Redox Regulation of Photosynthetic Genes

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Summary

Chloroplasts are the sites of photosynthesis and several other major biosynthetic pathways. A large number of proteins, comprising of products from both chloroplast and nuclear genes, participates in the biogenesis and function of the mature organelle. The dual genetic origin of the photosynthetic apparatus and other chloroplastidic supramolecular complexes requires mechanisms of intracellular integration, involving mutual exchange of information between the chloroplast and nucleo-cytoplasmic compartments. An important part of the signaling network that integrates cellular gene expression is the functional two-way connection between the photosynthetic apparatus and the gene expression machineries, both inside and outside the chloroplast. Apart from its primary role in light energy capture, photosynthetic electron transport acts as a source of redox signal(s) that initiates signal transduction events and gene expression responses at various levels and intracellular locations. The photosynthetic apparatus can adapt to environmental changes, including those in light quality and intensity,

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with associated changes in redox state of electron carriers. Photostress is known to accelerate deleterious effects that are part of normal oxygenic photosynthesis, i.e. degradation and replenishment of (reaction center) proteins. This inherent feature of photosynthesis requires a balanced supply of gene products in response to redox state. Accumulating evidence suggests that both transcriptional and posttranscriptional steps in gene expression are subject to control by photosynthetic electron flow, and gene expression both inside and outside the chloroplast is affected. Identified key mechanisms that provide regulatory feed-back connections between photosynthetic electron transport and gene expression are the phosphorylation and SH-group redox control of proteins. Despite this unifying picture, it has become increasingly clear, however, that the details can be quite variable, suggesting a possible existence of multiple and/or split signal transduction pathways.

I. Introduction

A. The Dual Role of Photosynthetic Electron Transport

Redox (reduction-oxidation) chemistry plays a fundamental role in living organisms. According to the Nernst equation (Fig. 1), the redox potential of a cellular electron carrier is given by the relative concentrations of its reduced versus oxidized forms. Metabolic changes in their concentrations will shift the redox potential, which can sequentially affect the redox state of a second, third, fourth etc. electron carrier connected in series. The power of biological electron transfer chains is highlighted by the photosynthetic apparatus, which consists of four multisubunit pigment-protein complexes that act together in the photoproduction of oxygen, ATP, and NADPH—the basis for autotrophic plant growth and, in general, most of life on earth (for review, see Simpson and von Wettstein, 1989; Bogorad and Vasil, 1991; Pakrasi, 1995; Allen and Williams 1998).

In addition to capture of light energy, a second function can be assigned to photosynthetic electro-chemistry. The efficiency of photosynthesis is dependent on the environmental conditions (most notably light intensity, quality and temperature), leading to both short and long-term responses.

Abbreviations: APX – ascorbate peroxidase; bromanil – tetrabromo-1,4-benzoquinone; CCCP – carbonal cyanide-m-chlorophenylhydrazone; DBMIB – 2,5-dibromo-3-methyl-6-isopropyl-1,4-benzoquinone; DCMU – 3-(3,4-dichlorophenyl)-1,1-dimethylurea; DCPIP – 2,6-dichlorophenolindophenol; DTT – dithiothreitol; FNR – ferredoxin-NADP reductase; GBF – G-box binding factor; GR – glutathione reductase; GS H – reduced dithiol form of glutathione; GSS G – oxidized disulfide form of glutathione; LH C – light-harvesting complex; NEP – nuclear-encoded plastid RNA polymerase; PE P – plastid-encoded RNA polymerase; PS I – Photosystem I; PS II – Photosystem II; PTK – plastid transcription kinase; ROI – reactive oxygen intermediate; SLF – sigma-like factor; SOD – superoxide dismutase

Resulting changes in the steady-state levels of reducing equivalents can affect the properties of many chloroplast proteins, as has been well-established e.g. for the Calvin cycle enzymes with known redox-regulated activity (Buchanan, 1991; Scheibe, 1991; Schürmann, 1995). Likewise, evidence has become available that plant gene expression—both inside and outside the organelle—can be modulated according to the energy state of the photosynthetic electron transport chain (Allen, 1993; Vener et al., 1998; Foyer and Noctor, 1999). Hence, in this respect the photosynthetic apparatus acts like a (photo)sensor, which by way of intermediate electron carriers initiates signal transduction pathways for downstream metabolic and/or gene regulatory responses.

B. Photosynthetic Redox Regulation of Gene Expression: How, When and Where?

Coupling of photosynthetic electron transport with mechanisms involved in both cellular maintenance and differentiation appears useful and necessary for several reasons: (i) The photosynthetic apparatus is

\[ E = E_m + \frac{RT}{nF} \cdot \ln \frac{[\text{ox}]}{[\text{red}]} \]

\[ E \] redox potential
\[ E_m \] midpoint (50%) potential
\[ R \] gas constant
\[ T \] abs. temperature
\[ n \] number of electrons
\[ F \] Faraday constant
\[ [\text{ox}] \] conc. of oxidized form
\[ [\text{red}] \] conc. of reduced form

Fig. 1. Concentration dependence of the redox potential.