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NEWSLETTER



EUROCAROTEN

EUROPEAN NETWORK TO ADVANCE CAROTENOID RESEARCH
AND APPLICATIONS IN AGRO-FOOD AND HEALTH

CAROTENOID FUNCTIONS IN PLANTS

Dámaso Hornero-Méndez

Department of Food Phytochemistry, Instituto de la
Grasa (IG-CSIC), 41013 Seville, Spain

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Introduction

Although carotenoids are primarily considered as ubiquitous pigments providing colour, there is a consensus on the hypothesis that these compounds appeared in Nature long before that the structures for colour perception and vision evolved in living organisms. As already referred by Meléndez-Martínez¹ in the first EUROCAROTEN Scientific Newsletter (2016), carotenoids can be considered as unique compounds presenting a wide range of functions that, in most cases, are directly involved in life-sustaining processes².

Functions of carotenoids in plants can be categorized in two major groups namely primary or essential and secondary or specialized³. In the essential group are those functions involving interactions with the sunlight in photosynthetic organisms, playing important roles such as light-harvesting and photoprotection. In addition, carotenoids are responsible for the colour of fruits and flowers, having a vital role in developing honest signals for attracting animals to act as pollinators and seed dispersion vehicles^{4,5}. The last processes also include the selection, acquisition and consumption of food by humans⁶. In the present article, these important functions and other less studied of carotenoids in plants will be presented in brief. For more detailed information readers are advised to consult specialized books⁷⁻⁹.



hornero@ig.csic.es

Carotenoids and light harvesting processes

Carotenoid pigments absorb light in the blue-green region of the spectrum of light coming from the sun (400-600 nm), and the absorbed energy is then efficiently transferred to chlorophylls (the main light-harvesting pigments), and consequently the wavelength range of light that is available for photosynthesis is expanded. For this reason carotenoids are referred as accessory light-harvesting pigments. Light energy harvested by carotenoids is passed on from the excited singlet state of the carotenoid molecule (¹Car) to the chlorophyll molecule (¹Chl) by singlet-singlet energy transfer. This feature is intimately linked to the structural features of these compounds; so that the long conjugated double bond system constitutes a chromophore with absorption properties markedly different and complementary in part to the one of chlorophylls (**Figure 1**). Consequently, the intervention of carotenoids in the light harvesting process enhances the overall efficiency of the photosynthetic light reactions^{7,10}.

In the chloroplasts of plants, where the photosynthetic process is performed, carotenoids are found, as part of the photosystems, in association with proteins and chlorophylls in the so-called pigment-protein complexes.



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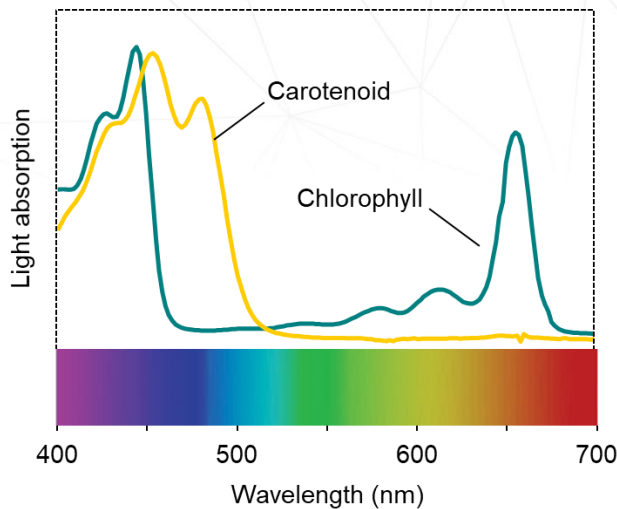


Figure 1. Light absorption spectrum of carotenoids and chlorophylls in the visible range (400-700 nm).

The presence of carotenoids is considered absolutely essential for oxygenic photosynthesis¹¹. Photosystems contain light-harvesting pigments (chlorophylls and carotenoids) which are organized into light-harvesting complexes (LHCs) that are coupled to reaction centres (RCs) where the absorbed light energy is eventually converted into chemical energy by photochemical reactions. Carotenoids are essential components of the RCs of photosystems of plants, being involved in the assembly and integrity of the pigment-protein complexes, and playing an important role in the electron flow cycle to chlorophyll¹⁰. The RCs use the absorbed solar energy to drive the initial electron transfer reactions within the photosynthetic membranes, eventually resulting in the production of reduced NADP and ATP which are then consumed in the CO₂ fixation reactions to produce carbohydrates.

The carotenoids present in the LHC of higher plants are represented by a highly conserved profile composed of β -carotene (20-25%) and three major xanthophylls, lutein (40-45%), violaxanthin (10-15%) and neoxanthin (10-15%) (**Figure 2**). In most RCs, β -carotene is almost the unique carotenoid. In some algae, and due to the adaptation to live in less illuminated environments, this profile changes drastically to increase the contribution of carotenoids to light-harvesting, e.g. fucoxanthin is the major carotenoid pigment in brown algae¹². In general, it has been found that pigment-protein complexes contain one carotenoid molecule per 3-4 chlorophyll molecules¹¹.

Carotenoids and photoprotection

As plants are not able to move away from light irradiation mechanisms for mitigating negative effects of direct irradiation are necessary. Carotenoids perform an essential photoprotection function against photooxidative damage by quenching triplet state chlorophyll molecules (³Chl) generated in the photosynthetic apparatus under excess of light conditions^{13,14}. This function is vital under aerobic conditions where the excess of excited chlorophyll molecules derive in the formation of singlet oxygen (¹O₂). This very reactive toxic oxygen species oxidize the lipids of the membrane, pigments, proteins and other components, subsequently destroying the photosynthetic machinery. Carotenoids act by scavenging both triplet state chlorophylls and the singlet oxygen, if formed, within the chloroplast of higher plants, and the corresponding excited carotenoid molecules (³Car; carotenoid triplets) decay harmlessly by emitting and dissipating the absorbed energy as heat. **Figure 3** depicts the photoprotection mechanisms. Interestingly, the mechanism of action of many herbicides is based on the inhibition of carotenoid biosynthesis and turn-over resulting in a lack of photoprotection and the concomitant “burning effect” derived from photooxidative harmful reactions¹⁵.

Another way of photoprotection involving carotenoids is the so-called non-photochemical quenching (NPQ), by which the excess of energy is dissipated as heat. NPQ implicates some conformational changes within the light-harvesting proteins of photosystem which are promoted by a combination of transmembrane proton gradient, and the enzymatic conversion of the carotenoid violaxanthin into zeaxanthin (the “xanthophyll cycle” or “violaxanthin cycle”)¹⁶⁻¹⁸. When light intensity increases there is an increase in the acidification of the thylakoid lumen leading to the activation of the violaxanthin de-epoxidase enzyme, which converts violaxanthin into zeaxanthin, via antheraxanthin (**Figure 4**). The resulting antheraxanthin and zeaxanthin can dissipate the energy from light as heat, preserving the integrity of the photosystem. In turn, the dissipation of the excess absorbed energy prevents the formation and negative consequences related to the formation of reactive oxygen species (ROS) such as superoxide, hydrogen peroxide and hydroxyl radical originated under oxidative stress conditions like drought, chilling, heat, senescence and salinity stress¹⁹. Under low irradiation levels of the normal violaxanthin levels are restored by the action of zeaxanthin epoxidase enzyme. The capacity of plants to respond to

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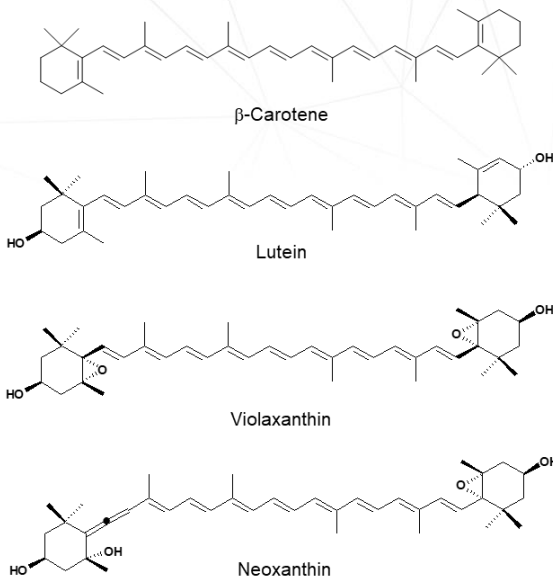


Figure 2. Major chloroplastic carotenoids.

light-mediated environmental stress by producing zeaxanthin must therefore be related with the ability of plants to adapt to certain environmental conditions such as the adaptation to sun/shade variations. Although, the violaxanthin cycle is the predominant xanthophyll cycle in most terrestrial plants, neotropical and some woody plant species use the lutein epoxide cycle²⁰.

Carotenoids as precursors for important molecules in plants

Another primary function of carotenoids is to serve as precursors of smaller molecules including phytohormones and volatile (aroma and essence) compounds. Phytohormones such as abscisic acid (ABA) and strigolactones are crucial molecules used for signalling and acting as regulators for growth, development, and stress responses in plants²¹.

ABA is formed from 9'Z-neoxanthin and 9Z-violaxanthin, both epoxycarotenoids, via xanthoxin by the cleavage action of 9-cis-epoxycarotenoid dioxygenase (NCED) enzyme²² (**Figure 5**). ABA was initially identified as the key compound promoting the senescence and subsequent abscission of leaves and inducing dormancy in seeds and repressing germination²³⁻²⁵. Nowadays, ABA has been implicated in the regulation of many other processes such as regulation of stomatal opening/closure for transpiration, tolerate to desiccation and cold and freezing temperatures, etc²⁶. The effects of ABA are usually opposed to those auxins, gibberellins and cytokinins which are growth-promoting hormones.

Strigolactones (SLs) are considered a novel carotenoid-derived plant hormone^{3,27}. These molecules are used by plants (released as root exudates to the soil) for the regulation of several developmental processes aimed to

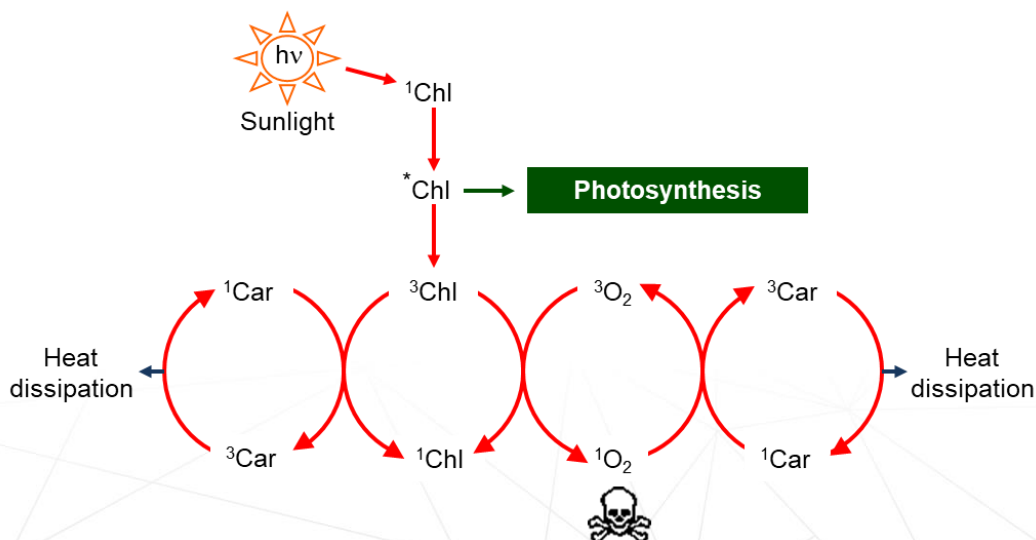


Figure 3. Photoprotection action of carotenoids.

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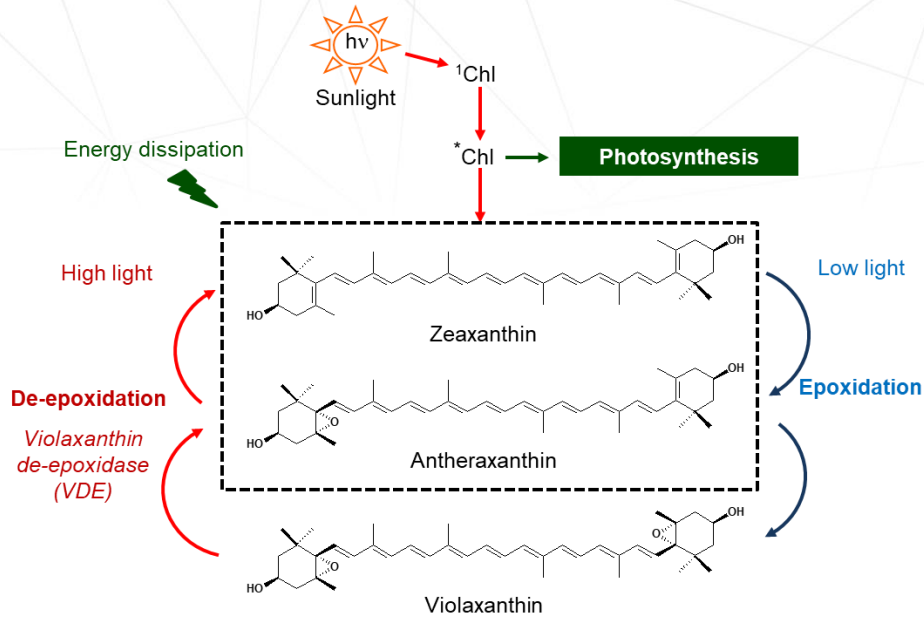


Figure 4. Xanthophyll cycle mechanism and non-photochemical quenching (NPQ).

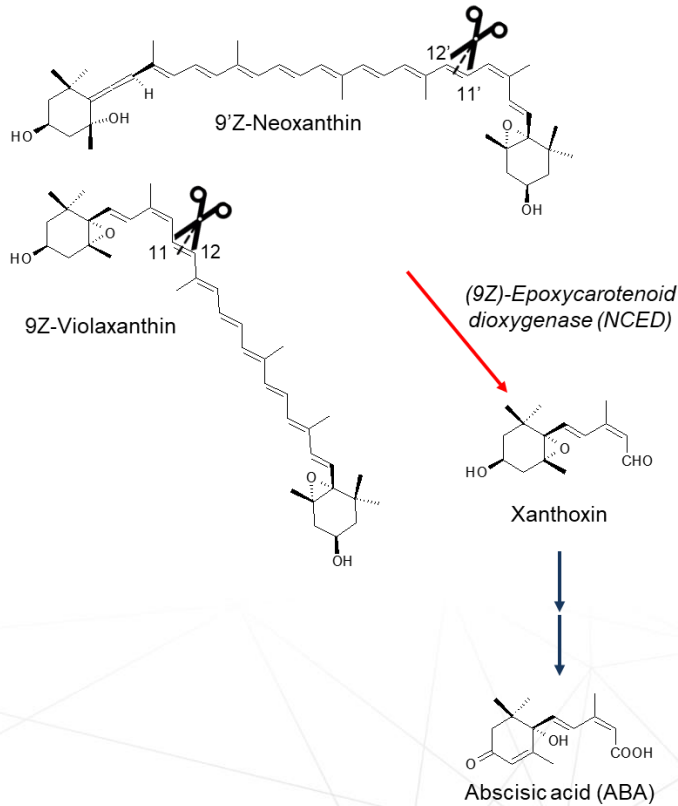


Figure 5. Biosynthesis of abscisic acid (ABA) from carotenoids.

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adapt the plant architecture to nutrient availability and for signalling and communication with root-symbiotic fungi and root-parasitic plants. SLs are biosynthesized from β -carotene by a set of reactions including the cis-isomerization into 9Z- β -carotene, the subsequent action of a carotenoid cleavage dioxygenase (CCD, similar to the NCED involved in ABA production) to produce carlactone which is the common precursor of SLs in different plant species²⁸ (**Figure 6**).

Within the carotenoid-derived compounds in plants there is another extensive and ubiquitous group of short-chain compounds playing an important role as aroma and fragrance substances²⁹. In a similar way to colour, these compounds exert important roles as sensory signals in the Nature. Thus, many of the flavours and aromas of fruit, as well as the scents of flowers, attract animals for ensuring efficient seed dispersal and pollination³⁰. These compounds are referred as “nor-isoprenoids” or “nor-terpenoids”, and they are formed by oxygenase enzymes that cleave carotenoids at in-chain bonds, mostly at the positions C(7,8), C(9,10) and C(11,12), resulting in a diversity of nor-isoprenoid fragments with 10, 13 and 15 carbon atoms back-bone, respectively (**Figure 7**). In addition, similar compounds can also be formed by non-enzymic unspecific cleavage promoted by some oxidizing conditions. Combination of both types of reactions leads to the formation of a wide range of volatile derivatives. Classical examples of some carotenoid-derived nor-isoprenoids are β -ionone (member of the ionones family) and β -damascenone (member of damascones family), both being detectable at very low concentration levels (flavor threshold of 0.007 and 0.002 ppb, respectively) and presenting a characteristic “rose-like” aroma (**Figure 7**). A variety of C13 nor-isoprenoids, including ionones, ionols, theaspiranes and edulanes are found in the ripe fruits of quince, passion fruit, raspberry and grapes (**Figure 7**). Processing grapes for wine is associated with the generation of characteristic nor-isoprenoids (vitispiranes and ‘Riesling acetal’) important to the sensory quality of the product. Similarly, the theaspirane and megastigmene nor-isoprenoids are formed during curing of tea and tobacco leaves, respectively.

Carotenoids as pigments for plant colours

As stated before, the colour of many fruits, tubers, seeds and flowers is due to the prevalent presence of carotenoids. The communication processes between

living organisms can be based on colour signals among others³¹. Thus, in the case of plants it is well-known that the contrasting colours of ripe fruits and flowers against the green background of the plant canopy are aimed to attract seed dispersers and pollinators, respectively, playing an essential role in propagation of the species^{4,5}. For instance, the processes by means of which these compounds exercise their positive health effects in humans and animals, after food ingestion, would not be possible without this previous attraction through colour⁶.

In plants, carotenoids are synthesized and accumulate in the chloroplasts of green tissues (together with chlorophylls), and in the chromoplasts of other plant parts, such as fruits, tubers and flower petals. In particular, chromoplasts are specialised in accumulating high amount of carotenoids within the plastoglobuli, a lipid-rich micro-compartments³². In certain cases, such as tomato (*Solanum lycopersicum*), carrot (*Daucus carota*), and pumpkin (*Cucurbita maxima*), carotenoids has also been reported to be deposited as carotenoid crystals, mainly carotenes, immersed in the stroma³³. Remarkably, the carotenoid profile in chloroplasts is very much conserved, presenting four major carotenoids (β -carotene, 25-30%; lutein, 40-50%, violaxanthin, 15% and neoxanthin, 15%), together with smaller amounts of other carotenoids (α -carotene, β -carotene, β -cryptoxanthin, zeaxanthin, antheraxanthin and lutein 5,6-epoxide). In some special cases, such as lettuce (*Lactuca sativa*), the major xanthophyll is lactucaxanthin (instead of lutein), a rare dihydroxylated xanthophyll with two ϵ -rings. Carotenoids in chromoplasts are presented in a greatest variety of structural forms compared to chloroplasts. Plastid carotenoids, with at least one hydroxyl group in their structure (known as hydroxy-xanthophylls or hydroxy-carotenoids) can be found either in their free form or esterified with fatty acids. Non-esterified is the native stage for carotenoids in chloroplasts (i.e. lutein, neoxanthin, violaxanthin, etc.), whereas in chromoplasts carotenoids are mostly in esterified form³⁴. The esterification of xanthophylls takes place during the ripening of most fruits and during the senescence of leaves. During ripening of the so-called carotenogenic fruits (for example pepper and tomato) there is a dramatic and rapid change in the colour which is usually accompanied by a change in the carotenoid profile of the fruit coinciding with the transformation of the chloroplasts into chromoplasts^{35,36}. A classic example are the *Capsicum* fruits, where a massive accumulation of characteristic carotenoids (capsanthin and capsorubin) in both free and esterified esters takes places in 2-3 days, changing from the characteristic chloroplastic carotenoid profile of green fruits (i.e.

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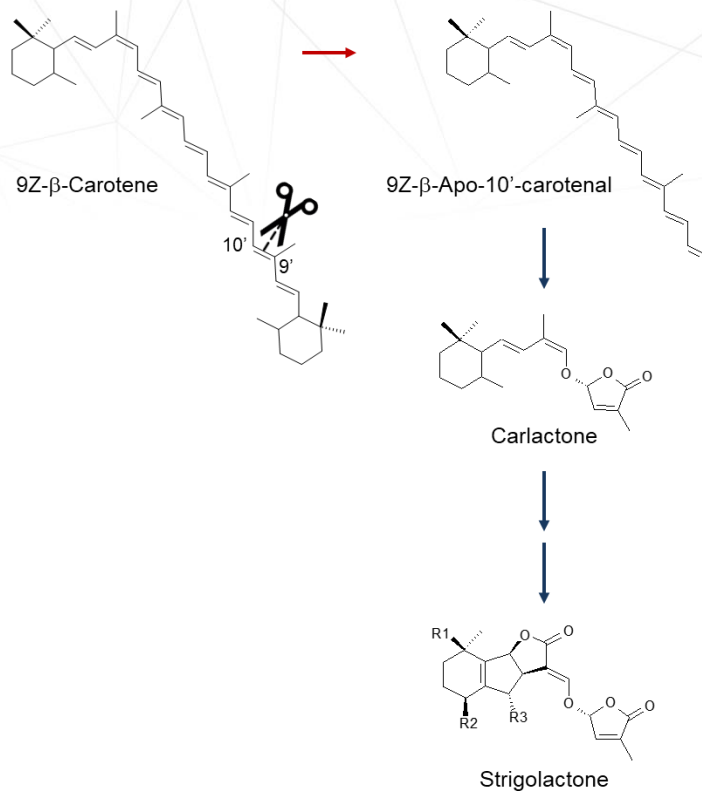


Figure 6. Biosynthesis of strigolactones.

neoxanthin, violaxanthin, lutein and β -carotene) to a more complex chromoplasmic profile of red fruits (capsanthin, capsorubin, capsanthin 5,6-epoxide, violaxanthin, zeaxanthin, cucurbitaxanthin A, antheraxanthin, beta-cryptoxanthin, beta-carotene, etc.)³⁷. The xanthophylls esterification process has been suggested as an important post-carotenogenic modification of carotenoids which mediates their accumulation in plant cells^{38,39}. Interestingly, a positive correlation between the total carotenoid content and the amount of esterified xanthophylls has been suggested by recent studies, indicating a role for the esterification process in the accumulation of carotenoids within chromoplasts⁴⁰⁻⁴².

The presence and distribution of the most common carotenoid pigments found in plant foods, mostly fruit and vegetables, are shown in **Table 1** (**Figure 8** shows the chemical structures). For a particular plant source the carotenoid composition is determined genetically, but the actual composition can be greatly affected by some genetic variation (cultivars) and by the cultivation and environmental conditions^{3,43}. Mango (*Mangifera indica*) and persimmon (*Diospyros kaki*) are characterized by

presenting high levels of β -cryptoxanthin and zeaxanthin. In certain fruits, a carotenoid, besides being the major one, is limited totally (exclusive) or almost totally to a single plant species. Thus, capsanthin and capsorubin are found almost exclusively in ripe fruits of the genus *Capsicum*, and are responsible for their attracting red colour. The orange (*Citrus sinensis*) contains varying amounts of β -citraurin and citranaxanthin (both apocarotenoids), together with β -cryptoxanthin, lutein, antheraxanthin, violaxanthin, and traces of their carotene precursors. In contrast, in tomato the major carotenoid is lycopene, a carotene. Similarly, carrots (*Daucus carota*) are rich in β -carotene and α -carotene. All green vegetables are characterised by containing a considerable amount of lutein, β -carotene, and β -cryptoxanthin, with the concentration varying greatly from one source to another. The best sources of α -carotene are carrots and pumpkins, while β -carotene is found more widely in fruits and vegetables such as carrots, red bell peppers, oranges, potatoes, broccoli, and green vegetables. β -Cryptoxanthin is usually found in minor concentration, although in ripe red peppers and tropical fruits like papaya in one of the major pigments. Tomato, watermelon and pink grapefruit are

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the main sources of lycopene. Green vegetables (such as spinach, Brussels sprouts, broccoli, and peas) are rich sources of lutein, whereas zeaxanthin is found in

lower concentrations. In corn grains (*Zea mays*) the predominant pigments are lutein and zeaxanthin, whereas lutein is the major carotenoid in wheat grains.

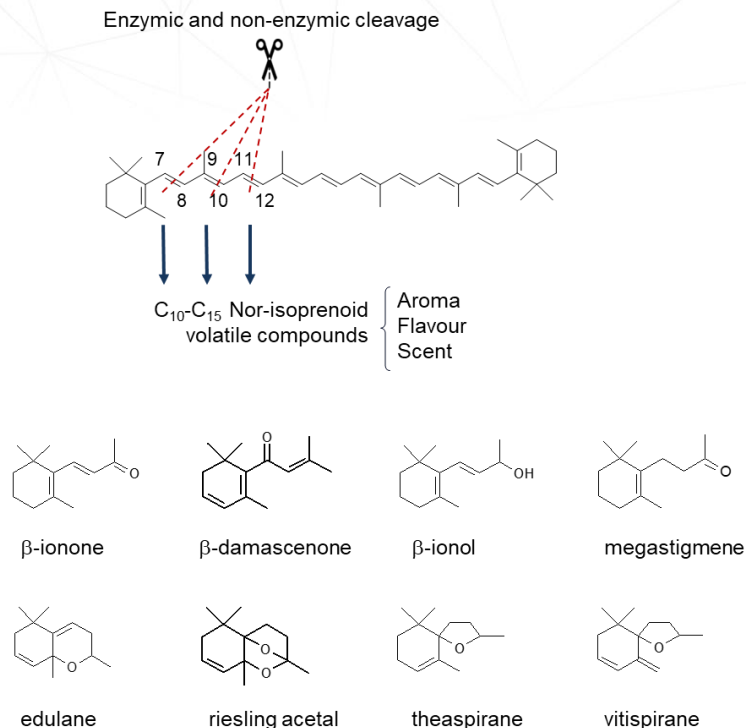


Figure 7. Formation of volatile nor-isoprenoid compounds from carotenoids.

Table 1. Common carotenes and xanthophylls in plants used for food.

| Carotenoid | Occurrence |
|--|---|
| Carotenes | |
| α-Carotene, β-carotene, δ-carotene, γ-carotene, ε-carotene, ζ-carotene | Fruits and vegetables, especially in carrots, sweet potato, palm tree fruit. Delta tomato mutant has δ-carotene as major carotene. Rose hips are good source for γ-carotene |
| Lycopene, neurosporene | Tomato, water melon and rose hips (<i>Rosa</i> spp.) |
| Phytofluene, phytoene | Carotenoid-rich fruits, flowers and roots (carrot) |
| Xanthophylls | |
| Antheraxanthin | Anthers and petals of many yellow flowers. Fruits and green vegetables. |
| Bixin, norbixin | Annatto (<i>Bixa orellana</i>) seeds |
| Capsanthin, capsanthin-5,6-epoxide, capsorubin | <i>Capsicum annuum</i> ripe fruits |
| β-Citraurin, citranaxanthin | <i>Citrus</i> fruits |
| Crocetin | Saffron (<i>Crocus sativus</i>) stigmas |
| Cucurbitaxanthin A | Pumpkin (<i>Cucurbita maxima</i>) flesh |
| Lactucaxanthin | Lettuce (<i>Lactuca sativa</i>) leaves |
| Lutein | Green fruits, vegetables, flowers and cereal grains (wheat). |
| Violaxanthin, neoxanthin | Green fruits, vegetables and flowers |
| Rubixanthin | Rose hips (<i>Rosa</i> spp.) |
| Zeaxanthin | Seeds (corn), potato tubers (<i>Solanum tuberosum</i>), red and orange pepper (<i>C. annuum</i>), goji berries (<i>Lycium barbarum</i>). |
| β-Cryptoxanthin, α-cryptoxanthin, cryptoxanthin-5,6-epoxide | Seeds (corn), flowers and fruits: mango, papaya, persimmon. Red, orange and yellow pepper (<i>C. annuum</i>). |
| Lactucaxanthin | Lettuce (<i>Lactuca sativa</i>) leaves |

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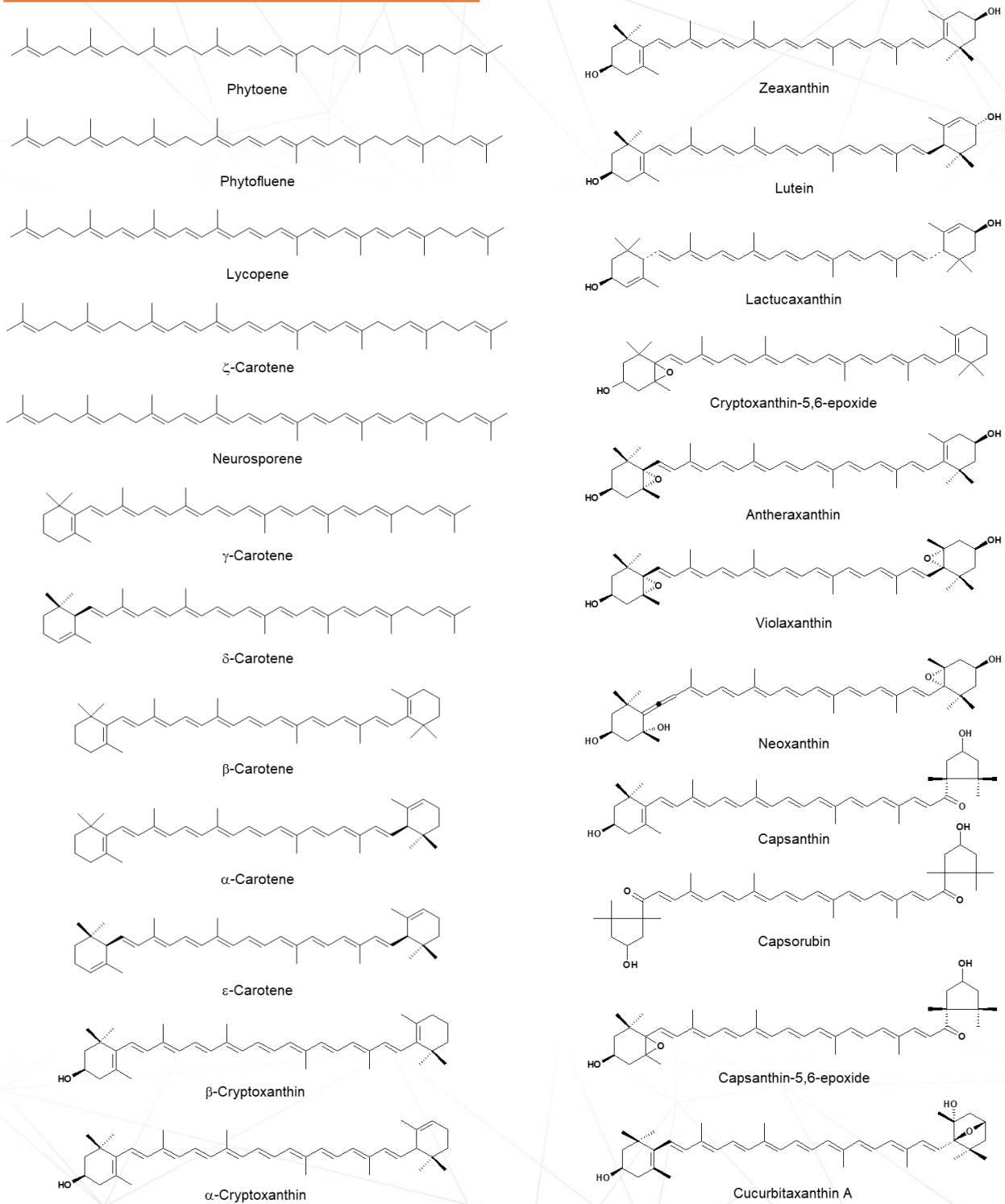


Figure 8. Chemical structures of carotenes and xanthophylls occurring in plants used for food.

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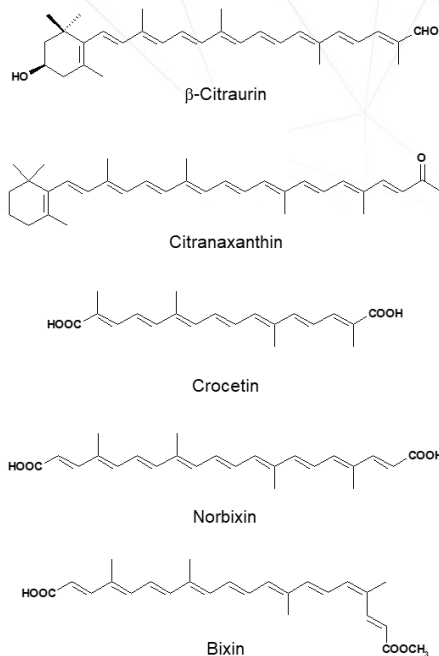


Figure 8 contin. Chemical structures of carotenes and xanthophylls occurring in plants used for food.

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