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Review

Carotenoids, versatile components of oxygenic photosynthesis

Ildikó Domonkos, Mihály Kis, Zoltán Gombos *, Bettina Ughy

Institute of Plant Biology, Biological Research Centre of Hungarian Academy of Sciences, P.O. Box 521, H-6701 Szeged, Hungary

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ABSTRACT

Carotenoids (CARs) are a group of pigments that perform several important physiological functions in all kingdoms of living organisms. CARs serve as protective agents, which are essential structural components of photosynthetic complexes and membranes, and they play an important role in the light harvesting mechanism of photosynthesizing plants and cyanobacteria. The protection against reactive oxygen species, realized by quenching of singlet oxygen and the excited states of photosensitizing molecules, as well as by the scavenging of free radicals, is one of the main biological functions of CARs. X-ray crystallographic localization of CARs revealed that they are present at functionally and structurally important sites of both the PSI and PSII reaction centers. Characterization of a CAR-less cyanobacterial mutant revealed that while the absence of CARs prevents the formation of PSII complexes, it does not abolish the assembly and function of PSI. CAR molecules assist in the formation of protein subunits of the photosynthetic complexes by gluing together their protein components. In addition to their aforementioned indispensable functions, CARs have a substantial role in the formation and maintenance of proper cellular architecture, and potentially also in the protection of the translational machinery under stress conditions.
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Contents

Abbreviations: AACT, acetoacetyl-CoA thiolase; ADP, adenosine diphosphate; APC, allophycocyanin; ATP, adenosine triphosphate; BChl, bacteriochlorophyll; CAR, carotenoid; CDP-ME2P, 4-(citidine 5′-diphospho)-2-C-methyl-D-erythritol; Chl, chlorophyll; CHYβ, β-hydroxylase; CHYε, ε-hydroxylase; CMP, cytidine monophosphate; CP43, chlorophyll–protein complex 43; CP47, chlorophyll–protein complex 47; CrtB, phytoene synthase; CrtH, *cis*-to-*trans* carotenoid isomerase; CrtI, bacterial type carotene isomerase; CrtISO, *cis*-to-*trans* carotenoid isomerase; CrtL, lycopene cyclase; CrtO, carotene β-ketolase; CrtP, phytoene desaturase; CrtQ, ζ-carotene desaturase; CrtR, carotene β-hydroxylase; CrtW, carotene β-ketolase; CruA, lycopene β-cyclase; CruE, β-carotene desaturase/methyltransferase; CruF, γ-carotene 1′-hydroxylase; CruG, 2′-*O*-glycosyltransferase; CruH, C-18 hydroxylase; CruP, lycopene β-cyclase; CTP, cytidine triphosphate; DDE, *diadinoxanthin de-epoxidase*; Ddx, diadinoxanthin; DEP, diatoxanthin epoxidase; DMAPP, dimethylallyl diphosphate; Dtx, diatoxathin; DXP, 1-deoxy-D-xylulose 5-phosphate; DXR, 1-deoxy-D-xylulose 5-phosphate reducto-isomerase; DXS, 1-deoxy-D-xylulose 5-phosphate synthase; EF-G, elongation factor G; GAP, D-glyceraldehyde 3-phosphate; GGPP, geranylgeranyl diphosphate; HMBDP, (*E*)-1-hydroxy-2-methyl-2-butenyl diphosphate; HMG-CoA, β-hydroxy-β-methylglutaryl-CoA; HMGR, HMG-CoA reductase; IPP, isopentenyl diphosphate; LCYβ, lycopene β-cyclase; LCYε, lycopene ε-cyclase; LHC, light harvesting complex; LHCI, light harvesting complex of PSI; LHCII, light harvesting complex of PSII; LHCSR, light harvesting stress response protein; MECDP, 2-C-methyl-D-erythritol 2,4-cyclodiphosphate; MEP, 2-C-methyl-D-erythritol 4-phosphate; MEP, methylerythritol phosphate; MVA, mevalonic acid; $NADP^+$, nicotinamide adenine dinucleotide phosphate; NADPH, reduced nicotinamide adenine dinucleotide phosphate; NPQ, non-photochemical quenching; NSY, neoxanthin synthase; OCP, orange carotenoid protein; PCP, peridinin–Chl *a* protein; PDS, phytoene desaturase; PSI, photosystem I; PSII, photosystem II; PSY, phytoene synthase; RC47, CP43-less CP47-containing reaction center of PSII; ROS, reactive oxygen species; VDE, violaxanthin de-epoxidase; ZDS, ζ-carotene desaturase; ZEP, zeaxanthin epoxidase; Z-ISO, 15-*cis*-ζ-carotene isomerase.

* Corresponding author. Tel.: +36 62599704; fax: +36 62433434.
E-mail addresses: gombos.zoltan@brc.mta.hu, gombos.zoltan@gmail.com (Z. Gombos).

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1. Introduction

CARs are ubiquitous protective agents in the membranes of all photosynthetic organisms. Although several aspects of CAR functions are still to be elucidated, a growing body of evidence suggests that they play important roles in cyanobacteria and the chloroplasts and other organelles of green plants. In cyanobacteria and plants that are capable of oxygenic photosynthesis the majority of CARs are found in thylakoid membranes where the light reactions of photosynthesis take place. Therefore it has been suggested that these compounds perform important functions in the primary processes of photosynthesis. Among CARs β-carotene and several xanthophylls serve as constituents of functional multiprotein complexes, such as photosystems I and II (PSI, PSII), cytochrome b_6/f complexes, and the light-harvesting complexes involved in photosynthetic electron transport. In these superstructures protein components are surrounded by and bound together by specific CARs, presumably by means of hydrophobic interactions.

The roles of various CARs in photosynthetic organisms have previously been studied using either biochemical or molecular genetic approaches. However, the information regarding their precise functions is still limited. The recent identification of genes encoding CAR biosynthetic enzymes in cyanobacteria and plants, and the subsequent isolation of mutants defective in these functions, have provided powerful molecular tools for studying the roles of individual CAR species in these organisms. It has become apparent that CARs are essential for the assembly and stabilization of protein complexes in thylakoid membranes, and also for some non-photosynthetic processes. In this review we summarize recent findings concerning the biosynthesis and functions of CARs in photosynthetic organisms, primarily in cyanobacteria and higher plants. We overview the effects of free, non-protein-bound CARs on membrane microviscosity and the ways how these molecules can modulate membrane dynamics via CAR-lipid–protein interactions. We also assess the structural changes observed in cyanobacterial CAR mutants and highlight the photoprotective roles of CARs, especially those of the orange carotenoid protein, in the defense mechanism against various stress effects. Furthermore, we also discuss a CAR-based mechanism that might have a role in protecting elongation factors of the translational machinery from oxidative damage.

2. Biosynthesis of CARs

CARs belong to the huge family of terpenoids and, accordingly, they are composed of the five-carbon units 2-methyl-1,3-butadiene, also referred to as isoprene [1]. CARs are tetraterpenoids, which are composed of eight condensed C5 isoprene precursors that generate a C40 linear backbone (Fig. 1). They can be divided into the class of hydrocarbons, the carotenes and their oxygenated derivatives, the xanthophylls. The biosynthesis of CARs involves successive condensations of the two interconvertible forms of active isoprene: isopentenyl diphosphate (IPP) and its double-bond-containing isomer dimethylallyl diphosphate (DMAPP).

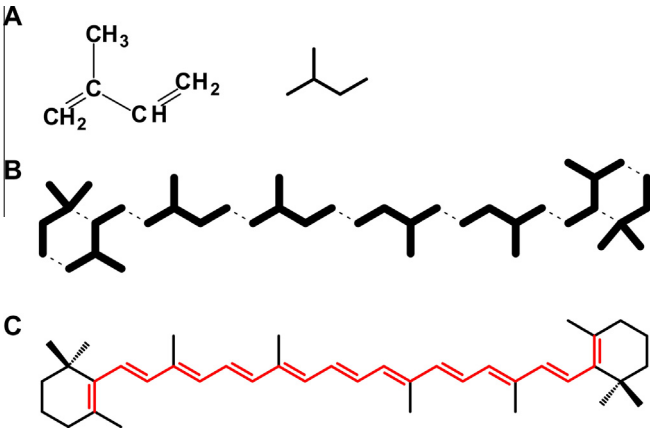

Fig. 1. Isoprenoids, including carotenoids, are derived from isoprene, 2-methyl-1,3-butadiene (A). β-Carotene is composed of eight five-carbon isoprenoid units (B). In the structure of β-carotene the central linear conjugated system contains eleven double bonds (shown in red) (C).

There are two non-related biosynthetic pathways for the synthesis of IPP and DMAPP, namely the mevalonic acid (MVA) and the methylerythritol phosphate (MEP) routes. Cyanobacteria possess only the MEP pathway. Eukaryotic phototrophs acquired MEP pathway genes by endosymbiosis with an ancient cyanobacterial lineage, the assumed ancestor of chloroplasts. Land plants and some groups of algae retained both pathways, while green algae (Chlorophyta) use only the MEP route. Among red algae there are examples for both the presence and absence of the MVA pathway. For a more detailed picture further studies are required, especially among the various groups of algae [2–5].

The MVA pathway is localized in the cytosol and it is responsible for the formation of steroids, sesquiterpenes, triterpenes, polyterpenes. It also supplies the IPP that is imported in the mitochondria and serves as precursor for the prenyl side chain of ubiquinones. The chloroplast-localized MEP pathway provides IPP and DMAPP for the biosynthesis of prenylquinones, monoterpenes and the phytyl side chain of chlorophylls (Chls). Although there is considerable exchange between the common intermediates of the two pathways, however, this is not sufficient for complementing the loss of either of the two pathways [3,6].

2.1. The MEP pathway

The first step in this pathway is the formation of 1-deoxy-D-xylulose 5-phosphate (DXP) by the condensation of pyruvate and D-glyceraldehyde 3-phosphate (GAP). The carboxyl group of pyruvate is lost as CO_2 (Fig. 2). The enzyme 1-deoxy-D-xylulose 5-phosphate synthase (DXS) catalyzing this reaction uses thiamine diphosphate as cofactor and requires a divalent cation, such as Mg^{2+} or Mn^{2+}. The sequel enzyme, 1-deoxy-D-xylulose 5-phosphate reducto-isomerase (DXR, also referred to as MEP synthase),

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