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REVIEW
Diversity of Carotenoid Composition in Flower Petals

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Abstract
Carotenoids are yellow, orange, and red pigments that are widely distributed in nature. In plants, carotenoids play important roles in photosynthesis and furnishing flowers and fruits with distinct colors. While most plant leaves show similar carotenoid profiles, containing carotenoids essential for photosynthesis, the carotenoid composition of flower petals varies from species to species. In this review, I present a list of carotenoid composition in the flower petals of various plants and discuss the possible causes of qualitative diversity.

Discipline: Horticulture
Additional key words: flower color

Introduction

Carotenoids are C_{40} isoprenoid pigments with or without epoxy, hydroxyl, and keto groups. More than 700 naturally occurring carotenoids, widely distributed in plants, animals, and micro-organisms, have been identified[4]. Carotenoids are essential structural components of the photosynthetic antenna and reaction center complexes[36]. Carotenoids protect against potentially harmful photooxidative processes and furnish flowers and fruits with distinct colors (e.g., yellow, orange, and red) that attract pollinators and seed dispersers. Some carotenoids are precursors for the biosynthesis of the plant hormones abscisic acid (ABA) and strigolactone[9,33]. Carotenoids are essential components of the human diet as they are precursors for vitamin A biosynthesis and have antioxidant functions[12].

The carotenoid biosynthesis pathway in plants is summarized in Figure 1 [7,12,17,42]. The initial step of carotenoid biosynthesis involves one isoprene unit, C_5 isopentenyl diphosphate (IPP). Four IPPs are condensed to form C_{20} geranylgeranyl diphosphate (GGPP), and two GGPP molecules are converted into phytoene, the first C_{40} carotenoid. Phytoene is then converted to lycopene, via the formation of ζ-carotene, by the addition of conjugated double bonds and the conversion of *cis*- to *trans*-configurations. The cyclization of the linear carotenoid lycopene is a branch point in the pathway, leading to the synthesis of α-carotene and its derivatives with 1 ε- and 1 β-ring (β,ε-carotenoids) or β-carotene and its derivatives with two β-rings (β,β-carotenoids) (Fig. 2). Subsequently, α- and β-carotenes are modified by hydroxylation, epoxidation, or isomerization to form a variety of structures. The oxygenated derivatives of carotenes are called xanthophylls.

Carotenoid composition in flower petals

Tables 1 and 2 show the carotenoids contained in petals of monocot and eudicot plants, respectively. There is considerable diversity in the carotenoid profiles of different plant species. The majority of carotenoids in flower petals are yellow xanthophylls, such as lutein, β-cryptoxanthin, and zeaxanthin. Epoxy xanthophylls such as violaxanthin, antheraxanthin, neoxanthin, and lutein-5,6-epoxide are also common. Yellow xanthophylls impart pale yellow and deep yellow to orange colors to flowers, depending on the carotenoid content in petals[27]. Some flowers contain carotenes such as lycopene and β-carotene and have a deep yellow to orange color.

The flower petals of most plants accumulate both β,β- and β,ε-carotenoids. Some flowers show distinctive carotenoid profiles. For example, the majority of carotenoids in the petals of sandersonia (*Sandersonia aurantiaca*), *Camellia chrysantha*, and *Ipomoea* sp. are

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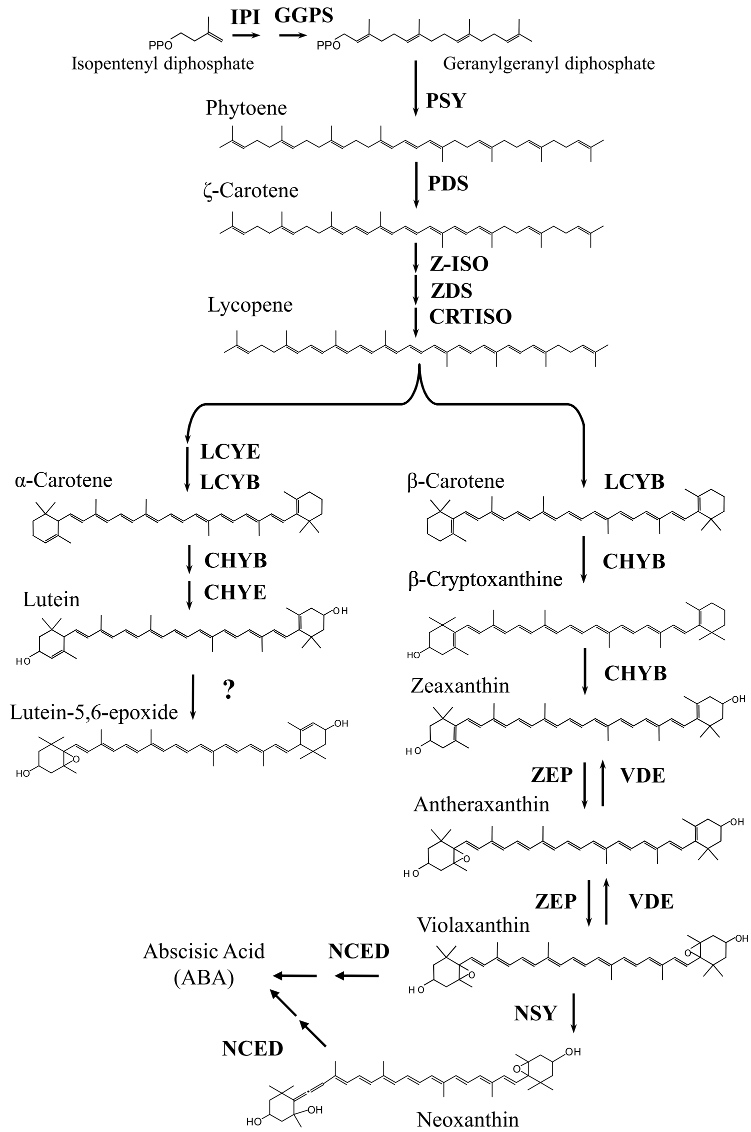

Fig. 1. Schematic of the carotenoid biosynthesis pathway in plants

IPI, Isopentenyl diphosphate isomerase; GGPS, Geranylgeranyl diphosphate synthase; PSY, phytoene synthase; PDS, phytoene desaturase; Z-ISO, 15-*cis*-ζ-CRTISO; ZDS, ζ-carotene desaturase; CRTISO, carotenoid isomerase; LCYE, lycopene ε-cyclase; LCYB, lycopene β-cyclase; CHYE, ε-ring hydroxylase; CHYB, β-ring hydroxylase, ZEP, zeaxanthin epoxidase; VDE, violaxanthin deepoxidase; NSY, neoxanthin synthase.

β,β-carotenoids, such as β-cryptoxanthin, zeaxanthin and β-carotene[34,43,48]. On the other hand, more than 90% of the carotenoids in the petals of marigold (*Tagetes* sp.) and chrysanthemum (*Chrysanthemum morifolium*) are lutein and its derivatives (β,ε-carotenoids)[19,27].

In general, the carotenoids present in flower petals differ from those found in leaves. However, the pale yellow petals of *Ipomoea obscura*[48] and *Eustoma* sp.[32] have similar carotenoid profiles to those of leaves (leaf-type carotenoids): an accumulation of lutein, β-carotene, violaxanthin, neoxanthin, and zeaxanthin. At the early stages of flower development, many flowers show a pale

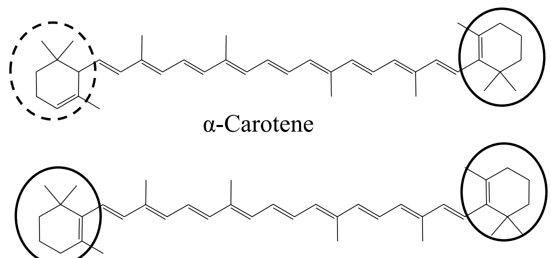

Fig. 2. Structure of β,ε-carotenoid (α-carotene) and β,β-carotenoid (β-carotene)

Solid and dotted circles indicate β- and ε-rings, respectively.

Table 1. Carotenoids contained in petals of monocot plants

Family species (cultivar)	Color	Carotenoids					Ref.
Araceae							
Zantedeschia hybrid ‘Florex Gold’	yellow	Lutein	β-Carotene				23)
Amaryllidaceae							
Narcissus poeticus ‘Scarlet Elegance’	orange (corona)	β-Carotene	Lutein	Rubixanthin-like	Lutein-epoxide	Flavoxanthin	45)
		Auroxanthin	ζ-Carotene	Zeaxanthin	Chrysanthe-maxanthin		
Narcissus poeticus ‘Scarlet Elegance’	pale yellow (perianth)	Lutein	Lutein-epoxide	β-Carotene	Flavoxanthin	Chrysanthema-xanthin	45)
		Antheraxanthin	5,6-Monoepoxy -β-carotene	5,6:5’,6’-Diepoxy-β-carotene	Zeaxanthin		
Naricissus pseudonarcissus ‘King Alfred’	yellow (corona)	Lutein	Auroxanthin	Lutein-epoxide	Flavoxanthin	5,6-Monoepoxy-β-carotene	45)
		cis-5,6:5’,6’-Diepoxy-β-carotene	5,6:5’,6’-Diepoxy-β-carotene	β-Cryptoxanthin	β-Carotene	Chrysanthema-xanthin	
Naricissus pseudonarcissus ‘King Alfred’	yellow (perianth)	*trans*-5,6:5’,6’-Diepoxy-β-carotene	Lutein	Flavoxanthin	Lutein-epoxide	*cis*-5,6:5’,6’-Diepoxy-β-carotene	45)
		5,6-Monoepoxy -β-carotene	β-Cryptoxanthin	β-Carotene	Chrysanthe-maxanthin	Zeaxanthin	
Iridaceae							
Crocosmia× *crocosmiiflora*	orange	Crocin					38)
Orchidaceae							
Oncidium ‘Gower Ramsey’	yellow	Violaxanthin	(9*Z*)-Viola-xanthin	Neoxanthin			16)
Hemerocallidaceae							
Hemerocallis disticha	orange	Zeaxanthin	*cis*-β-Crypto-xanthin	β-Cryptoxanthin	β-Carotene	Lutein	41)
		(13*Z*)-Lutein	Lutein-epoxide	Violaxanthin	Neoxanthin		
Liliaceae							
Lilium spp. ‘Conneticut King’	yellow (tepal)	Antheraxanthin	(9*Z*)-Viola-xanthin	*cis*-Lutein	Violaxanthin	Lutein	47)
		β-Carotene					
Lilium spp. ‘Montreux’	pink (tepal)	Violaxanthin	Lutein	Antheraxanthin	β-Carotene	(9*Z*)-Viola-xanthin	47)
		cis-Lutein					
Lilium spp. ‘Saija’	red (tepal)	Capsanthin	Antheraxanthin				47)
Lilium tigrinum ‘Red Night’	red (tepal)	Capsanthin	Capsorbin	(9*Z*)-Anthera-xanthin	Mutatoxanthin	Neoxanthin	26)
		(9’*Z*)-Capsanthin	(13*Z*)-Capsanthin	β-Citraurin	(9*Z*)-Capsanthin	(13’*Z*)-Capsanthin	
Tulipa sp. ‘Golden Harvest’	deep yellow (perianth)	5,6:5’,6’-Diepoxy-β-carotene	Flavoxanthin	β-Carotene	5,6-Monoepoxy-β-carotene	Chrysanthema-xanthin	45)
		Lutein	Lutein-epoxide	ζ-Carotene	Auroxanthin		
Cholchicaceae							
Sandersonia aurantiaca (Hook)	golden orange	β-Cryptoxanthin	Zeaxanthin	β-Carotene			34)
Cannaceae							
Canna indica	yellow	Lutein	Violaxanthin	β-Carotene	Zeaxanthin	β-Cryptoxanthin	44)

Carotenoids are listed basically in descending order of abundance. Compound names are described according to the terms adopted in the reference manuscripts. It should be noted that the accuracy of data may vary among manuscripts.

Table 2-1. Carotenoids contained in petals of eudicot plants

Family Species (cultivars)	Color	Carotenoids					Ref.
Nelumbonaceae							
Nelumbo lutea 'American Yellow'	greenish yellow	Lutein	Violaxanthin	Neoxanthin	β-Carotene		18)
Rununculaceae							
Adonis aestivalis	blood red	Astaxanthin	3-Hydroxyechinenone		Adonirubin	Adonixanthin	8)
Papaveraceae							
Eschscholzia californica Cham.	orange	Neoxanthin	Antherxanthin	Crocetin	Eschscholtz-xanthin	β-Cryptoxanthin	46)
		(3*S*,5*R*,3'*S*)-4'5-Retro-β, β-carotene-3,5,3'-triol					25)
Fabaceae							
Lotus japonicus	yellow	Violaxanthin	Antheraxanthin	β-Carotene	Neoxanthin	Lutein	40)
Hypericaceae							
Hypericum perforatum	yellow	β-Carotene	α-Carotene	Neoxanthin	Violaxanthin	Zeaxanthin	37)
Violaceae							
Viola tricolor	yellow	(9*Z*)-Viola-xanthin	Violaxanthin	Antheraxanthin	Lutein	(13*Z*)-Viola-xanthin	28) 29)
		β-Carotene	(15*Z*)-Viola-xanthin	Luteoxanthin	(9*Z*,9'*Z*)-Viola-xanthin	(9*Z*,13'*Z*)-Viola-xanthin	
		(9*Z*,13*Z*)-Viola-xanthin	(9*Z*,15*Z*)-Viola-xanthin				
Rosaceae							
Rosa hybrida 'Star of Persia'	yellow	Violaxanthin	Luteoxanthin				10)
Rosa hybrida 'Allgold'	yellow	Luteoxanthin	Auroxanthin				10)
Rosa hybrida 'Alister Stella'	yellow	β-Carotene					10)
Brassicaceae							
Brassica napus	yellow	Luteoxanthin	Neoxanthin	Violaxanthin	Flavoxanthin	Chrysanthema-xanthin	22)
Tropaeolaceae							
Tropaeolum majus	yellow	Lutein	Violaxanthin	Antheraxanthin	Zeaxanthin	Zeinoxanthin	35)
		β-Cryptoxanthin	α-Carotene	β-Carotene			
Malvaceae							
Hibiscus syriacus	pink	Lutein-5,6-epoxide	Auroxanthin	Chrysanthema-xanthin			15)
Rutaceae							
Boronia megastigma	brown	β-Ionone	Lutein	β-Carotene	*cis*-ζ-Carotene		5)
		10'-Apocaroten-10'-oic acid	Hydroxy 10'-apocaroten-10'-oic acid	10'-Apocaroten-10'-al	Methyl 10'-apocaroten-10'-oate		6)
Theaceae							
Camellia chrysantha	pale yellow	(9*Z*)-Violaxanthin	Violaxanthin	Antheraxanthin	Luteoxanthin	β-Cryptoxanthin	43)
		β-Carotene					

Carotenoids are listed basically in descending order of abundance. Compound names are described according to the terms adopted in the reference manuscripts. It should be noted that the accuracy of data may vary among manuscripts.

Table 2-2. Carotenoids contained in petals of eudicot plants

Family species (cultivars)	Color	Carotenoids					Ref.
Gentianaceae							
Eustoma	pale yellow	Lutein	Neoxanthin	β-Carotene	Violaxanthin	Zeaxanthin	32)
Gentiana lutea	yellow	Lutein Neoxanthin	Violaxanthin β-Cryptoxanthin	β-Carotene	Antheraxanthin	Zeaxanthin	49)
Allamanda cathartica	yellow	Lutein	β-Carotene	Violaxanthin	Zeaxanthin	Neoxanthin	44)
Scrophulariaceae							
Mimulus tigrinus	yellow	Taraxanthin	β-Cryptoxanthin	β-Carotene			14)
Mimulus cupreus 'Red Emperor'	dark red	β-Carotene	Taraxanthin				14)
Oleaceae							
Osmanthus frangrance Lour.	orange	β-Carotene	α-Carotene				1)
Verbenaceae							
Lantana camara	yellow	β-Carotene					39)
Acanthaceae							
Thunbergia alata	yellow	unknown	Lutein	β-Carotene			24)
Bignoniaceae							
Pyrostegia venusta	orange	Lutein Neoxanthin	β-Carotene	β-Cryptoxanthin	Violaxanthin	Zeaxanthin	44)
Tabebuia chrysantha	yellow	Lutein Neoxanthin	β-Carotene	β-Cryptoxanthin	Violaxanthin	Zeaxanthin	44)
Solanaceae							
Solanum lycopersicum 'M82'	yellow	Neoxanthin	Violaxanthin	Lutein			13)
Petunia x *hybrida* Vilm. 'Summer Sun'	pale yellow	β-Carotene	Lutein	Zeaxanthin			30)
Calibrachoa 'Million Bells Yellow'	yellow	β-Carotene	Lutein				31)
Nicotiana glauca	yellow	Lutein *cis*-β-Carotene	β-Carotene β-Cryptoxanthin	*cis*-Lutein	Violaxanthin	Antheraxanthin	50)
Convolvulaceae							
Ipomoea sp.	yellow	β-Cryptoxanthin	β-Carotene	Zeaxanthin			48)
Ipomoea obscura	pale yellow	Lutein	β-Carotene	Violaxanthin	Neoxanthin	Zeaxanthin	48)

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green coloration due to the accumulation of chlorophyll and leaf-type carotenoids, which disappear as the flower matures. It has been suggested that flowers containing leaf-type carotenoids have low rates of carotenoid degradation, and therefore small amounts of leaf-type carotenoids remain at later stages of flower development.

The petals of some plants have modified carotenoid biosynthetic pathways that produce specific carotenoid compositions associated with their respective genus or species. These express unique colors such as orange and red. Astaxanthin is a ketocarotenoid that is produced in a number of bacteria, fungi, and algae; it imparts a red color. The petals of *Adonis aestivalis* and *A. annua* accumulate large amounts of astaxanthin, resulting in their distinctive blood-red color[8].

The major carotenoids in the yellow tepals (indistinguishable petals and sepals) of the Asiatic hybrid lily cultivar 'Connecticut King' are yellow xanthophylls such as

Table 2-3. Carotenoids contained in petals of eudicot plants

Family Species (cultivars)	Color	Carotenoids					Ref.
Asteraceae							
Chrysanthemum morifolium 'Sunny Orange'	yellow	(9*Z*)-Lutein-5,6-epoxide	(9'*Z*)-Lutein-5,6-epoxide	(9*Z*)-Lutein	Lutein	Lutein-5,6-epoxide	19)
		(9'*Z*)-Lutein	(3*S*,5*S*,6*R*,3'*R*,6'*R*)-5,6-Dihydro-5,6-dihydroxy- lutein	(8*S*)-Lutein-5,8-epoxide (Chrysanthemaxanthin)	(9*Z*)-Violaxanthin	(9*Z*,9'*Z*)-Lutein-5,6-epoxide	
		(9'*Z*,13'*Z*)-Lutein-5,6-epoxide	(9*Z*,13*Z*)-Lutein-5,6-epoxide	(9*Z*,13'*Z*)-Lutein-5,6-epoxide	(13*Z*,9'*Z*)-Lutein-5,6-epoxide	(9*Z*-8'*R*)-Luteoxanthin	
		(8*R*)-Lutein-5,8-epoxide (flavoxanthin)					
Calendula officinalis 'Alice Orange'	orange	(8*R*)-Lutein-5,8-epoxide (flavoxanthin)	(8'*R*)-Luteoxanthin	Lycopene	(8*R*,8'*R*)-Auroxanthin	(9'*Z*)-Lutein-5,6-epoxide	20)
		(5'*Z*)-γ-Carotene	(5*Z*,9*Z*)-Lycopene	(5*Z*,9*Z*,5'*Z*,9'*Z*)-Lycopene	(5'*Z*,9'*Z*)-Rubixanthin	(5*Z*,9*Z*,5'*Z*)-Lycopene	
		β-Carotene	(5'*Z*)-Rubixanthin	γ-Carotene	Lutein	Lutein-5,6-epoxide	
		δ-Carotene	Antheraxanthin	α-Carotene	(9*Z*)-Lutein		
Calendula officinalis 'Alice Yellow'	yellow	(8*R*)-Lutein-5,8-epoxide (flavoxanthin)	(8'*R*)-Luteoxanthin	(8*R*,8'*R*)-Auroxanthin	(9'*Z*)-Lutein-5,6-epoxide	Lutein	20)
		Antheraxanthin	(9*Z*)-Lutein	β-Carotene			
Helianthus annuus 'Sunrich Orange'	yellow	Lutein	Antheraxanthin	Zeaxanthin	Violaxanthin		21)
Zinnia elegans 'Dreamland Coral'	orange	Zeaxanthin	Lutein	β-Carotene	Violaxanthin		21)
Osteospermum ecklonis 'Jury'	orange	Lycopene	(5*Z*,9*Z*,5'*Z*)-Lycopene	(5'*Z*)-γ-Carotene	β-Carotene	Lutein	21)
Osteospermum ecklonis 'Mikey'	yellow	Lycopene	Lutein	β-Carotene	(5*Z*,9*Z*,5'*Z*)-Lycopene	(5'*Z*)-γ-Carotene	21)
		(13*Z*)-Violaxanthin	β-Carotene	(15*Z*)-Violaxanthin	Luteoxanthin		
Tagetes petula 'Safari Tangerine'	orange	Lutein	Antheraxanthin	Zeaxanthin	Violaxanthin		21)
Tagetes erecta 'Orange Isis'	orange	Lutein	Violaxanthin	Neoxanthin			21)
Gerbera jamesonii 'Dancer'	orange	Antheraxanthin	Zeaxanthin	Violaxanthin	Lutein	Neoxanthin	21)
		β-Carotene					
Gazania spp. 'Daybreak Orange'	orange	(5'*Z*)-Rubixanthin	Lutein	(9*Z*)-Lutein	Antheraxanthin	(9*Z*)-Zeaxanthin	21)
		(9*Z*)-Violaxanthin	Lycopene	Lutein-5,6-epoxide	Violaxanthin	(5*Z*,9*Z*,5'*Z*)-Lycopene	
		(9'*Z*)-Lutein-5,6-epoxide	β-Carotene				
Gazania spp. 'Day Break Yellow'	yellow	Lutein-5,6-epoxide	Lutein	(9'*Z*)-Lutein-5,6-epoxide	(9*Z*)-Violaxanthin	Violaxanthin	21)
		Antheraxanthin	(9*Z*)-Lutein	β-Carotene	(9*Z*)-Zeaxanthin		

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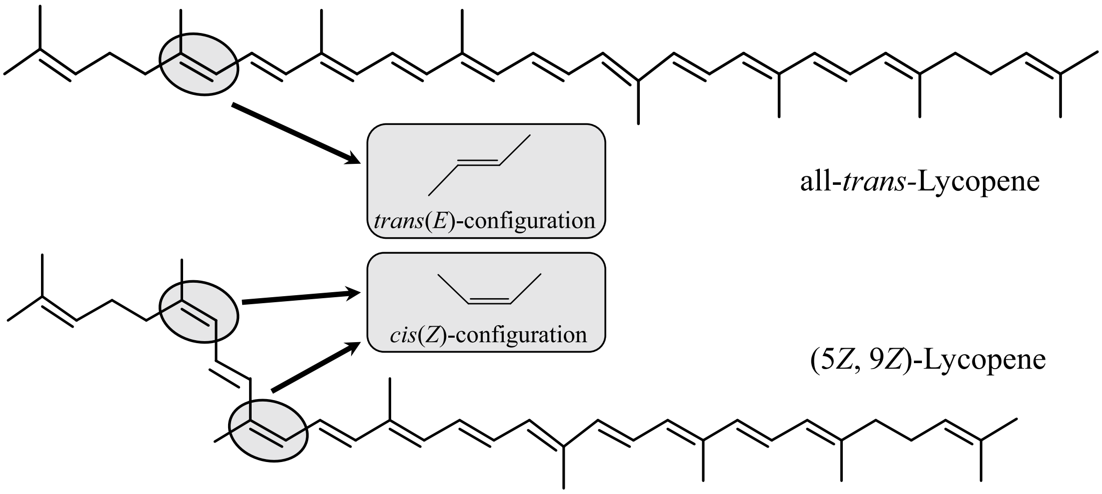

Fig. 3. Structure of geometrical isomers of lycopene

antheraxanthin, violaxanthin, and lutein, while the major carotenoid in the red tepals of the cultivar ‘Saija’ is capsanthin[47]. The red ketocarotenoid capsanthin is found in the fruits of red pepper[2] but is rarely found in flower petals. *Lilium leichtlinii* (syn. *L. tigrinum*), which is one of the parental species of Asiatic hybrid lilies, also accumulates capsanthin in the tepals[26].

Although the carotenoids in petals are generally in the all-*trans* forms, some plants accumulate *cis*-carotenoids. In particular, the petals of Asteraceae plants contain various types of *cis*-carotenoids, some of which are rarely found in plants; e.g., the orange petals of calendula (*Calendula officinalis*), osteospermum (*Osteospermum ecklonis*), and *Gazania* spp. accumulate (5*Z*)- and (5′*Z*)-carotenoids, which contain *cis*-structures at C5 and C5′, respectively[20,21] (Fig. 3). These carotenoids are reddish and are found only in negligible quantities in yellow petals. The petals of chrysanthemum, calendula, *Gazania* spp., and osteospermum produce di-, tri-, and/or tetra-*cis*-carotenoids[19,20,21]. Di-*cis*-carotenoids are also found in the petals of *Viola tricolor*[29].

Some orange and red petal colors are derived from apocarotenoids, which are compounds produced by the enzymatic cleavage of carotenoids. For instance, the petals of California poppy (*Eschscholzia californica* Cham.) accumulate crocetin and those of *Crocosmia* accumulate crocin[38,46]. Various apocarotenoids such as β-ionone, 10'-apocaroten-10'-oic acid, and hydroxy 10'-apocaroten-10'-oic acid are found in the petals of boronia (*Boronia megastigma*)[5,6]. The red stigma of crocus (*Crocus sativus*), from which the spice saffron is derived, accumulates a unique mixture of apocarotenoids—crocetin glycosides, picrocrocin, and safranal—which are responsible for the color, taste, and aroma of saffron.[3]

How does carotenoid diversity occur?

The leaves of most plants show similar carotenoid profiles, indicating a specific role for each carotenoid component; in contrast, flowers show distinctive carotenoid compositions that vary with the plant species. From an evolutionary perspective, it is of great interest to investigate the interspecific differences in carotenoid composition. Firn and Jones[11] have proposed a possible scenario for this chemical diversity. The accumulation of yellow carotenoids in flowers is a character that is not strictly linked to the detailed fine structure of the molecules because it does not involve any specific protein-ligand interactions, unlike plant growth regulators and their receptors. If a mutation occurs in a carotenogenic gene, which causes a new flower carotenoid profile, but the variants express yellow color with the same wavelength absorption, there may be no selection pressure on the original structure, and thus the diversity of carotenoids in flowers will be retained.

Future prospects

The carotenoid profiles in petals have been analyzed using modern technology such as nuclear magnetic resonance spectroscopy and gas chromatography-mass spectrometry in only a few plants[19,20,25]. Most of the carotenoid compositions listed in this review were analyzed by means of high-performance liquid chromatography. Carotenoids were identified by comparing retention times and absorbance spectra with known carotenoids as standards. With these methods, many unknown carotenoids remain unidentified, and their stereochemical properties undetermined. In addition, the petal carotenoid composition in many plant species has not yet been examined. Therefore, our knowledge of flower carotenoids is currently limited. I hope that future research will be undertaken to improve our understanding of the wide chemical diversity of petal carotenoids.

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