



Research review paper

Occurrence and biosynthesis of carotenoids in phytoplankton



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ABSTRACT

Naturally occurring carotenoids are important sources of antioxidants, anti-cancer compounds and anti-inflammatory agents and there is thus considerable market demand for their pharmaceutical applications. Carotenoids are widely distributed in marine and freshwater organisms including microalgae, phytoplankton, crustaceans and fish, as well as in terrestrial plants and birds. Recently, phytoplankton-derived carotenoids have received much attention due to their abundance, rapid rate of biosynthesis and unique composition. The carotenoids that accumulate in particular phytoplankton phyla are synthesized by specific enzymes and play unique physiological roles. This review focuses on studies related to the occurrence of carotenoids in different phytoplankton phyla and the molecular aspects of their biosynthesis. Recent biotechnological advances in the isolation and characterization of some representative carotenoid synthases in phytoplankton are also discussed.

Abbreviation: 1,3-BPGA, 1,3-bisphosphoglycerate; 3-PGA, 3-phosphoglycerate; aa, amino acids; ABA2, xanthoxin dehydrogenase; ABA3, abscisic aldehyde oxygenase; AS, antisense; APE, *al*-3 proximal element; ATP, adenosine triphosphate; CDMDE, 4-(cytidine 5'-diphospho)-2-C-methyl-D-erythritol; CEC, 2-C-methyl-D-erythritol 2,4-cyclodiphosphate; ChRs, channelrhodopsin photoreceptor proteins; CLD, chain length determination; CMK, 4-(cytidine 5'-diphospho)-2-C-methyl-D-erythritol kinase; CMS, 4-diphosphocytidyl-2-C-methyl-D-erythritol synthase; CrtA, spheroidene monooxygenase; CrtB, phytoene synthase; CrtC, hydroxyneurosporene synthase; CrtD, C-3',4' desaturase; CrtE, geranylgeranyl diphosphate synthase; CrtG, 2,2'-β hydroxylase; CrtH, *cis-to-trans* carotene isomerase; CrtI, cyanobacterial phytoene desaturase; CrtL/LYC/LCY, lycopene β-cyclase; CrtL-b, lycopene β-cyclase; CrtL-e, lycopene *e*-cyclase; CrtO, β-carotene monoketolase; CrtP, phytoene desaturase; CrtQ, ζ-carotene desaturase; CrtR, β-carotene hydroxylase; CrtU, β-carotene desaturase; CrtW/BKT, β-carotene diketolase; CrtY, bacterial lycopene cyclase; CrtZ/CHYB, microalgal β-carotene hydroxylase; CruA, lycopene cyclase; CruE, β-carotene desaturase/methyltransferase; CruF, C-1' hydroxylase; CruG, 2'-O glycosyltransferase; CruH, ring-hydroxylating dioxygenase; CruP, lycopene cyclase; DDE, diadinoxanthin de-epoxidase; DdxS, diadinoxanthin synthase; DEP, diatoxanthin epoxidase; Diox1, retinal synthesizing enzyme; DMAPP, dimethylallyl diphosphate; DME, 2-phospho-4-(cytidine 5'-diphospho)-2-C-methyl-D-erythritol; DOXP, 1-deoxy-D-xylylose 5-phosphate; DRE, dehydration responsive element; DXR, 1-deoxy-D-xylylose 5-phosphate reductoisomerase; DXS, DOXP synthase; FAD, flavin adenine dinucleotide; FARM, first aspartate-rich motif; FCP, fucoxanthin chlorophyll *a/c* binding proteins; FCPa, trimeric fucoxanthin chlorophyll *a/c* binding protein; FCPb, oligomeric fucoxanthin chlorophyll *a/c* binding protein; FPP, farnesyl pyrophosphate; FxS, fucoxanthin synthase; G3P, glyceraldehyde 3-phosphate; G3PD, glyceraldehyde 3-phosphate dehydrogenase; GDP, guanosine 5'-diphospho; GGPP, geranylgeranyl diphosphate; GGPPS, geranylgeranyl diphosphate synthase; GPP, geranyl pyrophosphate; GPPS, geranyl pyrophosphate synthase; GSB, green sulfur bacteria; HDR, HD reductase; HDS, (E)-4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase; hECN, 3'-hydroxyechinenone; HMED, 4-hydroxy-3-methylbut-2-en-1-yl diphosphate; H-type, Hypsochromic-type; IPP, isopentenyl diphosphate; IR, inverted repeat; J-type, Jelly-type; LC-MS, liquid chromatography-mass spectrometry; LCYB, lycopene β-cyclase; LCYE, lycopene *e*-cyclase; LHC, light-harvesting complex; Lhcf, light-harvesting complex with fucoxanthin; Lhcr, light-harvesting complex related to red algae; LhCSR, light harvesting complex stress-related; Lhcv, light-harvesting complex with violaxanthin; Lhcx, light-harvesting complex in green algae and diatoms; LSX, linoxanthin synthase; MCS, 2-C-methyl-D-erythritol 2,4-cyclodiphosphate synthase; MEP, 2-C-methyl-D-erythritol 4-phosphate/methylerythritol phosphate; MGDG, monogalactosyl-diacylglycerol; MgDV, magnesium 2,4-divinyl phaeoporphyrin *a5* monomethyl ester; MPTA, 2-(4-methylphenoxy) triethylamine hydrochloride; MVA, mevalonic acid; NADPH, nicotinamide adenine dinucleotide phosphate; near-UV, near-ultraviolet; NPQ, non-photochemical fluorescence quenching; NSY, neoxanthin synthase; NxS, neoxanthin synthase; OCP, orange carotenoid protein; ORF, open reading frames; PBS, phycobilisome; PCP, peridinin-chlorophyll *a* protein complex; PCR, polymerase chain reaction; PDS, phytoene desaturase; PGAK, phosphoglycerate kinase; PPPP, prephytoene pyrophosphate; PSII, photosystem II; Psy, microalgal phytoene synthase; Pys, cyanobacterial phytoene synthase; qPCR, quantitative PCR; ROS, reactive oxygen species; RuBisCo, ribulose-1,5-bisphosphate carboxylase oxygenase; RuBP, ribulose-1,5-bisphosphate; RuPK, ribulose 5-phosphate; SARM, second aspartate-rich motif; SRE, sterol regulatory element; TTET, triplet-triplet energy transfer; UFAs, unsaturated fatty acids; UTR, untranslated region; UV, ultraviolet; UVA, ultraviolet band A; UVB, ultraviolet band B; VCP, violaxanthin-chlorophyll *a* protein; VDE, violaxanthin de-epoxidase; WcaG, GDP-fucose synthetase; ZDS, ζ-carotene desaturase; ZEP, zeaxanthin epoxidase

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Table 1
Distribution of carotenoids in phytoplankton^a.

Carotenoids	Phytoplankton phyla																											
	Bac ^a	Bol ^b	Chc ^c	Chl ^d	Chm ^e	Chs ^f	Coc ^g	Cry ^h	Cyb ⁱ	Dic ^j	Dif ^k	Eug ^l	Eus ^m	Gla ⁿ	Hap ^o	Mes ^p	PeI ^q	Pha ^r	Pin ^s	Prat ^t	Pro ^u	Pry ^v	Rep ^w	Rho ^x	Syn ^y	Trv ^z	Xan ^y	
Carotenes																												
α-Carotene	++	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
β-Carotene	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
γ-Carotene																												
ε-Carotene																												
Lycopene																												
Xanthophylls																												
Alloxanthin																												
Antheraxanthin																												
Astaxanthin																												
Auroxanthin																												
19'-B-fucoxanthin ^A																												
Caloxanthin																												
Canthaxanthin																												
Crococanthin																												
Cryptoxanthin																												
Diadinoxanthin																												
Diatoxanthin																												
Dihydroleutin																												
Dinoxanthin																												
Echinenone																												
Eutryptellanone																												
Fucoxanthin																												
Gyroxanthin DE ^B																												
19'-H-fucoxanthin ^C																												
19'-H-4k-fucoxanthin ^D																												
Loroxanthin																												
Loroxanthin dodecenoate																												
Lutein																												
Micromonal																												
Micromonol																												
Monadoxanthin																												
Mutatoxanthin																												
Myxoxanthophyll																												
9'-cis-Neochrome																												
9'-cis-Neoxanthin																												
All-trans-Neoxanthin																												
Nostoxanthin																												
Oscillol diquinovoside																												
Peridinin																												
Prasincoxanthin																												
Siphonaxanthin																												
Siphonaxanthin D ^F																												
Uriolide																												
Vaucheriaxanthin																												
Vaucheriaxanthin EO ^F																												

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