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Distribution and dynamics of electron transport complexes in cyanobacterial thylakoid membranes☆

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ABSTRACT

The cyanobacterial thylakoid membrane represents a system that can carry out both oxygenic photosynthesis and respiration simultaneously. The organization, interactions and mobility of components of these two electron transport pathways are indispensable to the biosynthesis of thylakoid membrane modules and the optimization of bioenergetic electron flow in response to environmental changes. These are of fundamental importance to the metabolic robustness and plasticity of cyanobacteria. This review summarizes our current knowledge about the distribution and dynamics of electron transport components in cyanobacterial thylakoid membranes. Global understanding of the principles that govern the dynamic regulation of electron transport pathways in nature will provide a framework for the design and synthetic engineering of new bioenergetic machinery to improve photosynthesis and biofuel production. This article is part of a Special Issue entitled: Organization and dynamics of bioenergetic systems in bacteria, edited by Conrad Mullineaux.

1. Introduction

Cyanobacteria are the oldest oxygenic phototrophs on Earth. They were not only among the early microbial pioneers of life to produce oxygen that is indispensable for sustaining aerobic life in the atmosphere, but also have consistently served as a predominant contributor to our sustainable environment for around 3.5 billion years [1]. Cyanobacteria can adapt to a variety of environmental changes and have a wide variety of habitats, predominantly ascribed to the robustness and plasticity of their metabolic systems. The thylakoid membranes of many cyanobacteria that have been studied are uniquely capable of conducting both photosynthetic and respiratory electron transductions [2,3]. The dynamics and modulation of electron transport pathways are essential for cyanobacteria to optimize their metabolism towards environmental challenges. In the last decades, improvements in structural biology techniques have provided substantial information, in molecular detail, about the structures and functions of the electron transport complexes in cyanobacterial thylakoid membranes. However, we still have insufficient knowledge about the overall organization of the thylakoid membranes, the interactions between electron transport complexes and the dynamics of these functional modules. This is a major impediment to addressing many fundamental questions, such as how these electron transport components are biosynthesized and degraded, how their functions are regulated, and how they communicate with each other within the same membrane or between different cellular membranes.

This review focuses on the spatial organization and dynamics of electron transport chains in cyanobacterial thylakoid membranes, and discusses the functional significance of the distribution and mobility of electron transport modules in vivo. The dynamic modulation of the electron flow network produces optimized energy transduction in cyanobacteria. Extensive study of cyanobacterial photosynthetic membranes will provide essential information for the design and engineering of new photosynthetic machinery and devices, with the attempts to improve bioenergy production. In addition, given the close evolutionary relationship between cyanobacteria and chloroplasts, the photoheterotrophic cyanobacteria represent an important model for elucidating the structure and function of chloroplasts in higher plants. Alternatively, knowledge obtained from plant chloroplasts will also inform the study of cyanobacterial thylakoid membranes.

2. Cyanobacterial thylakoid membrane structure

2.1. Composition

A unique structural feature of cyanobacterial thylakoid membranes is that it harbors the elements of both photosynthetic and respiratory electron transfer chains, and thereby is capable of performing both oxygenic photosynthesis and aerobic respiration in the same cellular

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compartment. The major photosynthetic and respiratory electron transport complexes have been structurally characterized in the past decade. Fig. 1 depicts the thylakoid membrane structure based on our current knowledge obtained from a model unicellular cyanobacterium, *Synechocystis* sp. PCC6803 (hereafter *Synechocystis* 6803). The photosynthetic electron transport complexes in the thylakoid membrane include phycobilisome (the membrane associated antenna complex), photosystem II (PSII), photosystem I (PSI), cytochrome (cyt) b_6f and ATP synthase (ATPase). In addition, there are small electron transport molecules, such as plastoquinone (PQ), plastocyanin (PC) and cytochrome c_6, functioning as electron carriers to shuttle electrons between each electron transport complex and functionally link all the complexes together [4].

Cyanobacteria have evolved the extrinsic supramolecular phycobilisomes associated to the cytoplasmic surfaces of thylakoid membranes, serving as the major antenna for both photosystems [5–8]. Phycobilisomes are self-assembled supercomplexes composed of chromophore-containing phycobiliproteins and colorless linker polypeptides [9]. The ingeniously-created architecture allows phycobilisomes to absorb efficiently the visible light at the wavelength of 500–670 nm, greatly extending the absorbance range of chlorophyll *a* in photosystems (major absorption at 440 nm and 680 nm). Moreover, stepwise energy transfer within the phycobilisome could also act as a photoprotective mechanism to prevent the photodamage of photosystems by excess light energy [10]. Light energy captured by phycobilisomes is rapidly and efficiently transferred to PSII and PSI. At the reaction center of PSII, a series of light-induced electron transfer reactions occur, leading to the conversion of electrochemical potential energy and water splitting reaction. PQ accepts the electrons from PSII and contributes the electrons to PSI via cyt b_6f and PC. PSI catalyzes the light-driven electron transport including the oxidation of luminal electron carriers, PC and cyt c_6, and the reduction of ferredoxin. The electron transfer reactions are coupled with the formation of an electrochemical gradient across thylakoid membranes, which is essential for driving ATP synthesis by the ATPase. This electron flow pathway, namely the linear electron transport, is strictly correlated with the evolution of O_2. During the last steps of electron transfer, the ferredoxin, a strong reductant, transfers electrons to ferredoxin-$NADP^+$ oxidoreductase (FNR) to generate NADPH. Apart from the linear electron transport, PSI also participates in the cyclic electron transport, which generates only ATP without any accumulation of NADPH, in order to balance the ratio of ATP and NADPH in the cell [11]. The produced ATP and NADPH will then be utilized for CO_2 fixation and other cellular metabolism.

Likewise, some protein complexes are also related to the photosynthetic electron flow. A water-soluble orange carotenoid protein (OCP) was shown to mediate directly the fluorescence quenching of phycobilisomes, known as non-photochemical quenching, and possibly in the regulation of energy transfer between phycobilisomes and photosystems [12–14]. OCP contains a single bound carotenoid (3′-hydroxyechinenone), which can change the conformation between its orange (OCP^O) and red forms (OCP^R) [13,15]. The photoactivated OCP^R binds to the phycobilisome core, where it takes excitation energy from phycobilins and converts it to heat as an energy quencher, in order to prevent photodamage of reaction centers at high light. The reversal of OCP-induced energy quenching (conversion of OCP^R back to OCP^O) depends on a second cytoplasmic protein, the fluorescence recovery protein, which binds to OCP and weakens its association with phycobilisomes [16].

In contrast to the well-studied photosynthetic electron transport chain, the respiratory electron transport chain in cyanobacteria is much less understood. The main respiratory electron transport complexes include type-I NAD(P)H dehydrogenase (NDH-1), type-II NAD(P)H dehydrogenase (NDH-2), succinate dehydrogenase (SDH), cytochrome oxidase and alternative oxidases, as well as cyt b_6f [2]. NDH-1 and SDH were postulated as the principal respiratory electron donor complexes in cyanobacteria [2,17–19]. The cyanobacterial NDH-1 complex structurally and functionally resembles mitochondrial Complex I of the respiratory chain, and plays key roles in respiration, cyclic electron flow around PSI and CO_2 uptake [20]. Electrons from respiratory substrates enter the electron transport chain via PQ reduction by NDH-1 or SDH, and are passed on through cyt b_6f and the luminal electron carrier, PC or cytochrome *c*. Afterward, they could be transferred to either a terminal oxidase to perform conventional respiratory electron transport with net oxidation of the metabolite pool, or could be transferred to PSI to participate in the cyclic photosynthetic electron transport. The redox state of PQ pool has been demonstrated to play an important role in steering the electron flow into different directions [19].

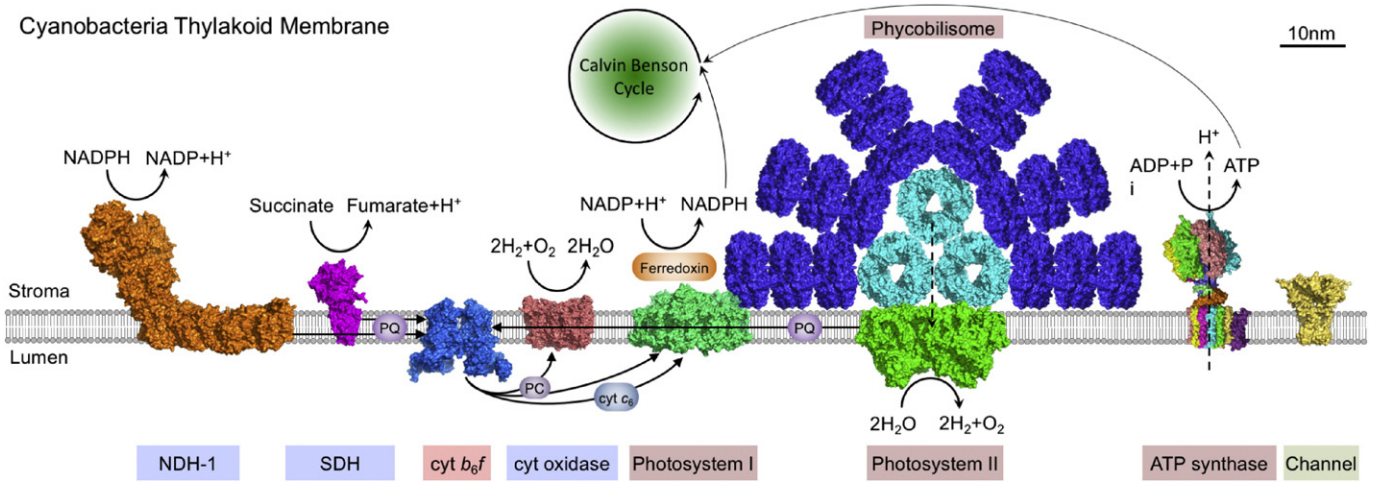

Fig. 1. Schematic model of cyanobacterial thylakoid membrane (based on knowledge of *Synechocystis* 6803 thylakoids), showing the interplay of photosynthetic and respiratory electron transport component in the same membrane. Photosynthetic electron transfer complexes include phycobilisome, PSII and PSI, cyt b_6f and ATPase. The presence of phycobilisome–photosystem supercomplex in vivo has been identified [38,39]. Complexes specific for respiratory electron transport chain are NDH-1, SDH and cyt oxidase. Some components, such as the cyt b_6f, PQ and PC are shared by both electron transport pathways. There are also potassium channel proteins in the thylakoid membrane. Arrows indicate the electron transduction reactions. Abbreviations: ADP — adenosine diphosphate, ATP — adenosine triphosphate, cyt b_6f — cytochrome b_6f, cyt c_6 — cytochrome c_6, cyt oxidase — cytochrome oxidase, NADP(H) — nicotinamide-adenine dinucleotide phosphate (reduced form), NDH-1 — type 1 NADPH dehydrogenase, PC — plastocyanin, PQ — plastoquinone, SDH — succinate dehydrogenase. The protein structures are achieved from PDB database: allophycocyanin, PDB ID: 1KN1; NDH-1, based on the Complex I structure from *Thermus thermophilus*, PDB ID: 4HEA; cyt b_6f, PDB ID: 4H13; cyt oxidase, PDB ID: 1OCO; potassium channel protein, based on the *Magnetospirillum magnetotacticum* KirBac3.1 potassium channel crystal structure, PDB ID: 1XL4; phycocyanin, PDB ID: 3O18; PSI, PDB ID: 1JB0; PSII, PDB ID: 3WU2; and SDH, based on the *E. coli* SDH crystal structures, PDB ID: 1NEK.