes in PETC balance upon changes in the light environment. Herein lies a paradox; signalling is based on unbalanced PETC, but balance is actively maintained in the midst of fluctuating environmental factors. It is not well understood how the regulation of photosynthetic light reactions interacts with the signalling cascades initiated from the chloroplast or what is the impact of regulation of the photosynthetic machinery for the signalling.

Current progress in understanding the regulation, assembly and damage of the photosystems has paved the way to studying the effects of specific disturbances in photosynthetic light reactions on the induction of retrograde signalling from chloroplasts to the nucleus. Perturbance in the photosynthetic apparatus as a response to environmental changes can be traced from the thylakoid-embedded electron transfer chain, to modifications in the metabolic status of the chloroplast stroma and even of the cytosol, and it is likely the interactions of various signals eventually relay the information to the nucleus for acclimation of the plant to prevailing conditions. This review will focus on recent progress towards defining signals that are emitted from the photosynthetic apparatus during environmental fluctuations, and how regulation of photosynthetic energy distribution and electron transfer mechanisms impact retrograde signalling pathways.

Failure to maintain redox balance in the photosynthetic electron transfer chain results in retrograde signalling

The fluency of electron flow in the PETC is defined by the redox state of the electron carriers, namely PQ, plastocyanin (PC) and redox components on the stromal side of PSI. Light-induced development of trans-thylakoid proton gradient (ΔpH) is crucially important for balanced function of the PETC and is highly dependent on the proton gradient regulation (PGR5) protein [19]. Thylakoid ΔpH controls the rate of electron flow via the Cyt b_6f complex [19,20] and induces dissipation of excess excitation energy as heat (NPQ) via the PSBS protein [21] (for review of integrated regulation, see [22]). Changes in environmental conditions transiently alter the redox balance in the PETC with consequences on the activation, inhibition and deactivation of the thylakoid protein kinases STN7 and STN8, and possibly also the respective phosphatases TAP38/PPH1 and PBCP, in order to rapidly re-establish the redox balance of PETC [23,24•]. In general, the ΔpH-dependent mechanisms maintain the balance between light reactions and energy-using stromal metabolism, while thylakoid protein phosphorylation maintains balance between PSII and PSI. However, recent evidence shows that phosphorylation-based increase in PSI excitation can function in thermal dissipation of excess energy [25••], demonstrating that phosphorylation also plays a part in maintaining the balance between the light reactions and metabolic reactions [23,24•,25••].

The biophysical and biochemical mechanisms that regulate photosynthetic energy transduction do not buffer all modifications in the energy state of the PETC. As a result, changing energy states cause a number of effects, such as the production of reactive oxygen species (ROS) and electrophilic by-products of oxidation of organic molecules, known as reactive electrophile species (RES) (discussed below), as well as inhibition of PSII activity through damage to the D1 reaction centre protein (for reviews, see [26,27]). PSI is also susceptible to photoinhibition in over-reducing conditions through damage to the iron-sulphur clusters in the PSI core (reviewed in [28]). Photoinhibition of PSI is a relatively irreversible phenomenon induced by ROS production, and recent evidence suggests that the more frequently-occurring and rapidly-repaired photoinhibition of PSII actually functions as a protection mechanism against PSI photoinhibition [29]. Products resulting from the failure to effectively maintain PETC balance, including ROS, RES and their targets of 'photodamage,' are recognised as signal components by which the chloroplast can transmit information about environmental stress conditions to the wider cell and induce long term acclimation responses through regulation of NGE [11••,14,30,31]. These messages are likely integrated with other information derived from the levels of photo-assimilated carbon, the abundance of metabolic cofactors and hormones, and from ROS and RES produced in other organelles, to send a cohesive and detailed message to the nucleus. The progressive redefinition of 'chloroplast retrograde signalling' as the cell's reaction to specific combinations of metabolites and stress-related side products, via reactions initiated by photosynthesis, is a concept that is gaining popularity in plant research [32,33,34,35••,36]. It is reasonable to assume that this type of complex signal from the chloroplast provides a feed of information regarding the current cellular status that is not limited to stressful conditions, but operates continuously. This is pertinent because plants must constantly assess their allocation of resources between growth and defence strategies, and adjust to changing situations by altering NGE (Figure 1).

The importance of energy distribution to PSI and PSII as a component of chloroplast signalling has been shown through analyses of changes in NGE when energy balance is disrupted through artificial light conditions ('State I' and 'State II' light: [37–39]) or chemicals that block electron flow (DCMU, DBMIB: for example, [40]). Under natural conditions, PETC energy balance is controlled by cooperation of numerous regulatory mechanisms that intersect and impact each other in ways that are slowly becoming understood. The 'state of the art' understanding of the regulation of photosynthetic electron transfer upon changes in environmental conditions is currently undergoing major revision, and this impacts our understanding of PETC balance in NGE signalling. For example, adjustments to the harvesting and distribution of light energy to the two photosystems, with concomitant changes in organisation of thylakoid protein complexes, is now known to maintain the excitation balance between PSII and PSI upon changes in light intensity. The mechanism is required to keep functional balance between PSII and PSI in low light conditions (reviewed in [22]), but under certain stress conditions it can also enhance excitation energy transfer to PSI where it can be safely dissipated [23,24•,25••]. Another example is the management of lumen acidification and the trans-thylakoid ΔpH, which modulates NPQ via thermal dissipation of absorbed energy from the light-harvesting antennae [41]. NPQ is required, but not sufficient, to maintain optimal oxidation of the PQ pool upon rapid increase in light intensity, and the role of ΔpH-dependent control of Cyt b6f in optimising the oxidation state of PSI electron donors is increasingly appreciated [42•] (Tikkanen et al., in revision).

PSII is not the only reducer of the PETC, and PSI not the only oxidiser, as cyclic and light-independent reduction