

Chapter 14

Photosystem I and Photoprotection: Cyclic Electron Flow and Water-Water Cycle

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Summary

Cyclic electron transport around photosystem I has been proposed to play dual roles in the regulation of photosynthetic electron transport: down-regulating PS II and adjusting the ATP/NADPH ratio. Recent molecular genetics revealed that cyclic electron flow is essential for normal photosynthesis and growth. The water-water-cycle would also play a role similar to cyclic electron transport, in addition to the effective scavenging of reactive oxygen species generated in PS I. Though their rates of electron flux are lower than that of linear electron transport at steady state,

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these alternative electron flows are indispensable for acute responses to environmental changes and stress. Recent biochemical and molecular studies at the protein and gene level have clarified the components participating in the alternative electron transport. These new findings, including the dual functions of cyclic electron flow and the water-water cycle, and their respective roles in stress responses, are discussed in this chapter.

I. Introduction

The photosynthetic electron transport system is often regarded as a single chain of electron transfer. However, there are actually diverging and converging routes of electron flows around the central chain known as the 'Z-scheme' or 'linear electron transport chain'. These alternative routes of electron flow have been studied for some time, but their physiological functions are still a matter of debate. Among these alternative electron transport routes, cyclic electron transport around photosystem I (PS I) and the water-water cycle have been most intensively studied.

Cyclic electron flow around PS I was discovered by Arnon's group over 40 years ago (Tagawa et al., 1963). Reduced electron carriers in the stroma, such as reduced ferredoxin (redFd) and NADPH photoproduced in PS I, can donate electrons to the intersystem plastoquinone and thus move electrons in a cycle around PS I. Fd-dependent cyclic flow, which has been shown to be inhibited by antimycin A, is thought to be mediated by the putative enzyme Fd-quinone reductase (FQR). NAD(P)H-dependent cyclic flow has been shown to be mediated by NAD(P)H dehydrogenase (NDH), a homologue of the respiratory NADH dehydrogenase in mitochondria and bacteria, which has been referred to as Complex I in the respiratory electron transport. Recent molecular biological studies have characterized FQR and NDH, which are one of the main topics of this review. Advances in the study of cyclic electron transport as well as chlororespiration have been reviewed previously by Nixon (2000) and Peltier and Cournac (2002). Although transcriptional and post-transcriptional regulation of the expression of *ndh* genes have been used by many researchers as models for studying plastid gene expression, these studies are not included in this review. Heber and Walker (1992) have proposed that cyclic electron flow has dual

functions, as an inducer of proton gradient-dependent down-regulation of PS II as well as a generator of additional ATP required for the CO₂-fixation cycle.

The very same dual function can also be applied to the water-water cycle, in addition to the effective scavenging of reactive oxygen species (ROS) in chloroplasts. The photoreduction of dioxygen was discovered by Mehler (1951), and has been referred to as the Mehler reaction. Subsequently, the primary photoreducing product of dioxygen was identified as superoxide anion radicals (O₂⁻), that are photoproduced in PS I instead of reducing NADP⁺ via ferredoxin (Asada et al., 1974). The hydrogen peroxide generated via SOD-catalyzed disproportionation of superoxide radicals is reduced to water via a series of enzymatic reactions in the vicinity of the PS I complex, by the electrons derived from the oxidation of water in PS II. Because the electrons derived from water reduce dioxygen to water, this effective scavenging system of reactive, reduced species of oxygen (superoxide and hydrogen peroxide) in PS I has been referred to as the water-water cycle. Molecular mechanisms and functions of the water-water cycle have been reviewed by Asada (1999, 2000) in plants and Miyake and Asada (2003) in algae.

The primary physiological function of the water-water cycle is the rapid scavenging of ROS generated in PS I prior to their interaction with target molecules in chloroplasts as a means for protection against photoinhibition. In addition, like the cyclic electron flow around PS I, the water-water cycle does not produce net reducing equivalents but only ATP through the generation of a proton gradient across the thylakoid membranes. This common property is a reason why both cyclic electron flow and the water-water cycle are thought to have similar physiological functions.

ATP production and generation of a proton gradient across the thylakoid membranes may both play roles in the protection against photoinhibition. ATP production is important for the fine-tuning of the ATP/NADPH ratio for effective CO₂-fixation, the chloroplastic and cellular requirements for which might vary from one condition to another. The ATP/NADPH ratio required for the Calvin cycle turnover is 1.5 in C₃ plants. Whether the linear or non-cyclic electron transport supports this molar ratio has been a matter of serious discussion.

Abbreviations: AsA – ascorbate; DHA – dehydroascorbate; Fd – ferredoxin; FNR – ferredoxin-NADP reductase; FQR – ferredoxin-quinone reductase; GSH – reduced glutathione; GSSG – oxidized glutathione; MDA – monodehydroascorbate; NDH – NAD(P)H dehydrogenase; PS I – photosystem I; PS II – photosystem II; redFd – reduced ferredoxin; ROS – reactive oxygen species; SOD – superoxide dismutase.