Chapter 17

Redox Regulation of Chloroplast Gene Expression[#]

Sacha Baginsky*
Plant Science Institute, ETH Center, Swiss Federal Institute of Technology, Universitätsstr. 2, CH-8092 Zurich, Switzerland

Gerhard Link*
University of Bochum, Plant Cell Physiology & Molecular Biology, Universitätsstr. 150, D-44780 Bochum, Germany

Summary

The chloroplast is the most important biosynthetic compartment of a green plant cell, being the site of photosynthesis and aspects of carbon, sulfur, and nitrogen assimilation as well as other pathways. At the same time, the complex enzymatic machinery of the organelle is a key target for photooxidative stress. The chloroplast contains an evolutionarily conserved set of genes and a specially adaptable gene expression machinery that is in close physical proximity to the photosynthetic apparatus, i.e. the primary source of reactive oxygen species. This adaptability somehow links the rapid gene expression response to the activity status of photosynthetic electron transport and accompanying redox reactions. In this chapter, we address the following questions: (i) which plastid gene products are subject to redox control? (ii) which stage(s) of organellar gene expression are redox-controlled? and (iii) what are the mechanisms and mediators involved?

*Author for correspondence, email: sbaginsky@ethz.ch or gerhard.link@ruhr-uni-bochum.de
[#]This chapter is dedicated to Professor Achim Trebst on the occasion of his 75th birthday

B. Demmig-Adams, William W. Adams III and A.K. Mattoo (eds), Photoprotection, Photoinhibition, Gene Regulation, and Environment, 269–287.

I. Introduction

A. The Chloroplast – a Center for Sensing, Transmission, and Expression of Responses to Environmental Signals

In "green" eukaryotes, from unicellular algae to higher plants, the chloroplast is the intracellular site of photosynthesis (Buchanan et al., 2000; Aro and Andersson, 2001). It is a member of the plastid family, i.e. a cell-specific group of organelles comprising a number of differentiated forms, each with a specialized function. In a given plant species, all plastid types contain closed circular plasmid-type DNA molecules with essentially the same organization, but with different copy numbers. A typical higher plant plastid DNA molecule harbors the genes for complete sets of rRNAs and tRNAs for protein synthesis on the organellar ribosomes as well as genes for more than a hundred proteins (Bogorad and Vasil, 1991; Sugita and Sugiura, 1996). Considering the large number of more than 3,000 (mostly nuclear-encoded and imported) putative chloroplast proteins, as suggested by proteomics and genomics database analyses (Kleffmann et al., 2004), the coding capacity of the organellar DNA seems surprisingly small. One may ask why the plant cell invests at all in the effort of establishing a complete gene expression system inside the plastid compartment. According to current views and consistent with a considerable body of compelling data, at least part of the answer lies in the integration of the plastid into the regulatory network that determines the differentiation and activity state of the entire cell. This complex network is based on the integration of different genetic compartments within the plant cell, i.e. the plastid, the mitochondrion, and the nucleus, necessitating a concerted regulation of gene expression. This is immediately obvious for the nuclear-encoded plastid proteins, which—in addition to many proteins involved in photosynthesis and other metabolic reactions—include proteins and regulatory factors involved in organellar gene expression itself. Conversely, it has become increasingly clear that the physiological status of the chloroplast is signaled back to the nucleus in a retrograde fashion. Although the biochemical nature of such (a) plastid signal(s) is only beginning to emerge, it is easily envisaged that both the forward and retrograde communication mechanisms, that have evolved together during evolution, have overcome the need to retain a full extra genome with thousands of genes initially brought in by (an) ancient endosymbiont(s).

Despite the small (less than 3%) proportion of chloroplast proteins that are encoded by organellar genes, these proteins comprise a group of essential components in photosynthesis and carbon assimilation as well as in plastid gene expression. In fact, the very first proteins to be identified as organellar gene products were the large subunit of RubisCO and the D1 protein of the PS II reaction center – both functionally important plant proteins that rank amongst the most extensively studied chloroplast gene products (Bogorad and Vasil, 1991; Sugita and Sugiura, 1996). It is interesting to note that, despite the overall small proportion of organelle-encoded (vs. imported) plastid proteins, the ratio is much higher (almost 1:1) in the case of the photosynthetic proteins. This emphasizes the importance of having genes for photosynthetic proteins—and their expression – inside the organelle, where their expression can be tightly regulated by the activity status of the photosynthetic electron transport chain. This is an obvious advantage in a situation such as photooxidative stress where there is a need for rapid replenishment of reaction center proteins (and possibly other photosynthetic proteins as well) (Aro and Andersson, 2001; Demmig-Adams and Adams, 2002). The question is which of the organelle-encoded proteins are affected by photosynthetic signals, and to what extent, and at which stage(s) of gene expression does the response to photostress operate? Before we focus on these specific points, we will review the general principles of reduction-oxidation (redox) regulation of gene expression.

B. Redox Regulation of Gene Expression – a Universal Theme in Biology

Redox chemistry is a universal aspect of living organisms. As defined by the Nernst equation, the redox potential of an electron carrier depends on the relative concentrations of its reduced versus oxidized forms. Redox reactions involve the transfer of electrons

Abbreviations: APX – ascorbate peroxidase; bromanil – tetrabromo-1,4-benzoquinone; CCCP – carbonal cyanide-m-chlorophenylhydrazone; CDK – cyclin-dependent kinase; CK2 – casein kinase 2; cpCK2 – chloroplast casein kinase 2; DBMIB – 2,5-dibromo-3-methyl-6-isopropyl-1,4-benzoquinone; DCMU – 3-(3,4-dichlorophenyl)-1,1-dimethyl urea; DCPIP – 2,6-dichlorophenolindophenol; DTT – dithiothreitol; FNR – fumarate and nitrate reduction regulator; GSSG – oxidized disulfide form of glutathione; GSH – reduced dithiol from of glutathione; GSK – glycogen synthase kinase; MAPK – mitogen-activated protein kinase; IBZ – iodosobenzoic acid; NEM – N-ethyl maleimide; NEP – nuclear-encoded plastid RNA polymerase; PDI – protein disulfide isomerase; PEP – plastid-encoded RNA polymerase; PTK – plastid transcription kinase; ROS – reactive oxygen species; RRM – RNA recognition motif; SLF – sigma-like factor; SOD – superoxide dismutase