POLISH JOURNAL OF FOOD AND NUTRITION SCIENCES
Pol. J. Food Nutr. Sci. 2006, Vol. 15/56, No 4, pp. 385–389

MOLECULAR VIEW ON THE CAROTENOGENESIS IN PLANTS – A MINI REVIEW

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Key words: carotenogenesis, carotenogenic enzymes, carotenogenic genes in plants

Carotenoids play an integral and essential role in photosynthesis and photoprotection in plants. They are isoprenoid pigments that also function as precursors of the plant growth hormone – abscisic acid (ABA) or components of flavor, colorants and nutraceuticals. Carotenogenesis (carotenoid biosynthesis) and its regulation have been studied in many plant species. The cloning and characterization of plant carotenogenic genes has provided new gene resources and molecular tools which are used to attain a new level of molecular understanding of carotenoid biochemistry and genetics. The knowledge can also be utilized to optimize carotenoids accumulation in crop plant.

INTRODUCTION

Photosynthetic plants are the most abundant carotenogenic organisms. Carotenoids are a diverse group of pigments that are important in many biochemical and biophysical processes of plants [Cunningham *et al*., 1998; Bouvier *et al.,* 2005; Moise *et al.,* 2005] and some microorganisms [Armstrong, 1994; Bhosale, 2004]. They are essential for the structure and function of pigment-binding protein complexes and the prevention of photooxidative damage. In the chloroplast, the majority of carotenoids are located in pigment-binding proteins embedded in the thylacoid membrane. This is the place where they provide structure and support to the associated proteins and participate in light-harvesting processes, by absorbing light at 450–550 nm [Moise *et al*., 2005]. Carotenoids dissipate excess light energy absorbed by antenna pigments which play a crucial role in the protection of the photosynthetic apparatus from photooxidative damage by quenching triplet chlorophyll and singlet oxygen. They are essential pigments responsible for the yellow, orange and red coloration of flowers and fruits important to attract animals for pollination and seed dispersion. Lutein and violaxanthin are the major carotenoids in chloroplast-containing tissue, whereas during fruit development cryptoxanthin, zeaxantin and violaxantin progressively accumulate in the tissue [Rodrigo *et al.,* 2004]. In addition, carotenoids are precursors of apocarotenoids, such as the plant growth hormone – abscisic acid (ABA). Volatile terpenoid compounds, derived from carotenoids, are important components of flavor and aroma in a variety of fruits, vegetables and ornaments [Simkin *et al*., 2004].

Carotenoids and their metabolites have complementary physiological actions in both plant and animals. Animals do not synthesize carotenoids *de novo,* but they share common carotenoid-modifying enzymes with plants [Moise *et al*., 2005]. The relationship between plant and animal carotenoid-modifying enzymes could lead to a new impetus for the discovery of more genes, enzymes and proteins involved in their metabolism [Moise *et al.,* 2005].

Ample papers have shown the important role of carotenoids as bioactive phytochemicals to maintain a good health status [Record *et al.,* 2001; Yamini *et al*., 2001; Panfili *et al*., 2004, Dembinska-Kiec *et al*., 2005; Kiec-Wilk *et al.,* 2005]. Based on extensive epidemiological observation, fruits and vegetables that are a rich source of carotenoids are thought to provide health benefits by decreasing the risk of various diseases, particularly certain cancers [Fenech *et al*., 2005; Dulinska *et al*., 2005; Bodzioch *et al*., 2005] and eye diseases. The carotenoids that have been most studied in this regard are beta-carotene, lycopene, lutein and zeaxanthin. In part, the beneficial effects of carotenoids are thought to be due to their role as antioxidants [Stahl *et al.,* 2000]. Beta-carotene may have added benefits due to its ability to be converted to vitamin A. In addition, lutein and zeaxanthin may be protective in eye disease because they absorb damaging blue light that enters the eye. Food sources of these compounds include a variety of fruits and vegetables, although the primary sources of lycopene are tomato and tomato products [Bhuvaneswari & Nagini, 2005]. Lycopene is reported to be one of the most stable carotenoid. Additionally, egg yolk is a highly bioavailable source of lutein and zeaxanthin. Carotenoids are available in a supplement form. However, until the efficacy and safety of taking supplements containing these nutrients can be determined, current dietary recommendations of diets high in fruits and vegetables are advised [Krinsky & Johnson, 2005].

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CAROTENOID BIOCHEMISTRY

Carotenoids are a widely distributed class of structurally and functionally diverse natural pigments, consisting of more than 600 isoprenoid compounds that contain up to 15 double bonds. These biologically-active components typically consist of a C_{40} hydrocarbon backbone in the case of carotenes, often modified by various oxygen-mediated functional groups to produce cyclic or acyclic xanthophylls. The degree of conjugation and the isomerisation state of the backbone polyene chromophore determine the absorption properties of each carotenoid. Compounds with at least seven conjugated double bonds, such as ξ-carotene, absorb visible light. Carotenoids can occur naturally as *trans*- and *cis*-isomers [Moise *et al.,* 2005].

Biochemistry of carotenoid biosynthesis pathway

Carotenoids are derived from general isoprenoid biosynthetic pathway. It has been recently described in details by Moise *et al.* [2005] (Figure 1).

The initial strategy of biosynthesis is to supply the isoprenoid precursor C_{20} – geranylgeranyl pyrophosphate (GGPP). It is formed by the condensation of isopentenyl diphosphate (IPP) and dimethyllyl diphosphate (DMAPP) usually in plastids [Botella-Pavia *et al*., 2004]. The condensation of two GGPP molecules results in 15-*cis*-phytoene. The formation of the colorless carotenoid precursor is the first committed step in the pathway and is catalyzed by the enzyme phytoene synthase (PSY). Conversion of phytoene to lycopene occurs through desaturation steps. In plants the process is carried out by two desaturases: phytoene desaturase (PDS) and ξ-carotene desaturase (ZDS). PDS produce the first colored carotenoid in the pathway, 9,9'-di-cis-ξ-carotene from phytoene by *trans*-H elimination at 11,11' using plastoquinone as an intermediate and oxygen as the final electron acceptor. The origin of the 9 and 9' *cis*-bonds is not well established [Moise *et al*., 2005]. The desaturation of 15-*cis*-phytoene to 9,9'-di-*cis*-ξ-carotene was shown to occur *via* PDS-mediated desaturation to 9,15,9'-tri-*cis*-ξ-carotene with a 15,9'-di-*cis*-phytofluene intermediate [Breitenbach & Sandmann, 2005]. The 15-*cis*-bond of 9,15,9'-tri-*cis*-ξ-carotene can be isomerized to *trans* by light or by unidentified enzyme [Moise *et al.,* 2005]. ZDS from plants catalyze *cis*-H elimination at 7,7' to produce 7,9,9',7'-tetra-*cis*-lycopene. The isomerization of 7,9,9',7'-tetra-*cis*-lycopene to all-*trans*--lycopene is carried out by the carotenoid *cis-trans*-isomerase (CRTISO). The synthesis pathway can act independently of the status of the other end of the polyene chain [Isaacson *et al.,* 2004]. Several observed reaction intermediates, such as 9,15-*cis*-phytofluene, 7,9,9'-tri-*cis*-neurosporene, 9'-*cis*-neurosporene or 7',9'-di-*cis*-lycopene, can be explained by desaturation and/or isomerization of one of the polyene chain and not the other [Isaacson *et al.,* 2004]. Modification of the carotenoid end group results in many variations in color. Lycopene can be cyclized by β-cyclases to generate only one β-ionone ring, as seen in γ-carotene, or it can be cyclized at both ends to produce β-carotene. There are also ε-cyclases that can cyclize one end of one β-ionone ring to generate δ-carotene or ε-carotene if both ends are cyclized. The action of ε- and β-cyclases produce α-carotene, the precursor of lutein. β-Hydroxylase converts β-carotene to xanthophyll zeaxanthin, whereas zeaxanthin epoxidase catalyzes the formation of violaxanthin by epoxidation at the 5,6 and 5',6' double bonds at the β-ionone ring. Hydroxylation of the 3 carbon of the ε-ionone ring of α-carotene generates α-cryptoxanthin. This reaction is carried out by ε-hydroxylase [Tian *et al*., 2004].

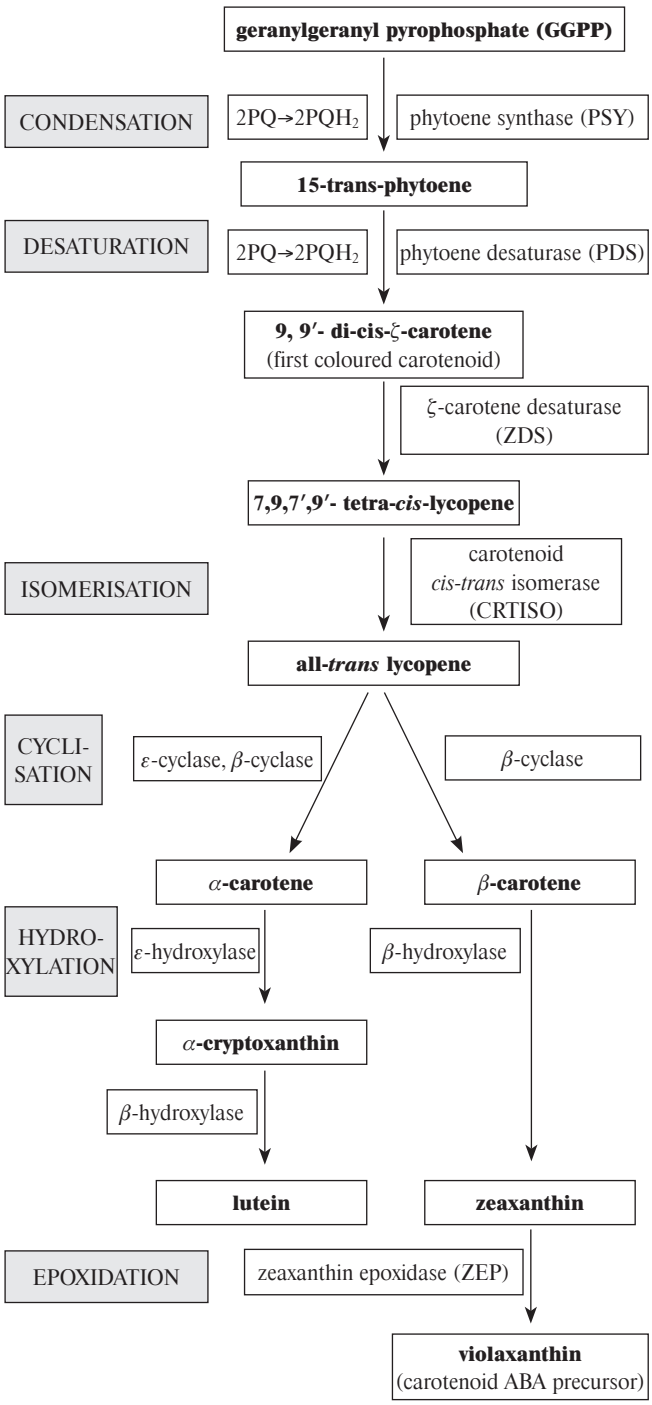

FIGURE 1. Synthesis of carotenoids in plants. The pathway is adopted from those proposed by Armstrong *et al.* [1994], Hirschberg [2001], Giuliano *et al.* [2002], and Moise *et al*. [2005]. (Abr: PQ – plastoquinone, PQH_2 – hydrogened plastoquinon; carotenoid and their precursors are marked in bold; detailed description in the text).

Hydroxylation of the carotenoid epsilon-ring is an essential reaction for the formation of lutein, the most abundant carotenoid in photosynthetic tissue. Tian and colleagues

[2004] as well as Inoue [2004] reported that plant cytochrom P450 monooxygenase is responsible for this reaction.

MOLECULAR REGULATION OF CAROTENOID BIOSYNTHESIS PATHWAY

The general scheme of carotenoid biosynthesis has been known for more than three decades. However, molecular description of the pathway in plants began only in the 1990s after the genes for the carotenogenic enzymes were cloned [Hirschberg, 2001]. Carotenoid biosynthesis regulation has been studied in various plant species, such as *Arabidopsis thaliana* [von Lintig *et al.,* 1997; Welsch *et al.,* 2003], bitterwort (*Gentiana lutea*) [Zhu *et al.,* 2002], orange (*Citrus sinesis*) [Rodrigo *et al.,* 2004], rice (*Oryza sativa*) [Paine *et al.,* 2005], tomato (*Lycopersicon esculentum*) [Fraser *et al.,* 1994; Simkin *et al.,* 2004], or sunflower (*Helianthus annuus*) [Salvini *et al.,* 2005]. Molecular comparative descriptions of the carotenogenic genes in plants are widely available [Welsch *et al.,* 2003; Salvini *et al*., 2005; Yan *et al.,* 2005]. The phytoene synthase gene (*psy*), the first gene within the carotenoid biosynthetic pathway, and its regulation seems to be the most detailed characterized.

A full-lengh nucleotide sequence of the *psy* cDNA differs in various plant species (Table 1).

Phylogenic analysis demonstrated that the sunflower *psy* (*Hapsy*) clustered with the marigold (*Tagetes erecta*) *psy* gene, with which it showed an overall amino acid identity of 97.7% [Salvini *et al.,* 2005]. The relationship between alga, *Dunaliella salina,* and higher plants amino acid PSY sequence is not so close and reaches 78–89% of similarity [Yan *et al*., 2005].

The sunflower phytoene synthase (HaPSY) predicted protein (46.8kDa) displays a sequence of 414 amino acid residues with a putative transite sequence for plastid targeting in the N-terminal region [Salvini *et al.,* 2005]. The molecular mass of a tomato single protein is 38 kDa and the size of the transit peptide of phytoene synthase from ripe tomato fruit is approximately 9 kDa (about 80 amino acid residues) [Misawa *et al.,* 1994].

The expression of the gene coding for the carotenogenic enzyme phytoene synthase is highly regulated. It has been reported that PSY from white mustard was regulated by light [Lintig *et al.,* 1997]. The full-length promoter of the gene from *Arabidopsis thaliana* was shown to be active in the dark, but mediated positive responses towards different light qualities (far-red, red, blue and white light). Response towards different light qualities was mediated by a TATA box-proximal promoter region (ATCTA) up to position -300, containing G-box-like elements involved in the distinction of different monochromatic light qualities [Welsch *et al.,* 2003]. A *cis*-acting ATCTA motif occurring in tandem between positions -854 and -841 represents an element capable of mediating a coordinated regulation of the expression of photosynthesis-related genes. The motif was found in several other promoter regions involved in carotenoid and tocopherol biosynthesis [Welsch *et al.*, 2003].

Light did not influence either PDS nor GGPS expression level from white mustard (*Sinapsis alba*) [Lintig *at al.,* 1997].

The carotenogenic genes show tissue-specific expression pattern. The phenomenon was investigated during flower [Zhu *et al.,* 2002] and fruit development and maturation [Fraser *et al.,* 1994; Rodrigo *et al.,* 2004]. The intense expression of *psy* and *pds* gene was detected in bitterwort and tomato flowers as well as in tomato fruits in parallel with the formation of carotenoids [Fraser *et al.,* 1994; Zhu *et al.,* 2002]. *Pds* gene expression from orange (*Citrus sinesis*) also corre-

TABLE 1. Major carotenogenic genes and gene products in plants.

Gene	Demonstrated gene product (protein)	Organism(s)	Gene length (mRNA)	References (The Entrez Nucleotide Database*) Accession numbers
psy	phytoene synthase (PSY)	*Oryza sativa*	1263 bp	AJ715786
		Capsicum annuum	1295 bp	X68017
		Tagetes erecta	1376 bp	AY099482
		Oncidium Gower Ramsey	1383 bp	AY973631
		Helianthus annuus	1598 bp	HAN304825
pds	phytoene desaturase (PDS)	*Tagetes erecta*	1156 bp	AY099483
zds1	zeta-carotene desaturase (ZDS1)	*Malus domestica*	2033 bp	AF429983
zds2	zeta-carotene desaturase (ZDS1)	*Malus domestica*	2155 bp	AF429984
crtiso	carotenoid isomerase (CrtISO)	*Lycopersicon esculentum*	2374 bp	AF416727
lcy-b	beta-cyclase	*Tagetes erecta*	1471 bp	AY099484
lcy-e	epsilon-cyclase	*Tagetes erecta*	1916 bp	AY099485
β-chx	*β*-carotene hydroxylase	*Crocus sativus*	891 bp	AY579207
lut1	*ε*-hydroxylase	*Arabidopsis thaliana*	1620 bp	AY424805
zep	zeaxantin epoxidase (ZEP)	*Citrus sinesis*	1995 bp	AB075547
		Arabidopsis thaliana	2314 bp	AF134578

* The Entrez Nucleotide Database-http://www.ncbi.nlm.nih.gov/entrez

lated with carotenoid content of developing fruit [Rodrigo *et al.,* 2004]. These results suggest that transcription of *psy* and *pds* genes is regulated developmentally, with elevated expression in chromoplast-containing tissue. This suggestion seems to be proved by *zds* gene expression in bitterwort, too. The gene transcript level was the lowest in young leaves and the highest in fully open flowers [Rodrigo *et al.,* 2004].

CONCLUSIONS AND FUTURE WORK

Fruits and vegetables, a rich source of carotenoids, are thought to provide health benefits by decreasing the risk of various diseases. Increasing evidences in biochemical studies of carotenogenesis and its regulation in plants *in vivo* are helpful to deeply understand the process as well as can be utilized to manipulate this pathway in crop plants [Paine *et al*., 2005]. The available molecular finding affect also the study of plant phylogeny and a comparative analysis of carotenoid metabolism pathway in plants and animals. However, methods based on genetic engineering applied in carotenogenic genes regulation analyses often cause uncontrolled change in genetic material in transgenic cells. Transgene copy number may differ or the chromosome complement can be doubled during the transformation process [Ducreux *et al.,* 2005]. In some cases, the amount of the enzyme protein analyzed does not correlate with gene expression [Simkin *et al.,* 2003], which is indicative of an unknown, more complex regulatory pattern including gene silencing on the transcriptional level. To avoid any uncertain scientific data, the cooperative research in the reviewed field is highly recommended.

ACKNOWLEDGEMENTS

I wish to thank Prof. Krzysztof Żyła for his helpful suggestions concerning the manuscript.

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Received October 2005. Revision received and accepted February 2006.

MOLEKULARNE SPOJRZENIE NA PROCES KAROTENOGENEZY U ROŚLIN – MINI-ARTYKUŁ PRZEGLĄDOWY

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Karotenoidy odgrywają zasadniczą rolę w procesach fotosyntezy i fotoprotekcji u roślin. Należą do barwników izoprenoidowych, funkcjonują także jako prekursory kwasu abscysynowego (ABA), roślinnego hormonu wzrostu, czy składniki aromatyczne, barwniki i nutraceutyki. Karotenogeneza (biosynteza karotenoidów) oraz mechanizmy regulacji procesu są przedmiotem badań u wielu gatunków roślin. Klonowanie i charakterystyka roślinnych genów karotenogenezy pozwoliły na rozwój nowych baz informacji genetycznych oraz narzędzi molekularnych, co stwarza możliwości osiągnięcia kolejnego poziomu zrozumienia biochemii, a także genetyki procesu. W przyszłości wiedza ta może zostać wykorzystana w celu optymalizacji akumulacji karotenoidów w roślinach uprawnych.