Emerging Roles of Carotenoids in the Survival and Adaptations of Microbes

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Abstract Carotenoids belong to the widespread group of lipophilic tetraterpenoids that play essential roles in plants, microbes, and animals. In photosynthetic microalgae and cyanobacteria, carotenoids are the fundamental components of photosynthesis and protect these organisms from excess radiations, and oxidative stress. Also, polar xanthophyll carotenoids are well known to regulate the biophysical properties of cellular membranes with respect to corresponding changes in temperature. In Zygomycetes fungi, carotenoids-derived trisporoids play crucial roles in early sexual reproduction and mycelial development. Considering these multifaceted roles, carotenoids are widely researched on. In this article, we highlighted the emerging roles of carotenoids in the survival and adaptations of microalgae, bacteria, and fungi under normal as well as extreme environmental conditions.

Keywords ROS · Non-photochemical fluorescence quenching (NPQ) · Trisporic acids · Cyanobacteria · Xanthophylls

Carotenoids are a subfamily of isoprenoids (also called “tetraterpenoids”) that are synthesized universally by all photosynthetic organisms, including macroalgae, microalgae, and plants, and some non-photosynthetic bacteria, insects and fungi [1]. The unique polyene chain $(-C=C-)_n$ structure with 8–13 conjugated double bond in carotenoid

molecules delivers a resonance-stabilized intermediate for the effective quenching of several classes of cellular oxidants, including singlet oxygen ($^1O^2$) and chlorophyll triplets [2]. These exceptional antioxidant properties of carotenoids channelize and orchestrate crucial pathways in microbes and higher organisms, including photosynthesis, photoprotection, cellular membrane stabilization, and detoxification of reactive oxygen species (ROS) [2, 3]. Also, carotenoids serve as a precursor for the biosynthesis of signaling compounds, which is the key player when it comes to root-mycorrhizal interactions (e.g., strigolactones), reproduction (e.g., trisporic acids in *Mucor*), and adaption under biotic and abiotic stress (e.g., abscisic acid) [4]. A significant correlation between carotenoid accumulation and aggregation and biofilm formation in *Rhodococcus* sp. was recently explored using Raman microspectroscopic approaches [5]. The observation showed a > 3-fold increase in the concentration of intracellular carotenoids within 1 week of biofilm development. Significantly increased levels of oxidative stress in biofilms of *Pseudomonas aeruginosa* has been reported in another study [6]. Thus, it is believed that the increased levels of oxidative stress trigger the enhanced production of cellular antioxidants, including carotenoids.

In photosynthetic organisms, the xanthophyll cycle provides a crucial photoprotective mechanism via dissipation of excess radiations energy; this is referred to as non-photochemical fluorescence quenching (NPQ) [2]. New emerging models for NPQ in plants and microalgae have been recently reviewed [2]. In plants, green algae, and brown algae, xanthophyll cycles consisted of pH-, light-, and transmembrane proton-dependent reversible conversion of violaxanthin (V; containing two epoxide groups) to antheraxanthin (A; one epoxide) and then to zeaxanthin (Z; no epoxide), referred to as the VAZ cycle (Fig. 1).

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Fig. 1 The representation of commonly existing xanthophyll cycles in photosynthetic microbes. The VAZ (violaxanthin-antheraxanthin-zeaxanthin), and diadinoxanthin (Dd)- diatoxanthin (Dt) cycles are modulated by light conditions

Similarly, in diatoms, diadinoxanthin (Dd)- diatoxanthin (Dt) cycle, involving a dynamic one-step de-epoxidation from the mono-epoxy xanthophyll Dd (one epoxide) to Dt (no epoxide group) provide enhanced photoprotection in high light-grown diatom cultures. In the cyanobacteria, NPQ mechanisms involving functional interactions between the Orange Carotenoid Protein (OCP), phycobilisome, and keto-carotenoids, including echinenone, 3'-hydroxyl echinenone, and canthaxanthin. The precise mechanism of OCP photoactivation is still largely unknown. However, Bandara et al. [7] recently explored that pigment (keto-carotenoid)-protein interactions at the β 1 end of the chromophore, followed by protein structural changes lead to OCP photoactivation.

Presence of significant amount of keto-carotenoid in cyanobacteria aids in their increased adaptation under challenging environmental conditions. The colonization of cryptoendolithic cyanobacterial populations dominated by *Chroococcidiopsis* sp., at a high-altitude of Atacama Desert, Chile has been recently studied [8]. Observation revealed that the change in the carotenoid composition (carotenoid red-shift) facilitates the adaptation under excessively light-conditions. Similarly, the cryptoendolithic and hypoendolithic colonization of horizons of algae and cyanobacteria under hyperarid and extremely high solar radiation conditions of Atacama Desert was also investigated [9]. The significantly enhanced accumulation of carotenoids and depletion of chlorophylls in the upper algal cells was observed as an adaptation strategy to counter the lethal effects of higher levels of photosynthetically active radiation (PAR), ultraviolet radiation (UVR), dehydration, and desiccation. In industries, this stress-driven enhanced production of cellular antioxidants possesses potent applications. For instance, UVR including UV band A (UVA, 315 – 400 nm) and UV band B (UVB, 280 – 315 nm), and PAR are used for the significantly enhanced production of commercially vital carotenoids and other metabolites in microbial cultures [1].

In Zygomycetes fungi (e.g., *Mucor*), early sexual morphogenesis and mycelial development are largely regulated by β -carotene derived apocarotenoids called trisporoids. These β -carotene derived singling compounds work as pheromones and assist in recognition of compatible mating partners (Fig. 2a). The key enzymes including 4-dihydrodromethyltrisporate dehydrogenase (TSP1), 4-dihydrotrisporin dehydrogenase (TSP2), and carotenoid cleavage oxygenase (TSP3) have been characterized from Zygomycetes Fungi. Similarly, several C18 trisporoid intermediates have been identified. However, the information regarding their receptors and signals transduction pathways are still not distinctly established [4]. The trisporic acid and sexual mating-induced have shown to significantly enhance production of β -carotene in *Blakeslea trispora* and other Zygomycetes fungi, and this phenomenon is therefore widely exploited by industry for the enhanced production of provitamin A carotenoids [10].

The polyunsaturated fatty acids (PUFA) and xanthophylls (polar carotenoids) are required for providing the proper structure, fluidity, and functioning of the cellular membrane under dynamic conditions of light and temperature. In the liquid crystalline state, xanthophylls restrict the molecular movements of lipids, thus increasing the rigidity of the membrane (Fig. 2b). Zakar et al. [11] studied the dynamic remodeling of xanthophylls, including myxoxanthophyll, zeaxanthin, and deoxymyxoxanthophyll, and PUFA in wild and xanthophyll- and PUFA-deficient mutants of *Synechocystis* sp.. The deficiencies in both PUFA and xanthophylls was found to destabilize photosynthesis I (PSI) trimers with the increased sensitivity of PSII to high mediated photoinhibition. Interestingly, these effects were more pronounced in xanthophyll deficient mutants. Kumar and Morrell-Falvey [3] also reported that *Pantoea* sp. mutants deficient in the gene encoding phytoene synthase (CrtB), which catalyzes the crucial step in the biosynthesis of first C40 carotenoid 15-Z-phytoene, failed to produce other downstream carotenoids and

Fig. 2 **a** A simplified overview of the biosynthetic steps towards trisporic acid in the mating partners of Zygomycetes fungi. The compounds, 4-dihydromethyltrispurate, and trispurin are specifically produced in the (+) and (−) mating type, respectively, which acts as

pheromones towards compatible mating. **b** Presence of polar carotenoids in the cell membrane can favorably modulate the membrane fluidity and other biophysical properties under the changing conditions of temperature

displayed enhanced sensitivity to ROS. The CrtB mutant also exhibited inability of aggregation and biofilm formation and root colonization. Additionally, CrtB mutant cells showed rigid membrane vesicles than wild cells, which indicated that such deficiency of carotenoids in cellular membranes modify the distribution and abundance of membrane lipids and proteins which significantly impact biophysical properties.

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Compliance with Ethical Standards

Conflict of interest The authors declare that there is no conflict of interest relevant to this study.

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