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Review

Regulation of photosynthetic electron transport ☆

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ABSTRACT

The photosynthetic electron transport chain consists of photosystem II, the cytochrome b_6f complex, photosystem I, and the free electron carriers plastoquinone and plastocyanin. Light-driven charge separation events occur at the level of photosystem II and photosystem I, which are associated at one end of the chain with the oxidation of water followed by electron flow along the electron transport chain and concomitant pumping of protons into the thylakoid lumen, which is used by the ATP synthase to generate ATP. At the other end of the chain reducing power is generated, which together with ATP is used for CO_2 assimilation. A remarkable feature of the photosynthetic apparatus is its ability to adapt to changes in environmental conditions by sensing light quality and quantity, CO_2 levels, temperature, and nutrient availability. These acclimation responses involve a complex signaling network in the chloroplasts comprising the thylakoid protein kinases Stt7/STN7 and Stl1/STN7 and the phosphatase PPH1/TAP38, which play important roles in state transitions and in the regulation of electron flow as well as in thylakoid membrane folding. The activity of some of these enzymes is closely connected to the redox state of the plastoquinone pool, and they appear to be involved both in short-term and long-term acclimation. This article is part of a Special Issue entitled "Regulation of Electron Transport in Chloroplasts".

1. Introduction

The primary light-driven reactions of photosynthesis occur in the thylakoid membranes and are mediated by photosystem II (PSII) and photosystem I (PSI). The existence of these two distinct light reactions was first inferred from studies on the enhancement of the photosynthetic yield observed by illuminating algae with two light sources of far red and short-wavelength light [1]. The coupling of the two light reactions in a linear electron transfer chain forms the basis of the Z-scheme, which was proposed by Hill and Bendall 50 years ago and which still prevails today [2]. In this scheme, the two light reactions operate in series whereby electrons extracted from water by PSII are transferred through the plastoquinone pool, the cytochrome b_6f complex (Cytb_6f), and plastocyanin to PSI and ultimately to ferredoxin and $NADP^+$ to produce NADPH. These electron transfer reactions are coupled with proton pumping into the thylakoid lumen, and the resulting proton gradient is harnessed to produce ATP. Both ATP and NADPH fuel the Calvin-Benson cycle for CO_2 fixation and other assimilatory processes.

In recent years, significant advances have been made in our understanding of the composition, structure, assembly, and regulation of the major photosynthetic complexes PSII, PSI, with their associated antenna systems, Cytb_6f and ATP synthase. The structures of PSII [3], PSI [4] and Cyt b_6f [5,6] have been determined at atomic resolution providing new insights into the electron transfer routes within these complexes. They contain multiple subunits, pigments, and redox cofactors and are synthesized through the coordinate action of the nuclear and chloroplast genetic systems (for review, see [7,8]). Thus, some of the photosynthetic subunits are encoded by chloroplast genes and translated on chloroplast ribosomes while others are encoded by nuclear genes, synthesized on cytoplasmic ribosomes and imported into the chloroplast where they are assembled, together with their chloroplast-encoded partners, into functional complexes. Such a dual genetic origin of photosynthetic proteins necessitates a complex regulatory network for their coordinated expression and raises questions on why the plastid genetic systems have been maintained during evolution. Among several possible reasons, one hypothesis proposed by John Allen [9] is that plastid genomes have been maintained because of the dependence of their expression on the redox state of the electron transport chain. The localization of these two systems within the same cellular compartment would allow for rapid adjustment of gene expression to changes in environmental cues. Expression of the genes involved in photosynthesis is indeed regulated by several factors among which light is particularly important. Besides its role in light energy capture and conversion, the photosynthetic apparatus also acts as a sensor for changes in the light environment. In particular, the redox state of various photosynthetic electron transport components and photosynthesis-dependent

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redox-active compounds are involved, at least in some cases, in the coupling of photosynthetic electron flow with gene expression (for review, see [10]).

A remarkable feature of the photosynthetic apparatus is its ability to adjust rapidly to changes in environmental and metabolic conditions and in micronutrient availability. While light is essential for photosynthesis, too much light can be harmful when the absorbed light energy exceeds the capacity of the photosynthetic machinery. Under these conditions, the excess photons and electrons need to be dissipated to protect the photosynthetic apparatus from light-induced damage. This occurs through a rapidly inducible non-photochemical quenching process, called ΔpH-dependent quenching in which the excess absorbed light energy is dissipated as heat [11]. In addition, several photoprotective mechanisms exist such as plastid antioxidant enzymes and molecules [11], repair processes for lipid peroxidation [12], and damaged PSII [13]. At the other extreme, under low light conditions, the photosynthetic machinery adapts to optimize its photosynthetic yield. In nature photosynthetic organisms are subjected to constant changes in light quantity and quality and need to adjust their photosynthetic electron transport system accordingly. The molecular mechanisms underlying the responses of the photosynthetic electron transport chain to these environmental changes and their regulation have been intensively studied in recent years and will be discussed in this review.

2. Photosynthetic electron transport pathways

Photosynthetic electron flow is driven by two photochemical reactions catalyzed by PSII and PSI, which are linked in series by the electron transport chain (Fig. 1). At one end of this chain, the photochemical activity of PSII creates a charge separation across the thylakoid membrane with a strong oxidant on the donor side capable of oxidizing water with the concomitant release of protons and molecular oxygen in the thylakoid lumen and the reduction of the primary electron acceptors of PSII, Q_A and Q_B, on the stromal side of the membrane. Once it has accepted two electrons, Q_B is released from PSII into the plastoquinone pool and reduced plastoquinol docks to the Qo site of Cytb_6f. This complex acts as a proton pump in a Q-cycle-like process [14]. Oxidation of plastoquinol releases two protons in the lumen and two electrons, one of which is transferred through the high potential chain to the Rieske protein and cytochrome *f* and subsequently to plastocyanin and PSI. The other electron is transferred through the low potential chain to cyt_L and cyt_H within the Cytb_6f complex and finally to a quinone at the Qi site to form a semiquinone. Upon oxidation of a second plastoquinol at the Qo site, this process is repeated and semiquinone is reduced to quinol and released from Qi. It can enter the Q-cycle again as described above. Electron transfer from Cytb_6f to PSI is mediated by the copper protein plastocyanin in the thylakoid lumen. PSI acts as a light-driven oxidoreductase by oxidizing plastocyanin and transferring electrons through its three internal 4Fe-4S centers F_X, F_A, and F_B to ferredoxin. Ultimately these electrons can be used by ferredoxin $NADP^+$ reductase (FNR) to produce NADPH, which together with the ATP generated by the ATP synthase will drive the Calvin–Benson cycle for CO_2 assimilation. In addition, ferredoxin donates electrons to other pathways such as cyclic electron transfer, sulfur and nitrogen assimilation, and to thioredoxins, which regulate carbon assimilation [15]. In some green algae, upon a transition from the dark to the light under anaerobic conditions, ferredoxin transfers transiently electrons to chloroplast hydrogenases, which catalyze the formation of hydrogen [16]. In these organisms, this process appears to act as an electron safety valve to dissipate excess reducing power when the Calvin–Benson cycle is not yet fully activated.

Besides the linear electron transfer mode (LEF), the system can also perform cyclic electron transport (CEF) [14,17]. In this case, reduced ferredoxin, the terminal acceptor of PSI, transfers its electrons back to the plastoquinone pool through NADPH or directly to the Cytb_6f complex, giving rise to cyclic electron flow around PSI, which is coupled with proton translocation and ATP formation. One cycle of the Calvin–Benson pathway, i.e., the fixation of one CO_2 molecule consumes 3 ATP and 2 NADPH molecules. However, estimates of the ATP/NADPH ratio arising from LEF are about 1.28, which is clearly not sufficient for driving the Calvin cycle [18]. This can be estimated from the fact that the transfer of 4 electrons from water to $NADP^+$ by the linear electron transfer chain produces 2 NADPH molecules and is coupled to the pumping of 12 protons into the thylakoid lumen

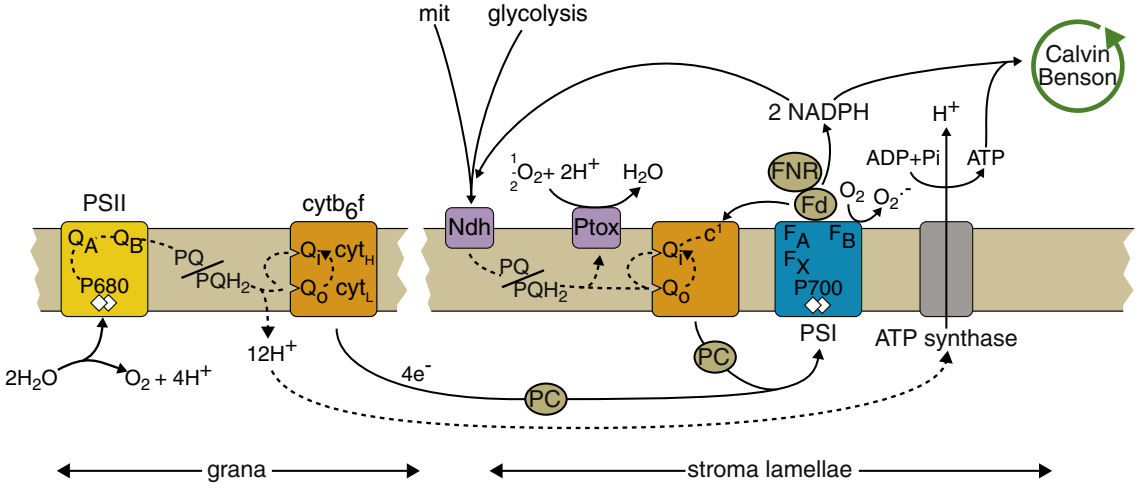

Fig. 1. Electron transport pathways of oxygenic photosynthesis. The thylakoid membrane with PSII, Cytb_6f, PSI, and the ATP synthase is shown. Electron transport pathways are shown by dotted lines with arrows to indicate the direction of electron flow. Linear electron transport (LEF) starts with the photo-induced water oxidation catalyzed by PSII. The stoichiometry of the reactions is indicated for 4 photons absorbed by PSII and 4 photons absorbed by PSI. Electrons are transferred from PSII through the PQ pool to Cytb_6f, which acts as proton pump through the Q cycle. Electrons are transferred from Cytb_6f to the soluble electron carrier plastocyanin (PC) and then to PSI, which acts as light-driven plastocyanin ferredoxin oxidoreductase. Ultimately FNR reduces NADP + to NADPH at the expense of reduced ferredoxin. Cyclic electron flow (CEF) involves PSI and Cytb_6f and occurs mostly in the stroma lamellae of thylakoids. Two different routes are indicated. The first uses ferredoxin, NADPH, and the Ndh complex. In the second pathway, ferredoxin transfers electrons directly to cyt *c′* in the Cytb_6f complex. Electron transport is coupled to proton translocation into the thylakoid lumen, and the resulting pH gradient drives ATP synthase to produce ATP. In addition pseudocyclic electron flow occurs in which molecular oxygen is reduced by PSI (Mehler reaction) to produce superoxide ($O_2^{\cdot-}$), which is converted to H_2O_2 by superoxide dismutase and to H_2O and O_2 by peroxidases and catalases (water–water cycle). Stromal reducing equivalents originating from mitochondria or from glycolysis are channeled into the PQ pool through the chlororespiratory chain, which includes the Ndh complex and PTOX as final electron acceptor.