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CYANOBACTERIAL PHOTOSYNTHETIC COMPLEXES AND THEIR ASSOCIATED BIOACTIVE COMPOUNDS: STRUCTURE, FUNCTION, AND BIOTECHNOLOGICAL APPLICATIONS

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ABSTRACT

All our food, fossil and biological fuels (biomass) are derived from the process of photosynthesis. This process is the fundamental and essential process where solar energy is converted into chemical energy, adenosine tri phosphate (ATP) and Nicotinamide adenine dinucleotide phosphate (NADPH). This chemical energy is required for the synthesis of the carbohydrates from CO_2. In addition to this, molecular oxygen is released as a result of an early event of photosynthesis. Thus all forms of life in the universe require the oxygen and energy for the growth and maintenance. In higher plants and green algae the entire process of photosynthesis takes place in chloroplast, where as in cyanobacteria which lacks chloroplast the same process occurs in intact cells. Photosynthesis consists of two phases, one is light phase and other is dark phase. In light phase the harvested light energy will be converted to chemical form (ATP and NADPH) during the photosynthetic electron transport. In the dark phase these energy rich compounds are utilized for the conversion of CO_2 into carbohydrates. In this present review we demonstrate on cyanobacterial photosynthetic complexes and its compounds. In this review we are exploring on the cyanobacterial photosynthetic pigments and its compounds.

KEYWORDS: Cyanobacteria, Photosynthetic complexes, Polypeptides, Pigments.

1. General view of photosynthesis

Photosynthesis is one of the most important biochemical pathways, fundamental and essential process, since nearly all life on Earth either directly or indirectly depends on it as a source of energy. Through this process higher plants and algae convert solar energy into chemically energy into energy rich compounds, which are necessary for their growth and development. In addition to this molecular oxygen is released as by product of in the early phase of photosynthesis. Thus life on our planet is dependent on this important biologica process. By the middle of the 19th century the key features of plant/algae photosynthesis were known, namely, that plants could use light energy to make carbohydrates from CO_2 and water.[1] The empirical equation representing the net reaction of photosynthesis for oxygen evolving organisms is: $CO_2 + 2H_2O + \text{Light Energy} \rightarrow (CH_2O) + O_2 + H_2O$

In higher plants and green algae the entire process of photosynthesis takes place in chloroplast, whereas in cyanobacteria the same process occurs in the intact cells. In the intact cell, the thylakoid membranes or thylakoids of chloroplast converts solar energy in to chemical energy. This process is known as "light reaction" of photosynthesis. The solar energy called visible light (380 nm to 800 nm) drives photosynthesis. Solar radiation is composed of electromagnetic energy that travels through space in a manner analogous to the motion of waves in water. The distance between the crests of waves is called the wavelength. The shortest wavelength is the greater the energy for each unit (photon) of electromagnetic energy; remember, energy cannot be created or destroyed. When light is absorbed by a green pigment, a small portion of that energy is converted into chemical energy in the process of photosynthesis. The term photosynthesis from greek means “assemblage of light” this process converts massive amount of sunlight into

electrical and then chemical energy. The input is carbon dioxide (CO_2), water (H_2O), minerals & light and the output is carbohydrates (food) that we need for our nourishment and oxygen that we need to breathe.[2] It is a complex process occurring in plants, algae, as well as bacteria such as cyanobacteria. Photosynthetic organisms are referred to as photoautotrophs. This oxygenic photosynthesis occurs in higher plants, green, red, brown, yellow algae and Blue Green Algae (BGA). Anoxygenic photosynthesizers are (e.g., purple and green bacteria, heliobacteria) that can produce carbohydrate (food), but no oxygen. Oxygenic photosynthesizers use the green pigment chlorophyll *a*, located in protein complexes in photosynthetic membranes, to run the photochemistry of the process, whereas the anoxygenic photosynthesizers use *Bacteriochlorophyll* instead. The set of photosynthetic reactions is divided into two types i.e., (I). Light phase (this phase produces the reducing power and ATP, the energy currency of life) & (II).Dark phase (The products of light phase are used to convert CO_2 to carbohydrates).

2. Cyanobacteria

Cyanobacteria also known as cyanophyta, a phylum of bacteria, which is aquatic and can manufacture their own food. Photosynthesis as a flexible molecular machine, cyanobacteria contribute about 40% present day global photosynthetic biomass production and its convert solar energy into biomass-stored chemical energy at the rate of ~450 TW. These are quite small and usually unicellular, though they often grow in colonies. Cyanobacteria are very important organisms for the health and growth of many plants. They have the distinction of being the oldest known fossils, more than 3.5 billion years old, in fact, it may surprise you to know that the cyanobacteria are still around; they are one of the largest and most important groups of bacteria on earth.[3] Cyanobacteria are oxygenic photosynthetic prokaryotes whose photosynthetic apparatus show resemblance to those of higher plants. In the thylakoid membrane of the cyanobacteria two photosystems work in series to convert the energy of solar photons into storable chemical energy. Plants and cyanobacteria contain similar photosystem (PS) II and PS I reaction center complex. PBsomes are major light harvesting complex (LHC) proteins in PS II of cyanobacteria which transfer the energy to the photochemical reaction center to perform photosynthesis.[4] (Fig 1). In addition to this,some of the cyanobacteria are able to fix nitrogen. Hence, they are known as 'Biofertilizers'. Some ion channels regulate photosynthesis in cyanobacteria and higher plants. A comprehensive review of the different aspects of primary reactions in photosynthesis was given by Messinger and Renger.[5] In higher plants and green algae the entire process of photosynthesis takes place in the chloroplast, whereas in cyanobacteria the same process occurs in the intact cells. The thylakoid membranes possess three distinct pigment protein complexes such as, PS II, PS I, ATP synthase and two carrier complexes of cytochrome b_6f, plastocyanin. The chlorophylls of the photosystems are driven to a higher energy state with the help of light energy. This gained energy could be utilized in different ways, such as photochemistry, energy transfer between the two photosystems, light emission and heat dissipation[6]

2.1. Photosystem I complex

PS II is large homodimeric and an integral membrane-protein complex within thylakoids of chloroplasts in cyanobacteria, that performs water splitting and the reduction of plastoquinone to plastoquinol at the start of the photosynthetic electron transport chain.[7,8] The PSII core complex is composed of at least 25 different protein subunits, pigments and lipids. This large homodimeric protein-cofactor complex consists of a "core" of at least five integral membrane proteins, the chlorophyll-binding proteins CP47 (*psb B*) and CP41, the 32-34 kDa proteins DI and D2 and cytochrome C_{559}.[9,10] In the reaction center (P_{680}) of photosystems, excitation is converted into charge separation, which drives electron flow from PS II to PS I via the cytochrome b_6f complex. PS II contains three protein complexes: the reaction center (RC), where the initial charge separation occurs and two internal Chl *a* light harvesting antennae, CP47 and CP43. The reaction center (P_{680}), strictly defined, contains four to six Chl *a* molecules, two pheophytins, and two quinines (Q_A and Q_B), which are involved in the initial charge separation, bound by a pair of hydrophobic polypeptides, D1 (psbA) and D2 (psbD). In addition to D1 and D2, PS II-RC contains three small proteins: cytochrome b559, Psb I, and Psb W,[11,12] none of which is thought to bind Chl.

CP47 (CPa-1) and CP43 (CPa-2) are internal light harvesting proteins of PS II The polypeptides of 52 and 48 kDa, encoded with psbB and psbC genes, which are very hydrophobic. CP47 and CP43 were reported to contain a small amount of lutein in addition to β-carotene.[13] This highly conserved PS II core protein consists of about 500 amino acids with a molecular mass of 47 kDa, predicted to have six transmembrane helices (I to V) with the N- & C- terminal exposed at the stromal surface.[14] According to Vermaas *et al.*,[15] CP 47 protein is an absolute requirement for photoautotrophic growth. *psb C* -CP 43 protein contains about 470 amino acids with a molecular mass of 43 kDa, in many ways it is homologous with CP 47 in that it is likely to have 6 transmembrane helices, binds about the same level of Chl and carotenoids and has a large lumenal loop between helices V and VI.[14]

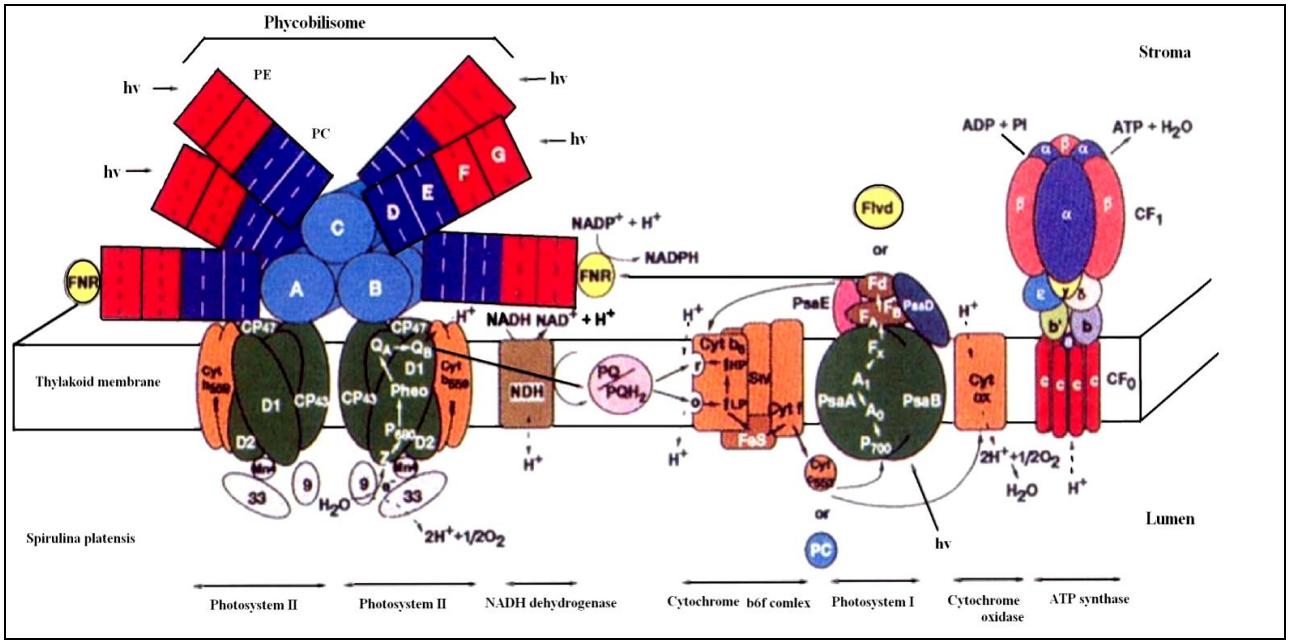

Fig 1: Organization of polypeptides in cyanobacterial thylakoid membrane.

Drwan based on Appel, et al., 2020

It differs from CP 47 in two main respects. (1). Its N-terminal threonine can be irreversibly phosphorylated in the case of higher plants.[16] (2). It is more weakly associated with the RC II and can be removed from the isolated core to yield a CP 47-RC complex.[17] D1protein is a highly conserved pigment-binding protein of RC II.[18] This protein is encoded by a single gene localized in the chloroplast genome with a molecular mass of 32 kDa depending upon the species.[19] It is an integral thylakoid membrane protein having five transmembrane α-helices (designated A to E).[6] The D1 protein is characterized by two important features: (1). It binds the majority of the cofactors involved in PS II mediated electron transport {Tyr 161 (Y_Z), P_{680} probably via His 198, Pheophytin (Phe) probably via Tyr 126, Tyr 147, Ala 150 and Glu 130, Q_B via interactions with Tyr 254, Phe 255, Gly 256 and others, Mn cluster possibly via Asp170, Glu 189, Gln 165, Ala 344, His 109, His 332 and His 377 and non-heme iron, probably via His 215 and His 272[16]}. (2). It turns over more rapidly than any other protein in the thylakoid membrane.[6,20] D2 protein is a 34 kDa chloroplast genome-encoded protein, homologous to D1 protein (Michel and Deisenhofer., 1988). It is integrally associated with the thylakoid membrane and forms D1/D2 heterodimer of the RC II, which binds the P_{680} as well as two peripheral Chl *a* and one α-carotene along with all the cofactors mediating the electron flow.[21] C-terminal domain of D_2 is important for the function and stability of PS II.[22] Down regulation of D2 resulted in the loss of the ability to grow photoautotrophically and the decrease in the number of functional RC II in thylakoid membranes.[23]

2.2. Cytochrome b_6f complex (Cyt b_6f)

The cytochrome b_6f complex can be considered as a plastoquinol-plastocyanin oxidoreductase. Plastoquinone is an important electron carrier between Q_B and Cytb_6f. It contains four major polypeptides, which are Cyt *f* (31 kDa), Cyt b_6 (22.5 kDa), the Rieske FeS protein (22 kDa) and 16.5 kDa protein of unknown function as major proteins; two minor proteins of 9 kDa are associated with this complex.[24] The stoichiometry of Cyt *f*/Cyt b_6 16.5 kDa polypeptides was estimated as 1:2:1, whereas the Rieske FeS protein was present in sub stoichiometric amounts. Cytb_6f complex operates an electron transfer in cyclic process known as Q cycle.[25,26] This cycle helps in the transfer of protons across the membrane, the oxidation of quinol and the reduction of the plastocyanin. 2,5-Dibromo-6-isopropyl-3-methyl-1,4-benzoquinone (DBMIB) is an inhibitor of the Q cycle.

2.3. Plastocyanin (PCy)

Plastocyanin (PCy) serves as a mobile carrier between Cyt b_6f complex to P_{700} reaction centre of PS I (Haehnel., 1984). PCy is a copper containing peripheral membrane protein (10.5 kDa) which is located on the luminal side of the thylakoid membrane.[27] It accepts electrons from Cyt *f* and form a pool of electrons, from here it can be passed to PS I.[28] In some algae and cyanobacteria the biosynthesis of plastocyanin are controlled by availability of Cu in the growth medium. In the absence of Cu, these cells are able to accumulate plastocyanin and instead synthesize a C-type cytochrome, cytochrome C_{553}, which is functionally interchangeable with plastocyanin.[29]

2.4. Photosystem I

Cyanobacterial PS I can exist in the photosynthetic membrane in both trimeric and monomeric forms. The trimeric form is the prominent oligomeric state at low light intensity. These low light conditions may correspond to the natural habitats of most cyanobacteria. The monomeric unit of PS I consists of 12 protein

subunits to which 127 cofactors are non-covalently bound. In cyanobacteria and plants, the PS I reaction center (P_{700}) is a membrane-bound, multisubunit complex, which functions as the light-driven plastocyanin (or cytochrome c6)/ferredoxin (flavodoxin) oxidoreductase.[30] The PS I complex of cyanobacteria is structurally and functionally equivalent to the PS I core complex of higher plants. In some cyanobacterial and green algae, cytochrome c6 can replace plastocyanin as an electron donor to PS I.[31,32]

2.5. ATP synthase complex

ATP synthase complex consists of the proton core CF_0, which is embedded in the thylakoid membrane and CF_1 the extrinsic enzyme that catalyzes the ATP synthesis and hydrolysis. The molecular weight of CF_1 is 320 kDa. It consists of five subunits of molecular weight 53.4 kDa, 51.6 kDa, 36 kDa, 21.1 kDa and 14.7 kDa respectively.[33] This occurs in a symmetrical ring of six alternating x and p subunits with a hole in α subunits. The CF_0 is oligomeric in nature and comprises four different protein subunits in both green algae and higher plants. It is self assembled in the membrane bilayer to form a proton conducting "core" as well as the site to which CF_0 binds [34]. The transport of electrons from PS II to PS I will liberate the protons (H^+) from the stroma to the lumen of the thylakoids. The protons are also released into the lumen due to oxidation of H_2O by PS II.[35] This electrochemical gradient is responsible for the synthesis of ATP from ADP and Pi.

3. Thylakoid membrane lipids and their role

The thylakoid membrane is unique in plant cell in having a high proportion of glyceroglycolipids and phospholipids. The glycerolipids are monogalactosyl diacylglycerol (MGDG) digalactosyl diacylglycerol (DGDG), sulpholipids (SQDG) and they account for 40-50%, 20-30% & 5-10%, respectively.[36] The phospholipid in the thylakoid membrane is phosphotidylglycerol (PG), which accounts for 10-20% of the total lipids. The specific binding of glycerolipids of protein complexes from the thylakoid membranes has been well studied, specifically the association of SQDG and DGDG with the ATP synthase that of phospholipids, PG with Cyt b_6f complex and that of PG with LHCP complex.[37] It has been shown that the activity of ATP synthase is stimulated by MGDG that contains polyunsaturated fatty acids.The Cyt b_6f activity, i.e. the plastoquinol/plastocyanin oxidoreductase activity was stimulated by DGDG, PG, and PC, but not MGDG and SQDG.[38] Lipase treatment studies and catalytic hydrogenation studies[39] indicated that lipid to protein ratio and/or the extent of lipid unsaturation determine the fluidity which is essential for thylakoid membrane stability and function. PG is necessary for oligomeric organization of LHCP and its monomeric form. Lipids are also shown to be essential for a stable charge separation between P_{680+} and Q_A.[40] Recently Murata *et al*[41] reported that the presence of the phospholipids varies with the nature of PS II complex preparation. One MGDG molecule, containing high saturated fatty acids is associated with active PS II reaction centre complex which performs only the charge separation.[42] This is essential for the proper confirmation of the PS II reaction centre complex. About ten lipid molecules, including MGDG, DGDG and PG are associated with active PS II core complex, which perform both charge separation and O_2 evolution suggests the participation of lipids in photosynthetic oxygen evolution.

4. Interaction of the respiratory and photosynthetic electron transport in cyanobacteria

Brown and Webster[43] observed the inhibition was insensitive to DCMU and promoted by the presence of far red light. To explain that processes an existence of the common segment of the electron transport carriers between respiratory and photosynthetic electron transport chains have been proposed.[44] These electron transport carriers are PQ, plastoquinol, Cyt C_{553}, oxidoreductase and PCy or Cyt C_{553}. PQ is found to be involved in dark $NADH^+$ oxidation. Hence it is carotenoid as a part of the respiratory process. Cyanobacteria are photosynthetic prokaryotes can evolve oxygen.[45] The main differences with other algae are the lack of particular organelles such as chloroplasts or mitochondria, but have different types of membranes. Cyanobacteria contain Cyt C_{553} in the place of PCy which not only takes participation in photosynthetic electron transport, but also acts as a good electron source of cyt oxidase.[46,47] Reconstitution experiments of the complete photosynthetic and respiratory electron transport chains of *Nostoc muscorum* provided evidence that Cyt C_{553} is involved in both in electron transport. The location and interaction between respiratory and photosynthetic electron transport was reviewed by Takahashi *et al*.,[48] (Fig 2).

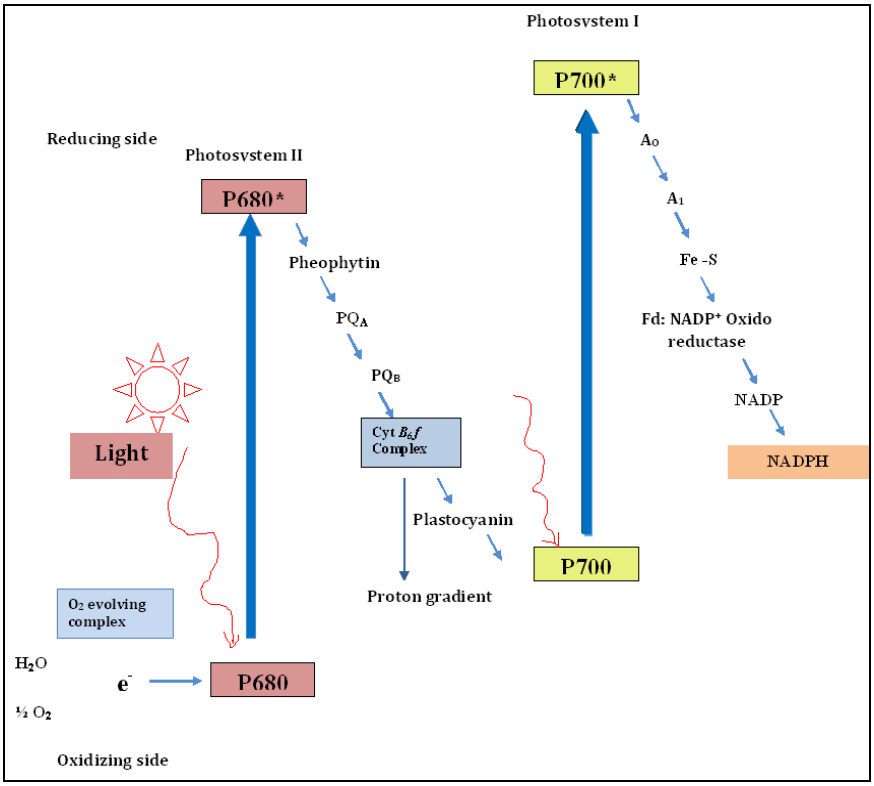

Fig. 2: Electron transport from PS II to PS I in cyanobacteria.

5. Biotechnological Applications and Emerging Technologies

Cyanobacterial photosynthetic complexes and their associated bioactive compounds have attracted considerable attention owing to their diverse applications in pharmaceuticals, renewable energy, environmental sustainability, agriculture, food, and cosmetics. Bioactive molecules such as phycocyanin, phycoerythrin, chlorophyll, carotenoids, polysaccharides, peptides, and phenolic compounds exhibit potent antioxidant, anticancer, antiviral, antibacterial, antifungal, anti-inflammatory, and neuroprotective properties, making them promising candidates for the development of novel therapeutics and nutraceuticals.[50,51] Owing to their efficient photosynthetic machinery, cyanobacteria are also regarded as sustainable microbial cell factories for the production of renewable biofuels, including biohydrogen, biodiesel, bioethanol, biomethane, and sustainable aviation fuel (SAF) precursors, while simultaneously capturing atmospheric CO_2 and contributing to climate change mitigation through enhanced carbon sequestration.[52,53] Furthermore, cyanobacteria play an important role in environmental biotechnology by removing nutrients, adsorbing heavy metals, degrading organic pollutants, and improving wastewater quality. Their nitrogen-fixing ability, production of phytohormones, and secretion of extracellular polysaccharides make them valuable biofertilizers, plant growth promoters, soil conditioners, and biopesticides for sustainable agriculture. In addition, cyanobacterial biomass serves as an excellent source of protein, omega-3 fatty acids, vitamins, and natural pigments for functional foods and dietary supplements, while antioxidant pigments and mycosporine-like amino acids (MAAs) are increasingly incorporated into cosmetic formulations as anti-aging, moisturizing, UV-protective, and skin-whitening agents.[54,55]

Recent advances in biotechnology have considerably expanded the industrial potential of cyanobacteria through the integration of CRISPR–Cas genome editing, synthetic biology, metabolic engineering, nanobiotechnology, artificial photosynthesis, bio-photovoltaic systems, omics technologies, and artificial intelligence. CRISPR-based genome editing enables precise modification of genes involved in photosynthesis, carbon fixation, pigment biosynthesis, lipid metabolism, and hydrogen production, whereas synthetic biology and metabolic engineering facilitate the construction of highly efficient cyanobacterial cell factories for producing biofuels, pharmaceuticals, biodegradable polymers, and other high-value biochemical.[52,53] Moreover, nanobiotechnology improves light harvesting, electron transfer, biosensing, and targeted drug delivery, while artificial photosynthesis and bio-photovoltaic devices exploit cyanobacterial photosystems for sustainable solar energy conversion and electricity generation. The application of integrated omics approaches—including genomics, transcriptomics, proteomics, metabolomics, and fluxomics—combined with machine learning enables predictive metabolic modeling, optimization of cultivation conditions, rational strain engineering, and enhanced production of valuable metabolites at an industrial scale **[50]**. Collectively, these emerging technologies are transforming cyanobacteria into versatile and sustainable biotechnological platforms

capable of addressing global challenges related to renewable energy, environmental remediation, carbon neutrality, food security, and human health, thereby supporting the development of a circular bioeconomy.

CONCLUSION AND FUTURE ASPECTS

Photosynthesis is the fundamental biochemical process that sustains life on Earth by converting solar energy into chemical energy while simultaneously releasing molecular oxygen. Cyanobacteria, as ancient oxygenic photoautotrophs, have played a pivotal role in shaping Earth's atmosphere and continue to contribute significantly to global primary productivity. The close structural and functional resemblance between the photosynthetic machinery of cyanobacteria and higher plants highlights the evolutionary conservation of this process. The coordinated action of Photosystem II, cytochrome b_6f complex, plastocyanin (or cytochrome c_6), Photosystem I, and ATP synthase enables efficient electron transport, proton gradient formation, and ATP synthesis. In cyanobacteria, the integration of photosynthetic and respiratory electron transport chains through shared components such as plastoquinone and cytochrome c_{553} represents a unique metabolic flexibility that allows adaptation to fluctuating environmental conditions. Thylakoid membrane lipids play a crucial structural and functional role by stabilizing photosynthetic protein complexes, regulating membrane fluidity, and supporting efficient charge separation and oxygen evolution. The dynamic turnover of key proteins such as the D1 and D2 subunits further emphasizes the finely regulated nature of the photosynthetic apparatus. Altogether, the studies discussed demonstrate that photosynthesis in cyanobacteria is a highly organized, lipid–protein–cofactor–dependent process essential for both cellular metabolism and global biogeochemical cycles.

Despite extensive knowledge of the photosynthetic electron transport system, several important areas remain open for future research:

a. **Molecular Regulation and Dynamics**: Further investigation is needed to understand the real-time regulation, assembly, repair, and turnover of photosynthetic complexes, particularly under stress conditions such as high light, nutrient limitation, and temperature fluctuations.
b. **Role of Lipids in Photosynthetic Efficiency** Although the importance of thylakoid membrane lipids is well recognized, the precise molecular mechanisms by which specific lipid species influence photosystem stability, electron transport, and oxygen evolution require deeper structural and biophysical analysis.
c. **Integration of Photosynthesis and Respiration**: The shared electron transport components between respiratory and photosynthetic pathways in cyanobacteria present an attractive model to study metabolic integration. Elucidating the regulatory switches controlling electron flow between these pathways may reveal new principles of energy optimization.
d. **Genetic and Synthetic Biology Approaches :** Advances in genome editing and synthetic biology can be used to engineer cyanobacteria with enhanced photosynthetic efficiency, improved stress tolerance, or optimized carbon fixation pathways for biofuel and bioproduct generation.
e. **Environmental and Applied Perspectives:** Understanding cyanobacterial photosynthesis at the molecular level has direct implications for climate change research, carbon sequestration strategies, and the development of sustainable biofertilizers and renewable energy resources.

In conclusion, continued interdisciplinary research combining structural biology, biophysics, molecular genetics, and systems biology will not only deepen our understanding of photosynthesis but also enable the rational exploitation of cyanobacteria for environmental and biotechnological applications.

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