Chapter 19

The Role of Peroxiredoxins in Oxygenic Photosynthesis of Cyanobacteria and Higher Plants: Peroxide Detoxification or Redox Sensing?

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Summary

Peroxiredoxins (Prx) constitute a group of recently identified peroxidases that detoxify a broad range of peroxides in distinct subcellular compartments, including chloroplasts. They are ubiquitously expressed in all organisms, i.e. bacteria, fungi, and animals, as well as in cyanobacteria and plants, in which they frequently represent a considerable fraction of total cellular and organellar protein. At least seven *prx* genes are expressed in leaves of *Arabidopsis*. The gene products of four of them are targeted to chloroplasts. Five genes encoding (putative) Prx are found in *Synechocystis* sp. PCC 6803. Based on such circumstantial evidence, as well as biochemical analysis and observations on photosynthetic organisms with modified levels of Prx, it has been established that a subset of Prx plays a role in the context of photosynthesis. The conclusion is further strengthened by studies that showed a modulation of *prx* gene expression in response to photosynthetic activity. This chapter describes the properties of peroxiredoxins in general and focuses on the role of Prx in protecting the photosynthetic apparatus from oxidative damage and, possibly, in redox signaling in photooxygenic cells.

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I. Oxidative Stress

Many non-enzymatic as well as enzymatic reactions in cell metabolism involve the formation of radicals, reactive oxygen species (ROS), and reactive nitrogen species (RNS) (Patel et al., 1999; Foyer and Noctor, 2000; Janssen-Heininger et al., 2002). These highly reactive compounds are also implicated in signaling (Van Breusegem et al., 2001; Vranova et al., 2002; Neill et al., 2003). To prevent damage to cell structures, ROS and RNS levels need to be tightly regulated. A delicate antioxidant network, consisting of low molecular mass antioxidants and enzymes, suppresses the accumulation of these reactive and harmful intermediates under normal growth conditions. Defense against oxidative and radical damage is particularly crucial for photosynthetic organisms. Generation of singlet oxygen and H_2O_2 in PS II (Melis, 1999), of superoxide anion radicals by PS I, and of hydrogen peroxide during photorespiration (Foyer and Noctor, 2000) are examples for ROS production associated with photosynthesis. ROS production may proceed at high rates under certain unfavorable environmental conditions, such as excess light, low temperature, drought, and limited electron acceptor availability. High levels of ROS production are frequently associated with lipid peroxidation and initiation of radical chain reactions that may lead to membrane damage and destruction (Smirnoff, 1993; Rawyler et al., 2002).

A set of antioxidant metabolites and enzymes detoxify ROS, RNS, and lipid peroxides in the various cell compartments such as chloroplasts, cytosol, mitochondria, and peroxisomes (Noctor and Foyer, 1998). Prominent antioxidant enzymes are superoxide dismutases, ascorbate peroxidases, glutathione peroxidases, and catalases (Foyer et al., 1994; Baier and Dietz, 1998). In 1996, 1-Cys and 2-Cys peroxiredoxins were identified as new players within the antioxidant network of barley (Baier and Dietz, 1996; Stacy et al., 1996). Since then, peroxiredoxins have been cloned from various photosynthetic organisms, identified in proteomes, and characterized *in vitro* and *in vivo*. Many of these findings have been summarized in recent reviews (Dietz et al., 2002; Rouhier et al., 2002; Dietz, 2003a). Recent advancements concerning function, regeneration, and regulation of peroxiredoxins and their role in photosynthetic cells, including cyanobacteria, are the focus of this review.

Abbreviations: aa – amino acid; ABA – abscisic acid; *Apx2* – cytosolic ascorbate peroxidase gene; Cys – cysteine; Fd – ferredoxin *katG* – catalase-peroxidase; ORF – open reading frame; *PetE* – plastocyanin gene; Prx – peroxiredoxin (protein); *prx* – peroxiredoxin (gene or transcript); PS – photosystem; RNS – reactive nitrogen species; ROS – reactive oxygen species; SOD – superoxide dismutase; Trx – thioredoxin

II. Cyanobacteria as Model Organisms to Study Oxygenic Photosynthesis

Cyanobacteria are a remarkable group of phylogenetically old prokaryotic organisms that probably evolved up to 3.5 billions years ago (Schopf, 2000) and contribute about 40 % of the present-day global photosynthetic primary biomass production (Paerl, 2000). In evolutionary terms, cyanobacteria represent the link between heterotrophic bacteria and algae or higher plants (Fay, 1983). Cyanobacteria are characterized by their ability to synthesize chlorophyll *a* (Whitton and Potts, 2000) and perform oxygenic photosynthesis (Carr and Whitton, 1982), thus driving the switch from an anoxygenic to an oxygenic atmosphere and the development of complex eukaryotic life forms. Due to their considerable morphological diversity (Whitton and Potts, 2000) and metabolic flexibility (Vermaas, 2001), cyanobacteria are able to colonize virtually all terrestrial and aquatic habitats. Cyanobacteria lack the eukaryotic type of compartmentation. Thus, oxygenic photosynthesis, respiration, and nitrogen assimilation take place in the same compartment (Schmetterer, 1994; Vermaas, 2001). Moreover, most cyanobacteria contain two distinct and fully functional respiratory chains, one located in the cytoplasmic membrane and the other in the thylakoid membrane. The latter uses, in part, the same components as the photosynthetic electron transport chain implying a complex interrelationship between respiratory and photosynthetic electron transport.

Cyanobacteria were the first photosynthetic organisms with an oxygenic type of photosynthesis, utilizing water as electron donor and producing dioxygen as a by-product. Therefore, they are the most ancient organisms to have coped with the production of reactive oxygen species (ROS) as a result of incomplete reduction of molecular oxygen via electron transport processes. Cyanobacteria have evolved effective mechanisms to prevent large-scale ROS production, such as modification of their light harvesting antenna, evolution of state transitions, changes in the stoichiometry of PS II to PS I, excitation energy dissipation by carotenoids, and, of course, enzymes for the detoxification of inevitably formed ROS (Nishiyama et al., this volume). Since the redox state of the cell and the electron transport