



Metabolites and chloroplast retrograde signaling

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Intracellular signaling from chloroplast to nucleus followed by a subsequent response in the chloroplast is called retrograde signaling. It not only coordinates the expression of nuclear and chloroplast genes, which is essential for chloroplast biogenesis, but also maintains chloroplast function at optimal levels in response to fluxes in metabolites and changes in environmental conditions. In recent years several putative retrograde signals have been identified and signaling pathways have been proposed. Here we review retrograde signals derived from tetrapyrroles, carotenoids, nucleotides and isoprene precursors in response to abiotic stresses, including oxidative stress. We discuss the responses that these signals elicit and show that they not only modify chloroplast function but also influence other aspects of plant development and adaptation.

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What is retrograde signaling?

Chloroplasts of higher plants are not only responsible for photosynthesis, but also for the synthesis of many essential compounds, such as fatty acids, amino acids, phytohormones and secondary metabolites. Thus chloroplasts are essential for the viability of plants. Many chloroplast functions are regulated by nuclear factors; this control is referred to as anterograde control or signaling. Conversely, changes in the developmental or metabolic state of chloroplasts can evoke massive changes in the expression of nuclear genes, some of which directly affect chloroplast function. This process is called retrograde signaling [1–3]. Chloroplast retrograde signaling not only coordinates the expression of nuclear and chloroplast genes, which is essential for chloroplast biogenesis, but also maintains chloroplast function at optimal levels in response to fluxes

in metabolites and changes in environmental conditions [1–3]. Other signals arising in the chloroplast such as some phytohormones that elicit responses elsewhere in the cell, are usually not considered to be retrograde signals.

Since the concept of chloroplast retrograde signaling was originally conceived nearly 40 years ago [4], different types of retrograde signaling pathways have been defined based on the sources of the corresponding signals. Retrograde signals can largely be grouped into two categories: biogenic control and operational control signals [5]. The biogenic retrograde signals regulate early chloroplast biogenesis as a seedling shifts from a heterotrophic to a photoautotrophic lifestyle. Such knowledge has been derived primarily from studies that used herbicides which inhibit organelle function and development [6]. In contrast, operational signals are important for the normal function of chloroplasts in mature plants. The ‘operational’ retrograde signals from mature photosynthesizing chloroplasts can regulate nuclear genes to alter photosystem stoichiometry or to induce stress responses [5].

Originally, four distinct putative chloroplast retrograde signaling pathways have been recognized based on the sources of the signals. They include tetrapyrrole biosynthesis, chloroplast gene expression, chloroplast redox homeostasis and reactive oxygen species (ROS) [1,2]. In addition to these classical pathways several novel retrograde signaling pathways have been recently reported. These findings indicate that many metabolic pathways can act as potential sources of retrograde signals during different developmental stages of plants or upon different stress responses. More importantly, unlike the previously identified signals generated during artificial conditions, these novel signaling molecules were identified during physiologically relevant responses to adverse growth conditions such as drought or high light (HL). Here, we will review novel metabolite retrograde signaling pathways defined in recent years and summarize their diverse functions in plant development and adaptation.

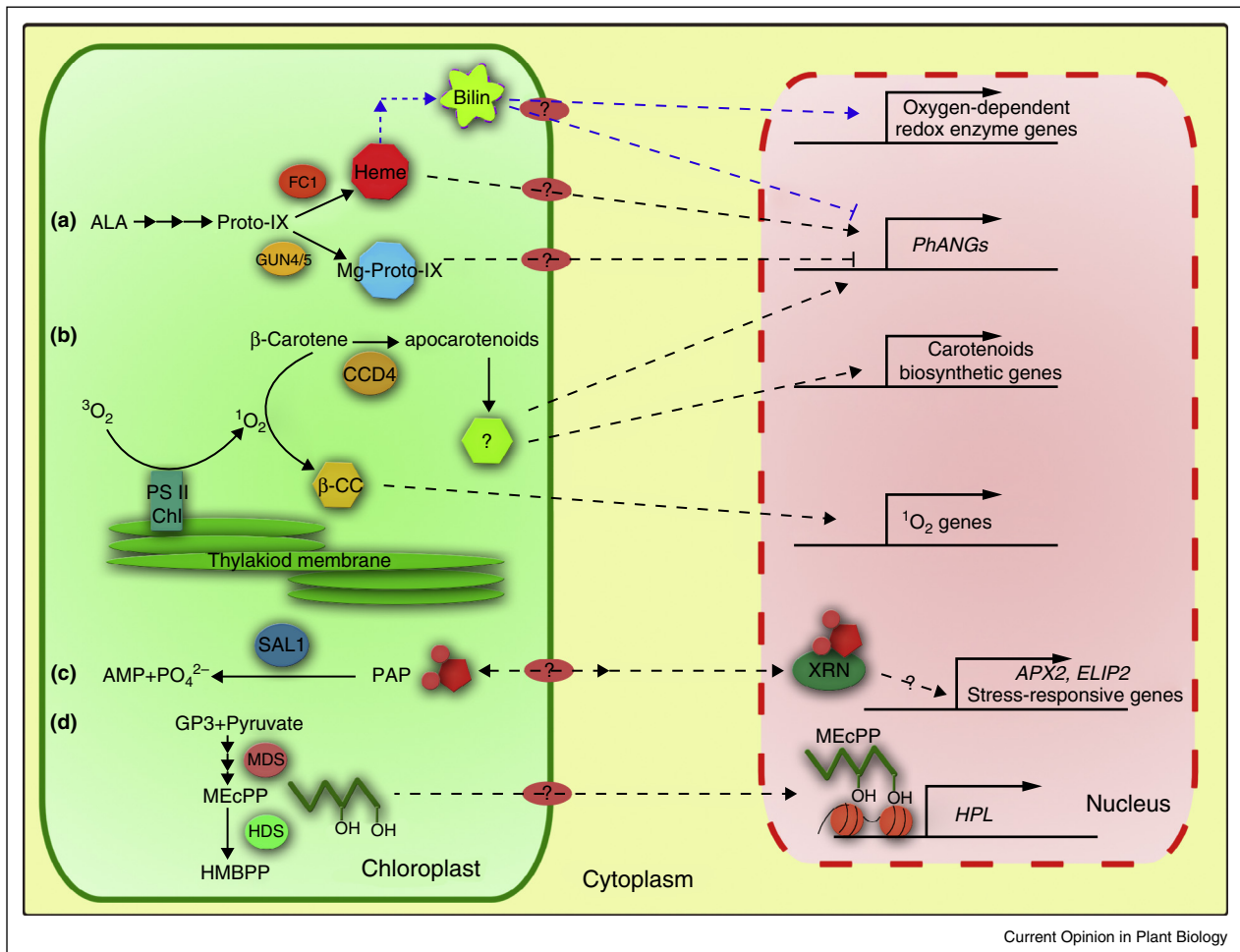
Tetrapyrrole signaling

Support for tetrapyrrole involvement in retrograde signaling came first from studies on the expression of nuclear genes of *Chlamydomonas reinhardtii* (*C. reinhardtii*) [7–9]. However, major insights arose from the analysis of *genome uncoupled* (*gun*) mutants of *Arabidopsis*. Wild-type plants grown on norflurazon (NF) expressed *Lhcb* (the gene encoding the chlorophyll a/b binding proteins of photosystem II) in lower amounts due to photo-bleaching of chloroplasts whereas *gun* mutants retain high levels of *Lhcb* expression under the same conditions, suggesting

disruption of retrograde signaling [6]. Four mutants (*gun2-gun5*) were shown to have lesions in enzymes involved in tetrapyrrole biosynthesis [10–12]. Analysis of *gun2-5* suggested that Mg-Proto IX, the first committed chlorophyll precursor might act as a negative retrograde signal to regulate nuclear gene expression [7–9]. However, the role of Mg-Proto IX in retrograde signaling after NF treatment was seriously questioned in later reports based on a lack of correlation between Mg-Proto IX levels and *Lhcb* gene expression [13,14].

gun6 is a gain-of-function mutant overexpressing the conserved chloroplast ferrochelatase1 (FC1, heme synthase). Increased flux through the heme branch of the tetrapyrrole biosynthesis pathway increases the expression of *PhANGs* (photosynthesis-associated nuclear genes) in the *gun6* mutant, suggesting that heme acts as a positive retrograde signal to regulate nuclear gene expression [15*] (Figure 1). Compared to Mg-Proto IX, heme appears to be a more likely candidate molecule for retrograde signaling, in part because heme is known to be

Figure 1



Metabolic retrograde signaling pathways. **(a)** The tetrapyrrole intermediates are involved in retrograde signaling. The plastid ferrochelatase 1 (FC1, heme synthase) is involved in the heme branch of tetrapyrrole biosynthesis. Heme acts as a positive regulator of *PhANGs* but the exact mechanism by which this compound reaches the nucleus and the nuclear components involved in heme signaling are unknown. In *C. reinhardtii*, bilins are also generated to regulate nuclear gene expression. GUN5 (H subunit of Mg-chelatase) and GUN4 (binding the substrate and product of the reaction catalyzed by the Mg-chelatase and activating the Mg-chelatase) are involved in the biosynthesis of Mg-ProtoIX from the chlorophyll branch of tetrapyrrole biosynthesis. Mg-ProtoIX might negatively regulate the expression of *PhANGs*. **(b)** The carotenoid oxidation products are involved in retrograde signaling. One product of the $^1\text{O}_2$ oxidation of carotenoids, $\beta\text{-CC}$, may act as a second messenger involved in the $^1\text{O}_2$ signaling pathway in plants. Carotenoid oxidation can also occur *in vivo* through CCD4 to generate apocarotenoids. An unknown apocarotenoid-derived signal regulates the expression of *PhANGs* and carotenoid biosynthetic genes. **(c)** SAL1-PAP signaling pathway. Plant stress triggered by drought or high light inhibits the activity of SAL1 and enhances the accumulation of PAP in the plastid. PAP is transported to the nucleus by unknown mechanisms and inhibits XNR activities, thereby inducing gene expression associated with stress responses. **(d)** A precursor of isoprenoids, MEcPP, derived from the MEP pathway for isoprenoid biosynthesis in the chloroplast, is induced by stress and functions as a sensor and communication signal to the nucleus where it induces selected stress-responsive genes through alteration of nuclear architecture and functional dynamics.

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