



Preface

Chloroplast Biogenesis



Chloroplasts play essential roles not only in photosynthesis but also in other important metabolic pathways; therefore, they are crucial for life on earth [1]. This special issue of BBA-Bioenergetics highlights recent advances of our understanding on chloroplast biogenesis. Reviews cover various aspects of chloroplast biogenesis at the molecular level, including chloroplast gene expression, chloroplast protein import, the synthesis, assembly and maintenance of thylakoid protein complex and signal transduction involved in chloroplast biogenesis.

Chloroplasts are originated from a cyanobacterial ancestor, whose uptake was followed by massive gene transfer to the nucleus but modest coding capacity of the extant chloroplast genome retains. Chloroplast gene expression is essential for chloroplast biogenesis but depends on nucleus-encoded proteins recruited from cyanobacterial or host-cell origins [2]. **Börner et al** reviewed the function of nuclear-encoded phage-type RNA polymerase and cyanobacterium-derived chloroplast-encoded RNA polymerase in chloroplast gene expression [3]. **Chi et al** highlighted the role of the individual functions and regulation of chloroplast sigma factors in chloroplast gene expression, focusing on the mechanisms that modulate the activity of sigma factors to optimize plastid function in response to developmental cues and environmental signals [4].

An important characteristic of chloroplast gene expression is the predominance of posttranscriptional control [5, 6]. RNA editing is a process that modifies the genetic information on RNA molecule at the post-transcriptional level, which has been extensively studied in chloroplasts. **Shikanai** summarized the recent advances in machinery and flexibility of the site recognition of chloroplast RNA editing and the functions of PPR proteins, *trans*-factors required for site recognition. PPR proteins are a large family of modular RNA-binding proteins which mediate several aspects of gene expression primarily in organelles. The mTERF (mitochondrial transcription termination factor) proteins are likewise defined by tandem degenerate helical repeats and share several key features with the PPR family. Functional roles for plant mTERFs are just beginning to emerge [7]. **Kleinea and Leister** reviewed recent advances in the characterization of mTERF function in photosynthetic organisms [8]. In this specific issue, **Schmitz-Linneweber et al** described the chloroplast splicing machinery in the context of organellar maturases [9]. With respect to chloroplast translational control, **Sun and Zegers** reviewed the translational regulation in chloroplasts, focusing on changes in translation rates which occur in response to requirements for proteins encoded by the chloroplast genome for development and homeostasis [10].

Chloroplast thylakoid membranes mediate photosynthetic electron transfer and represent one of the most elaborate energy-transducing membrane systems and much remains to be learned about how the machinery is formed [1, 11]. The papers presented in this special issue provide the integrating current knowledge in these various aspects of

thylakoid biogenesis. The concerted synthesis and assembly of lipids, proteins and cofactors like pigments and transition metal ions require a high level of spatiotemporal coordination [12]. The paper of **Rast et al** described how different biosynthetic pathways for thylakoid membrane constituents might be interconnected to enable coordination of biogenesis in the temporal domain [13]. The paper of **Zhang and Sakamoto** summarized the function of vesicle-inducing protein in plastids 1 (VIPP1), whose function was expanded significantly in recent years, such as vesicle budding from inner envelope to deliver lipids to thylakoids, maintenance of photosynthetic complexes in thylakoid [14]. **Yang et al** and **Rühle and Leister D** reviewed the assembly mechanism of the photosystem I and ATPase complexes, respectively. The assembly factor 'toolbox' is not conserved in different organisms and both papers highlight the assembly mechanism of thylakoid protein complexes in an evolutionary context [15, 16]. PSI and PSII complexes contain LHC with flexible peripheral moiety for enhancing light-harvesting cross-section. **Dall'Osto et al** provided a review on the current knowledge on LHC biogenesis, ranging from organization of pigment-protein complexes to the modulation of gene expression, import and targeting to the photosynthetic membranes, and regulation of LHC assembly and turnover [17]. Finally, in the paper of **Trösch et al**, the composition and function of ATP-dependent molecular chaperones in chloroplasts, especially Cpn60/Cpn10, Hsp70, Hsp90, and Hsp100 classes of molecular chaperones were summarized [18].

A number of papers deal with the dynamic aspects of the thylakoid membranes, and how these are integrated into the physiology of the whole plant. **Rottet et al** described plastoglobules as thylakoid membrane microdomains and discuss their involvement in lipid remodeling during stress and in the conversion from one plastid type to another [19]. It has well established the susceptibility of the PSII D1 protein to damage upon exposure of plants to light in their natural environments, and similarly, the basic concept for replacement of the damaged D1 protein by a newly-synthesized copy during the repair cycle of PSII has been extensively investigated [20]. The paper of **Järvi et al** paid emphasis on the sequential function of a number of PSII auxiliary proteins involved both in the biogenesis and repair of PSII [21]. The paper of **Adam** reviewed the intramembrane proteases localized in the thylakoid as well as the inner envelop and possible function of intramembrane proteases involved in thylakoid biogenesis and chloroplast development were discussed [22]. **Nishimura and van Wijk** described the organization, function and substrates of the Clp protease system, which is essential for chloroplast biogenesis, differentiation and chloroplast protein homeostasis [23]. Cyclic electron transport around photosystem I generates ATP without the accumulation of NADPH in chloroplasts and it is also important for the regulation of photosynthesis adaption. A study of **Wang et al** in this issue assayed the role of cyclic electron transport in regulating proton motive force of thylakoid [24].

Most subunits of thylakoid protein complexes are encoded by the nuclear genome and they are produced in cytosol and then are transported into chloroplasts [25, 26]. The knowledge for the dedicated translocon machineries for protein import, comprising the TOC (translocon at the outer envelope membrane of chloroplasts) and TIC (translocon at the inner envelope membrane of chloroplasts) complexes are referred to in this specific issue. **Ling and Javis** summarized recent advances in protein import regulation, particularly in relation to control by the ubiquitin-proteasome system (UPS), and how such regulation changes chloroplast development [27]. The chloroplast protein import is constantly changing depending on varying environmental conditions, as well as external and internal stimuli or different developmental stages. The reviews of **Bölter et al** described the impact of redox-mediated processes on protein import into chloroplasts, which might help readers understand the mechanisms of the dynamics of chloroplast protein import [28]. In contradiction to the classical view, **Nakai** proposed an alternative view regarding the TIC transport system in his paper of this issue [29].

An important characteristic of this specific issue is that the signaling transduction involved in chloroplast biogenesis was concerned. One topic of this area is the plastid retrograde signaling and reader can find some useful information from the paper of **Brzezowski et al**. In this review, the authors discuss the potential role of tetrapyrroles in retrograde signaling and also highlight new findings of research on tetrapyrrole biosynthesis in plants and algae [30]. In the review of **Rochaix and Ramundo**, a new plastid signaling pathway resulted from the depletion of the ClpP protease was discussed [31]. The paper of **Hochmal et al** concerned how the interplay of Ca^{2+} , thylakoid acidification and redox status regulated linear and cyclic electron flow and the novel function of Ca^{2+} in chloroplasts was discussed [32].

At the end of this specific issue, two papers present the overview of chloroplast biogenesis and many factors influencing chloroplast biogenesis in plants are integrated. The readers can find much knowledge that has not been covered above. Especially, the paper of **Belcher et al** summarizes contributions from a genetic resource in maize, the Photosynthetic Mutant Library (PML) [33]. The comparison between maize and other organisms reveals the divergence between monocot and dicot plants in chloroplast biogenesis, which is also highlighted in the paper of **Pogson et al** [34].

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Dr. Lixin Zhang is a professor and deputy director of Institute of Botany, Chinese Academy of Sciences. He received his bachelor's degree in Biology from Sichuan University in 1992 and obtained his Ph.D in Biology from Lanzhou University. He has been a postdoctor with Eva-Marie Aro from Department of Biology, University of Turku, and Klaas Jan van Wijk from Department of Biochemistry, Stockholm University. He now works in Photosynthesis Research Center, Institute of Botany, Chinese Academy of Sciences. His research interests include synthesis, assembly and degradation of photosynthetic protein complexes, chloroplast protein import, gene expression and intracellular signaling.

Lixin Zhang
Photosynthesis Research Center, Key Laboratory of Photobiology,
Institute of Botany, Chinese Academy of Sciences Nanxincun 20,
Xiangshan, Beijing, 100093, CHINA
Corresponding author at: Tel.: +86 10 62836256
E-mail address: zhanglixin@ibcas.ac.cn.