

Contents lists available at ScienceDirect

Biochimica et Biophysica Acta

journal homepage: [www.elsevier.com/locate/bbabbio](http://www.elsevier.com/locate/bbabbio)

## Q4 Carotenoids are essential for the assembly of cyanobacterial photosynthetic complexes

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### 1 0 A R T I C L E I N F O

11 Article history:  
12 Received 27 April 2015  
13 Received in revised form 26 May 2015  
14 Accepted 29 May 2015  
15 Available online xxx

16 Keywords:  
17 Carotenoid deficiency  
18 Cyanobacterial photosynthesis  
19 Phycobilisome  
20 Photosynthetic complexes  
21 Time-resolved fluorescence

### A B S T R A C T

In photosynthetic organisms, carotenoids (carotenes or xanthophylls) are important for light harvesting, photoprotection and structural stability of a variety of pigment–protein complexes. Here, we investigated the consequences of altered carotenoid composition for the functional organization of photosynthetic complexes in wild-type and various mutant strains of the cyanobacterium *Synechocystis* sp. PCC 6803. Although it is generally accepted that xanthophylls do not play a role in cyanobacterial photosynthesis in low-light conditions, we have found that the absence of xanthophylls leads to reduced oligomerization of photosystems I and II. This is remarkable because these complexes do not bind xanthophylls. Oligomerization is even more disturbed in *crhH* mutant cells, which show limited carotenoid synthesis; in these cells also the phycobilisomes are distorted despite the fact that these extramembranous light-harvesting complexes do not contain carotenoids. The number of phycocyanin rods connected to the phycobilisome core is strongly reduced leading to high amounts of unattached phycocyanin units. In the absence of carotenoids the overall organization of the thylakoid membranes is disturbed: Photosystem II is not formed, photosystem I hardly oligomerizes and the assembly of phycobilisomes remains incomplete. These data underline the importance of carotenoids in the structural and functional organization of the cyanobacterial photosynthetic machinery.

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### 1. Introduction

In all living systems carotenoids (Cars) are the most widespread pigments with important structural and functional roles [1]. They can be classified as carotenes and their oxygenated derivatives, the xanthophylls. These pigments can be essential for the assembly of protein complexes [2,3], and for maintaining the membrane integrity [4], but

they might also contribute to the regulation of membrane fluidity [5]. In photosynthetic organisms Cars can function as accessory light-harvesting pigments [6,7], but they also serve as photoprotective agents, especially when the organisms are exposed to excess light [8,9]. In particular, Cars are able to quench triplet excited states of chlorophylls (Chls), and directly scavenge singlet oxygen. Due to their hydrophobic characteristics Cars are mostly localized in the thylakoid membrane, most often in the vicinity of or incorporated in pigment–protein complexes.

Cyanobacteria are prokaryotic photosynthetic organisms, the ancestors of plant chloroplasts. They were fundamental participants in the formation of the oxygenic atmosphere on Earth. Nowadays cyanobacteria represent an ecologically important group especially in the oceans; they have a major role in carbon- and nitrogen-fixation and are often present as symbiotic partners. In cyanobacteria the most abundant Cars are  $\beta$ -carotene and various xanthophylls, such as synechoxanthin, canthaxanthin, caloxanthin, echinenone, myxoxanthophyll, nostoxanthin and zeaxanthin [10,11]. X-ray crystallographic studies have revealed that in the cyanobacterium *Thermosynechococcus elongatus* 22 and 12  $\beta$ -carotene molecules are located in photosystem I (PSI) [12] and photosystem II (PSII) [13] [7

*Abbreviations:* APC, allophycocyanin; Car, carotenoid; DAS, decay associated spectrum/spectra; EET, excitation energy transfer; FLIM, Fluorescence Lifetime Imaging Microscopy; LAHG, light activated heterotrophic growth;  $L_R^{33}$ , 33 kDa rod linker protein; PAG, photoautotrophic growth; PC, phycocyanin; PBS, phycobilisome; PSI and PSII, photosystems I and II; RC, reaction center; RC47, PSII monomeric core complex lacking CP43;  $\tau_{av}$ , average lifetime; PPF, Photosynthetic Photon Flux Density; TEs, terminal emitters of the phycobilisomes.

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<http://dx.doi.org/10.1016/j.bbabbio.2015.05.020>

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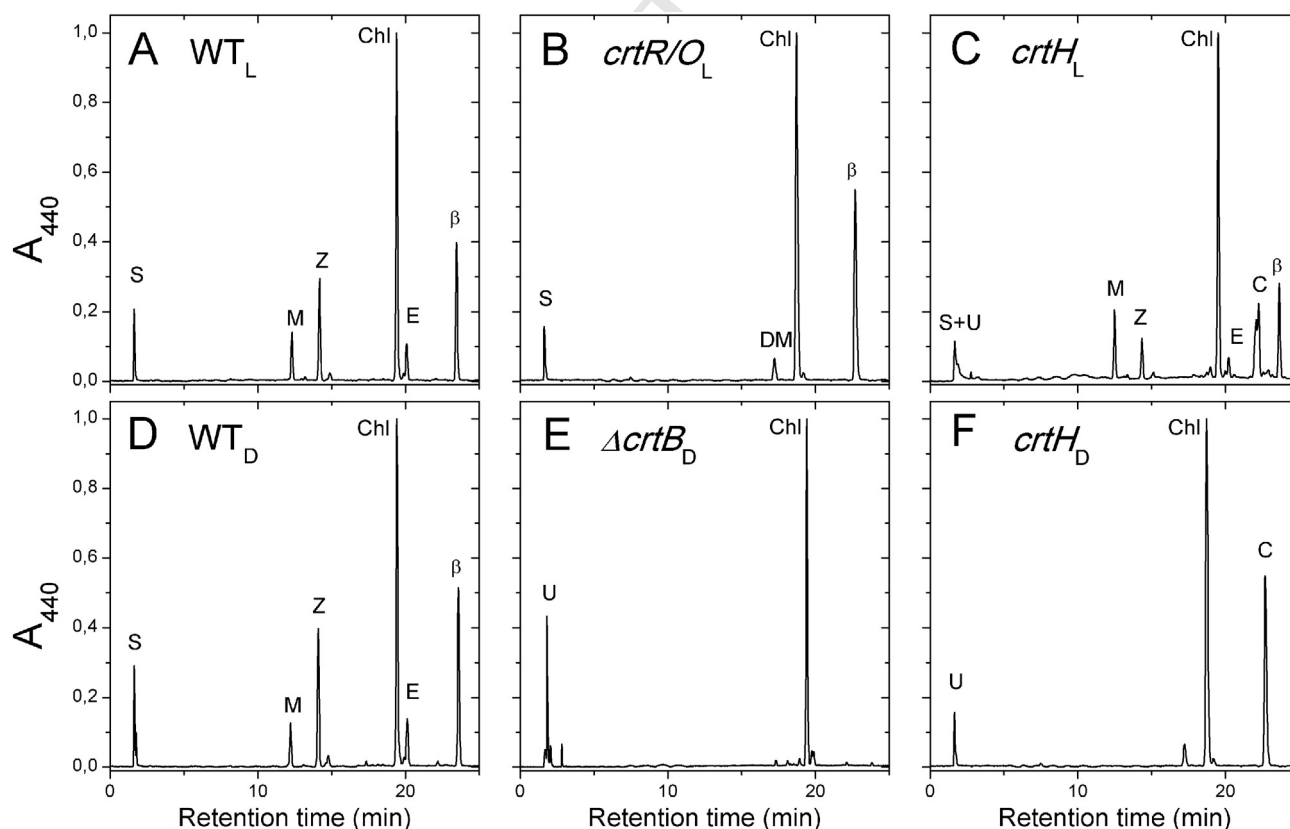
Please cite this article as: T.N. Tóth, et al., Carotenoids are essential for the assembly of cyanobacterial photosynthetic complexes, Biochim. Biophys. Acta (2015), <http://dx.doi.org/10.1016/j.bbabbio.2015.05.020>

monomers, respectively. Also the electron transport component, cytochrome *b<sub>6</sub>f* (cyt*b<sub>6</sub>f*) complex, contains a  $\beta$ -carotene molecule [14]. Recently a new, less abundant  $\beta$ -carotene–protein complex, Ycf39–Hlip, was observed in cyanobacteria, which is involved in the early steps of PSII assembly [15]. In the most often used model organism, *Synechocystis* sp. PCC 6803 (hereafter *Synechocystis*), the most common xanthophylls are zeaxanthin, myxoxanthophyll (myxol-2'-fucosid), echinenone, hydroxy-echinenone and synechoxanthin. Hydroxy-echinenone or echinenone serves as an activator switch in the orange carotenoid protein (OCP), which is responsible for non-photochemical quenching in cyanobacteria [16,17] and protects the cells from oxygen radicals [18]. Occasionally, zeaxanthin can also be inserted into OCP, but with lower affinity and eventually this leads to lower efficiency of OCP [19]. The hydrophobic character of carotenoids leads to their preferential presence in the lipid membrane environment. The majority of Cars, especially xanthophylls are located in the outer, cytoplasmic and thylakoid membranes. Most of them are bound to proteins but they can also be constituents of the lipid phase [10], where they can influence the membrane dynamics and microviscosity [5] and perform protective roles [5,20]. Although the amounts of the xanthophyll molecules and their distribution among the cell compartments are influenced by environmental conditions [21,22], they can be predominantly found in the thylakoid membranes. It is generally accepted that in cyanobacteria zeaxanthin and myxoxanthophyll provide efficient protection against photooxidation and lipid peroxidation under various stress conditions [20,22,23]. In addition, myxoxanthophyll appears to be an important factor in maintaining extended thylakoid membrane sheets [4]. Less information is available about the role of synechoxanthin [24], but it seems that it is mostly present in the

cell membrane, and participates in protecting the cells against high light exposure [25].

Biosynthesis of carotenoids in cyanobacteria has been intensively studied and several mutants deficient in different Cars are available [10,11]. In the  $\Delta crtRO$  double mutant strain of *Synechocystis* an almost complete loss of xanthophylls was obtained by the inactivation of two biosynthetic enzymes (carotene  $\beta$ -ketolase and carotene  $\beta$ -hydroxylase) [26] and thus the mutants contain only  $\beta$ -carotene, synechoxanthin and a myxoxanthophyll precursor, namely deoxy-myxol-2'-dimethyl-fucoside (Fig. 1). The basic photosynthetic processes and membrane integrity appear to be unaffected in this mutant; only the light sensitivity of the cells in high-light intensities increases [26,27]. The *crtH* mutant strain is deficient in the CrH enzyme, which catalyzes the *cis*-to-*trans* isomerization of carotenoids at the early steps of their synthesis. Photo-isomerization can still occur if the cells are cultivated under continuous light conditions [28]. However, photo-isomerization is unable to completely replace the enzymatic *cis*-to-*trans* isomerization [28,29]; the light-grown *crtH* and wild-type cells contain the same Car species, but the ratio of the various Cars is somewhat different [28] (Fig. 1), whereas the dark-grown *crtH* cells are unable to synthesize *trans*-carotenoids due to the lack of both enzymatic and photo-isomerization. This strain can produce only some Car precursors, primarily *cis*-lycopenes and a small amount of all-*trans* carotenes, but no xanthophylls [28,29].

Recently, a completely Car-free  $\Delta crtH/B$  mutant strain has been generated by the inactivation of the *crtB* gene, encoding the phytoene synthase in *crtH* cells [30]. The  $\Delta crtH/B$  mutant cells do not contain phytoene or any downstream carotenoid biosynthesis intermediates. The  $\Delta crtH/B$  cells are extremely light sensitive and only capable of growing in the dark, under light-activated heterotrophic growth (LAHG) [27



**Fig. 1.** HPLC analysis of photosynthetic pigment extracts of wild-type and mutant cells. Chromatograms of WT<sub>L</sub> (A); *crtR/O<sub>L</sub>* (B); *crtH<sub>L</sub>* (C); WT<sub>D</sub> (D);  $\Delta crtB_D$  (E), and *crtH<sub>D</sub>* (F) cells were recorded at 440 nm. The samples containing equivalent chlorophyll concentrations were loaded. Car derivatives were identified on the basis of both their absorption spectra and their retention times.  $\beta$ ,  $\beta$ -carotene; C, *cis*-carotenes; Chl, chlorophyll; DM, deoxy-myxoxanthophyll; E, echinenone; M, myxoxanthophyll; U, unknown non-carotenoid derivatives; Z, zeaxanthin.

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