AGRO PRODUCTIVIDAD

Colegio de Postgraduados

Pigmentation and vitamin production in mango (*Mangifera indica* L.)

Hernández-Estrada M. E., Rosas-Quijano R., Vázquez-Ovando A., Gálvez-López D.*

Instituto de Biociencias, Universidad Autónoma de Chiapas. Tapachula, Chiapas, México. C.P. 30798.
* Correspondence: didiana.galvez@unach.mx

ABSTRACT

Objective: To describe the main genes involved in mango and the biosynthetic routes of the most common pigments, considering the impact on human health when consuming them, and highlighting challenges and opportunities that could arise from the use of pigments from Mexican mango germplasm.

Design/methodology: A review that gathers and discusses information that contributes to the understanding of the biochemical and genetic processes that determine pigmentation and vitamin production in mango.

Results: Color is a visual attribute that defines consumer preference. The diversity of pigmentation is defined by families of genes that code for the production of proteins, which lead to biosynthetic pathways responsible for the production of vitamins and their precursors. In Mexico there is a wide range of colors in the native mango germplasm, which could represent an important source of antioxidants, pigments and would bring benefits to the health of Mexicans, through the consumption of fresh fruit, or the commercial/industrial exploitation of these.

Limitations/implications: One way to classify the mango is according to the color of the skin, they are classified as green, yellow and red, however, little has been explored about the benefits they could provide.

Conclusion: The diversity of colors in the mango fruit is determined by different genes and biosynthetic pathways. Red, green and yellow colors in mango fruit, are a source of carotenoids, betalains, flavonoids and chlorophylls, precursors of vitamins A, B, C and E.

Keywords: biosynthesis, flavonoids, anthocyanins, carotenoids, chlorophyll.

Citation: Hernández-Estrada M. E., Rosas-Quijano R.,Vázquez-Ovando A., & Gálvez-López D. (2022). Pigmentation and production of vitamins in mango (*Mangifera indica* L.). *Agro Productividad*. https://doi.org/10.32854/agrop.v15i2.2094

Editor in Chief: Dr. Jorge Cadena Iñiguez

Received: July 21, 2021.
Accepted: January 23, 2022.
Published on-line: March 3, 2022.

Agro Productividad, 15(2). February. 2022. pp: 109-125.

INTRODUCTION

In Mexico, the cultivation of mangoes (*Mangifera indica* L.) is an agricultural activity that stands out for the volume of domestic production and exports to the United States and Canada (SIAP, 2017). During 2020, the state of Chiapas produced 270,695 tons of mangoes (SIAP, 2020). Harvesting is done when physiological maturity has been reached and during sensory ripening, or consumption of the fruit. At this stage, the pigmentation of the epicarp (mango skin) is a visual attribute of quality that determines its acceptance in the market.

Pigment accumulation is attributed to various genetic events that occur at different stages of maturation. Phenolic compounds such as anthocyanins and flavonoids have been associated with pigmentation (Falcone Ferreyra *et al.*, 2012); and it has been found that in fruits they accumulate more frequently in the skin during the ripening process. Genes that

Image by Rattakarn at Pixabay

control the production of these pigments, such as Phenylalanine ammonia-lyase (PAL), Chalcone synthase (CHS), Cinnamate 4 hydroxylase (C4H), 4-Coumarate: Coenzyme A ligase (4CL), among others, have also been associated.

The role of phenolic compounds in pigment accumulation is known. For example, some specific ones are phenylpropanoid flavonoids (PFP), precursors of chalcones, flavones, anthocyanins and condensed tannins (Vogt, 2010). The biosynthetic pathway that regulates these compounds is highly conserved among plant species and is well documented in *Arabidopsis thaliana* and in some fruit species such as grape, tomato, olive (Groenenboom *et al.*, 2013; Martinelli and Tonutti, 2012; Saito *et al.*, 2013); however, it is unknown whether in all major fruit trees such as apple, peach, pear, mango or others, such pathway could be similar, although it is known that such biosynthetic pathways and genes are associated with the production of vitamins A, B, C, E and K (Maldonado-Celis *et al.*, 2019).

According to information regarding pigment accumulation, the mango fruit has high nutritional value because it is a rich source of antioxidants, vitamins and other compounds that can promote human health benefits (Hoang *et al.*, 2015a). The metabolic pathways of some pigments are described (Hichri *et al.*, 2011; Yonekura-Sakakibara *et al.*, 2008). The production of these compounds is regulated by various genes, which control the expression pathways and proportion of these compounds. On the other hand, in some mango varieties it has been reported that PAL, CHS, C4H, 4CL genes are responsible for regulating the synthesis and production of such pigments and vitamins.

In Mexico there is a high diversity of criollo varieties of mango (Galvéz-López *et al.*, 2007a), with a wide spectrum of colors, ranging from green, yellow, red, among other intermediate colors, which could represent an important source of antioxidants with impact on the human health of Mexicans, through the consumption of fresh fruit. However, given the scarce information so far available on the genetic control of mango fruit pigmentation, it would be useful to know the possible biochemical and genetic processes that determine such pigmentation. Therefore, this study describes the biosynthetic pathways of the main pigments and the genes associated with the production of these pigments in various fruit trees, and their possible application to pigment diversity in Mexican criollo mango germplasm is discussed.

What is pigmentation?

Fruit color is an index of quality and is the visual characteristic that most attracts consumers (Kayesh *et al.*, 2013). Flavonoids (FL) are synthesized in the cytosol and stored mainly in the vacuole. LFs are also found in cell walls, the nucleus, chloroplasts, and even in the extracellular space, depending on the plant species, tissue or stage of development (Hichri *et al.*, 2011). Some pigments have also been reported to be stored in chromoplasts, which are a type of fully developed plastids (Li and Yuan, 2013). Pigment accumulation is a mechanism attributed to biochemical pathways that are triggered during fruit ripening. Some of the pigments that have been identified are carotenoids, betalains, flavonoids and anthocyanins, chlorophyll, among several others (Yuan *et al.*, 2015a; Sudhakar *et al.*, 2016).

Carotenoids

Carotenoids are lipid-soluble pigments responsible for yellow, orange and red coloration; β-carotene is a type of carotenoid produced by plants and is the one found in highest proportion in them; therefore, it is one of the most studied pigments. Carotenoids are classified into oxygenated (lutein, violoxanthin and neoxanthin), and non-oxygenated (β-carotene and lycopene) (Subburaj *et al.*, 2019). The main interest lies in the fact that it is a precursor of vitamin A (Arscott and Tanumihardjo, 2010) (Olson, 1999; Perera and Yen, 2007; Stahl and Sies, 2005).

Betalains

Betalains are nitrogen-containing, water-soluble pigments derived from tyrosine. However, their presence is restricted to only a few plant families related to the order Caryophyllales, among which the genera *Beta*, *Amaranthus*, *Opuntia* and *Hylocereus* stand out. Betalains are divided into two groups: betacyanins, which provide red hues and are formed by condensation of a cyclo-DOPA (dihydroxyphenylalanine) structure with betalamic acid, and betaxanthins which provide yellow colorations and are synthesized from different amino compounds and betalamic acid (Polturak and Aharoni, 2018). Both have antioxidant and anti-inflammatory activity (Gandía-Herrero and García-Carmona, 2013). Betalains are the least known pigments, although the vitamins associated with these pigments are vitamin B and C (Rahimi *et al.*, 2019; W.S., 2018).

Flavonoids

Flavonoids are a group of natural compounds with variable phenolic structures produced by the metabolic pathway of PFP compounds, which also contribute to fruit coloration and plant protection from ultraviolet radiation (Agati *et al.*, 2012; Pandey, 2013). In 1930 a new substance was isolated from oranges (*Citrus sinenesis*), at that time believed to be a member of a new class of vitamins and designated as vitamin P; this substance was later found to be the flavonoid rutin and to date, more than 4000 flavonoid variants have been identified. Recently, there has been interest in flavonoids due to their potential health effects as antioxidant, antibacterial, anti-inflammatory, anticancer and antiviral substances. Thus, they also play an important role in plants by decreasing oxidative stress and as growth regulators (Pandey, 2013). Quercetin is one of the most abundant flavonoids found in fruits and vegetables, and has been linked to vitamin C and E (Colunga Biancatelli *et al.*, 2020; Srivastava *et al.*, 2016).

Anthocyanins

They are water-soluble pigments that belong to the flavonoid group, a subclass of the polyphenol family. Anthocyanins give colors to fruits that, in spectrum, range from red and purple, to blue (Sudhakar *et al.*, 2016). More than 700 different anthocyanins have been identified, including pelargonidin, delphinidin, cyanidin, petunidin, peonidin, malvidin, among many others (Wallace and Giusti, 2014). Some of the functions of anthocyanins in red mango fruits that have been reported are tolerance to cold and fungal pathogens, especially when the red color is intense (Sivankalyani *et al.*, 2016; Sudheeran *et al.*, 2018).

Some vitamins associated with anthocyanins are vitamins C and E (Leong and Oey, 2012; Martín *et al.*, 2017).

Chlorophylls

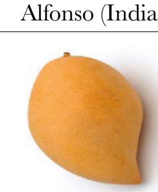
Chlorophylls are lipid-soluble green pigments found in all algae, higher plants and cyanobacteria that photosynthesize. Chlorophyll in plant foods is converted into pheophytin, pyropheophytin and pheophorbide, after ingestion by humans; these valuable bioactive compounds show an anti-mutagenic effect, so they are likely to play an important role in cancer prevention, specifically through inhibition of myeloma cell multiplicity through pheophorbide. In addition, it is used as a natural food colorant and has antioxidant properties (Guedes *et al.*, 2019).

Pigment diversity of mango fruit

Mango has a diversity of colors in both skin and flesh. In mango fruit, color development is an important phenomenon during ripening. Mango varieties can be classified according to their skin color spectrum or pigmentation, and consumers in some countries have preferences for a particular color in their imports market. The red mango varieties most in demand for export are Kent, Tommy Atkins, Haden and Keitt, which are less fibrous, firmer and suitable for long distance transport (Evans, 2008).

Among the green mango varieties, and mostly known in the world, are Bombay, Amrapali, Bennet Alphonso, Arroyos, Carabao, Carrie, Chok Anan, Fazli, Himayat, Jean Ellen, Neelam and Saigon mangoes, all of them rich in beta-carotene. Other well-known red varieties include Haden, Irwin and Tomy Atkins, Edward, Palmer, Badami, Cogshall, Vado, San Felipe and Van Dyke mangoes, rich in vitamin A. Meanwhile, the most popular

Table 1. Example of common pigmentation in international mango varieties.

Green varieties	Red varieties	Yellow varieties
 Saigon (USA)	 Irwin (USA)	 Ataulfo (Mexico)
 Alampur Baneshan (India)	 Van Dyke (USA)	 Alfonso (India)
 Amparali (India)	 Tommy Atkins (USA)	 Nam Doc Mai (Thailand)

yellow varieties are Alfonso, Ataulfo, Banganapalli, Punto, Duncan, Gir Kesar, Glenn, Nam Doc Mai, Sindhri, Manila, Mallika, Francis and Kesar (Mitra, 2016), rich in vitamin B, C and E. Table 1 shows some examples of widely traded mango varieties with green, red and yellow pigmentation.

In Mexico there is also a wide diversity of colors in mango germplasm. The best known and most widely cultivated variety in the country is the Ataulfo mango, although there are also other varieties cultivated in smaller proportions, as well as a wide range of criollo mangoes, all of which are high in nutrients, vitamins and antioxidants. Some registered varieties are Cotaxtla-1, Cotaxtla-2, Diamante and Zafiro mangoes (SNICS 2020).

Authors such as Gálvez-López *et al.* (2007b) reported a broad and diverse range of Mexican criollo mangoes, among which green, red and yellow mangoes can be distinguished (Table 2). This indicates that genetic recombination of mango germplasm since its introduction to Mexico has been favored by climatic conditions.

Within the spectrum of green coloration reported in Mexico there are the Criollo mangos, Tecolote, Madura Verde and Piña. In turn, the red mango germplasm consists of the varieties Manzanillo Núñez, Suchitoto, as well as the criollo Coche, Manzana, Cachetio and Pepino. Among the yellow mangoes there are Ataulfo, Diamante Ataulfo, Elite Ataulfo, Diplomatic and Criollos Manililla, Amate or Amatillo, Alcanfor, Plátano, Oro, Agua and Ajo. There are also criollo mangos with yellow peels with red dots and yellow with green dots. This variability of colors could represent an important source of

Table 2. Diversity of colors in native mango germplasm from Chiapas, Mexico (Taken from: Gálvez López *et al.*, 2007b).

Name	Ripe fruit	Name	Ripe fruit	Name	Ripe fruit
Manililla		Plátano		Agua	
Canela		Viejita		Plátano	
Coche		Tecolote		Sin nombre 1	
Amatillo		Pepino		Ajo	
Cachetio		Manzana		Sin nombre 2	
Oro		Alcanfor		Ataulfo 50	

antioxidants and pigments that would bring benefits to the human health of Mexicans through the consumption of fresh fruit, or the commercial/industrial exploitation of these.

The high variability in coloration and pigments in the native Mexican mango germplasm constitutes a source of genetic wealth, and makes this species a genetic potential for human nutritional use and benefit, since most of the criollo mango cultivated in Mexico is not used.

Pigment biosynthesis

It is evident that the range of coloration that may happen in fruits depends on the triggering of the biosynthetic pathways of the different pigments present in mango germplasm. This also applies to all fruits consumed by humans. The main biosynthetic pathways that convert pigments into products beneficial to human health are described below.

Carotenoids

Carotenoid biosynthesis in plants begins with the conversion of geranylgeranyl pyrophosphate (GGPP) by condensation of two molecules to form phytoene via phytoene synthase (PSY) (Figure 1). Phytoene is subsequently converted to lycopene by the activities of two desaturases, phytoene desaturase (PDS) and ζ-carotene desaturase (ZDS), and two isomerase enzymes, ζ-carotene isomerase (ZISO) and carotene isomerase (CRTISO). The conversion of linear lycopene to β-carotene or α-carotene represents a bifurcation of the biosynthetic pathway (H. Yuan *et al.*, 2015b).

Betalaines

The biosynthetic pathway of betalains, as well as the enzymes and genes involved in this pathway, are less well known than those of flavonoids and carotenoids. Betalains are synthesized from tyrosine (Figure 2), an aromatic amino acid that is mainly produced in plants through the shikimate pathway. Tyrosine is initially hydroxylated to form 3,4-dihydroxy-L-phenyalanine (L-DOPA) by the enzyme tyrosine hydroxylase. L-DOPA is subsequently converted to betalamic acid, the central backbone of all betalain compounds, in a two-step reaction initiated by the enzyme DOPA dioxygenase (Polturak and Aharoni, 2018). The

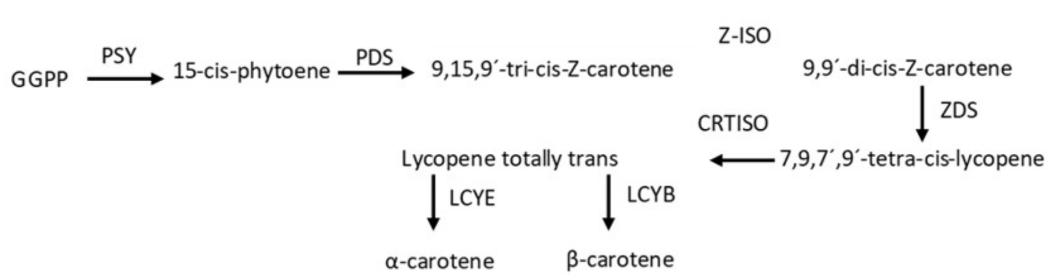


Figure 1. Schematic representation of carotenoid biosynthesis. GGGP: Geranylgeranyl pyrophosphate, PSY: Phytoene synthase, PDS: Phytoene desaturase, ZISO: Z-carotene isomerase, ZDS: Z-carotene desaturase, CRTISO: Carotene isomerase, LCYE: Lycopene β-cyclase, LCYB: Lycopene β-carotene (Liang *et al.*, 2020).

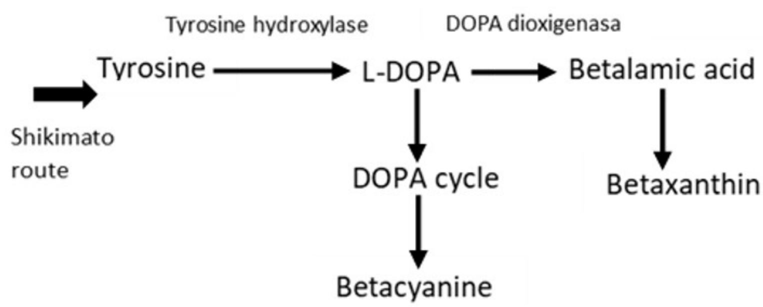


Figure 2. Schematic representation of the biosynthesis of betalains. L-DOPA: 3,4-dihydroxy-L-phenylanaline (Gengatharan *et al*., 2015).

formation of cycle DOPA is carried out by the enzyme DOPA oxidase. Betalamic acid then spontaneously condenses with an amine to produce the yellow pigment betaxanthin, or with DOPA cycle to produce the red pigment betacyanin, the pigmentation depending on condensation in the pathway.

Flavonoids

The phenylpropanoid flavonoid pathway in plants is responsible for the biosynthesis of a large number of secondary metabolites. Both flavonoids and anthocyanins are synthesized at the end of this very diverse metabolic pathway, as well as many intermediate molecules whose precise biological functions remain largely unknown.

Phenylpropanoids are a group of physiologically active secondary metabolites derived from phenylalanine, such as lignins, flavonols, isoflavonoids and anthocyanins (Vogt, 2010). All of these perform different important functions, such as protecting plants against photooxidative damage and UV radiation (Xie *et al*., 2012). The products of the PFP biosynthetic pathway have been extensively studied. Phenylpropanoid metabolism is a key biosynthetic pathway in plant cells, but the regulation of the genes involved is specific to plant tissue type and the species (Vogt, 2010). The relationship between the fruit ripening process and the biosynthesis of phenolic compounds is a complex issue to address (Rinaldo *et al*., 2010). As the first step in the phenylpropanoid pathway in plants, phenylalanine is deaminated to produce cinnamic acid through the action of phenylalanine ammonium lyase (PAL). Cinnamic acid is hydroxylated to coumaric acid, which is then activated to 4-coumaroyl-CoA by the action of 4-coumarate: CoA ligase (4CL). Chalcone synthase (CHS) catalyzes the tiered condensation of three malonyl-CoA acetate units with p -coumaroyl-CoA to produce naringenin chalcone. Naringenin chalcone is converted to naringenin by chalcone isomerase (CHI) (Figure 3). Subsequently, flavanone 3-hydroxylase (F3H) converts naringenin to dihydrokaempferol. Dihydroflavonol 4-reductase (DFR) is an important enzyme in the next step of anthocyanidin synthesis and can use any of the dihydroflavonols as substrates to produce anthocyanidin precursors. Afterwards, anthocyanins have three main branches. Each branch corresponds to the use of one, two or three hydroxyl groups on the B-ring of dihydrokaempferol. The flavonoid enzyme 3'hydroxylase (F3'H) is responsible for the different hydroxylations during the pathway.

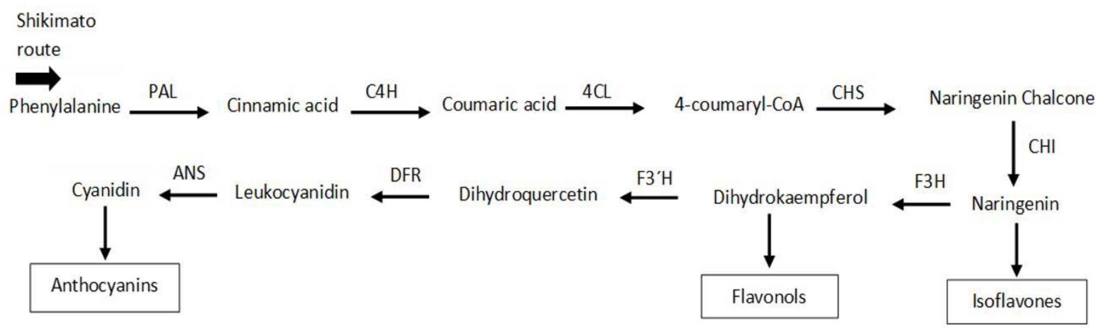


Figure 3. Schematic representation of phenylpropanoid flavonoid biosynthesis. PAL: Phenylalanine ammonium lyase, C4H: Cinnamate 4- mono-oxygenase, 4CL: 4-coumarate: CoA ligase, CHS: Chalcone synthase, CHI: Chalcone isomerase, F3H: Flavanone 3-hydroxylase, DFR: Dihydroflavonol 4-reductase and ANS: Anthocyanidin synthase (Ferreyra *et al.*, 2012).

Chlorophylls

Chlorophyll is synthesized in the chloroplast. In the first phase, the acid glutamic amino acid is converted to 5-aminolevulinate acid (Figure 4). In this metabolic pathway, the presence of light is necessary during the reaction that produces protoporphyrin IX. Other chloroplast enzymes can add either Mg^{2+} to initiate chlorophyll synthesis or Fe^{2+} to initiate the synthesis of heme groups. Protoporphyrin IX can also be exported from the chloroplast to the mitochondrion, where it is used to produce large amounts of cytochromes. This biosynthetic pathway is also important because heme groups serve as substrate for the synthesis of phytochrome, an essential photosensitive molecule for normal plant photomorphogenesis (Rüdiger *et al.*, 2006).

Therefore, all pigments have defined biosynthetic pathways that determine the different colorations in fruits, which are regulated by a series of genetic elements, not yet fully

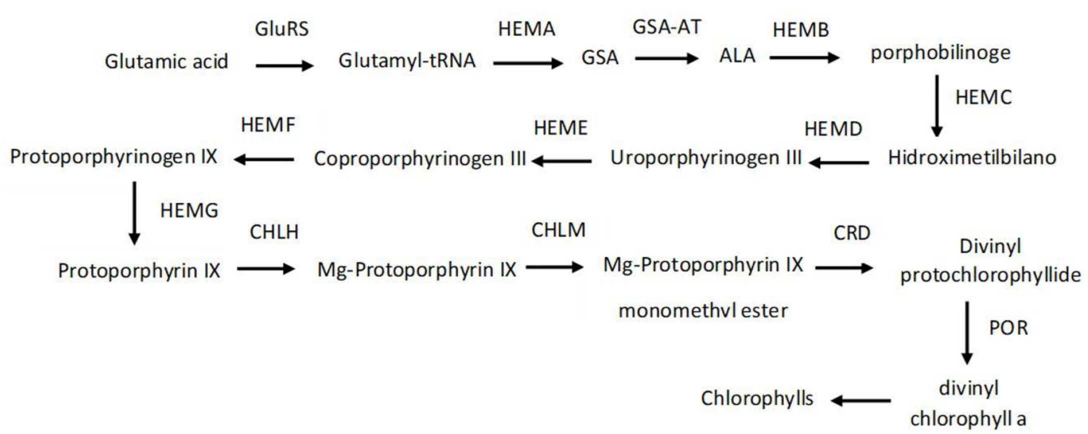


Figure 4. Schematic representation of chlorophyll biosynthesis. GluRS: Glutamyl-tRNA synthase, HEMA: Glutamyl-tRNA reductase, GSA: Glutamate-1-semialdehyde, GSA-AT: Glutamate-1-semialdehyde 2,1-aminotransferase, ALA: 5-aminolevulinic acid, HEMB: 5-aminolevulinate dehydrogenase, HEMC: Porphobilinogen deaminase, HEMD: Uroporphyrinogen III synthase, HEME: Uroporphyrinogen III decarboxylase, HEMF: Coproporphyrinogen III oxidase, HEMG: Protoporphyrinogen oxidase, CHLH: Mg-chelatase, CHLM: Mg-protoporphyrin IX methyltransferase, CRD: Mg-protoporphyrin IX monomethyl ester cyclase, POR: Protochlorophyllide oxide reductase (Ohmiya *et al.*, 2014).

known or elucidated. Some associated elements are, for example, genes, SNPs, proteins, transcription factors, miRNA, among other key elements (Castillejo *et al.*, 2020).

Genes associated to pigmentation

Fruit pigment production and degradation depend on complex events. Particularly some genes have been related to the modulation of biosynthetic pathways, generating key enzymes and byproducts in fruit pigmentation. Generally speaking, two types of genes are required for pigment production: structural genes that encode enzymes involved in each reaction step, and regulatory genes that control the transcription of structural genes (Liu *et al.*, 2018).

The PSY gene coding for the enzyme phytoene synthase was found to control the production of the elements responsible for the limiting reactions of the carotenoid pathway; therefore, the resulting enzyme is one of the most studied enzymes in plant carotenogenesis (Yao *et al.*, 2018). This gene presents diverse alleles depending on the species; for example, in Arabidopsis, only one copy of the PSY gene has been found in chromosome 5, while two alleles have been found in carrot (*Daucus carota*) (Clotault *et al.*, 2008; Rodríguez-Villalón *et al.*, 2009); in tomato (*Solanum lycopersicum*), maize (*Zea mays*), rice (*Oryza sativa*) and sorghum (*Sorghum bicolor* L. [Moench]) there are three alleles of the PSY gene (Chaudhary *et al.*, 2010; Dibari *et al.*, 2012; Fantini *et al.*, 2013). For its part, the PDS gene encoding the phytoene desaturase enzyme is involved in the carotenoid biosynthesis pathway.

In the modulation of gene expression, the presence of regulatory sequences and proteins capable of directing gene expression is necessary. Gene expression is the process by which the information encoded in a gene is used to direct the assembly of a protein molecule. Regulation of gene expression is one of the most important events in the control of development and in the responses to environmental changes. Gene regulation is the process of activating and deactivating genes. The master proteins in the regulation of gene expression are known as transcription factors.

Transcription factors are proteins that bind to DNA to stimulate or repress the transcriptional rate of genes by binding to specific promoter regions. This activates or deactivates gene signaling cascades. Transcription factors have fundamental functions in almost all biological processes (development, growth and responses to environmental factors).

In plants, transcription factors have been used to manipulate various metabolic pathways, of growth and development, and stress responses (Garcia-Morales *et al.*, 2013). For example, it has been reported that the structural genes of the flavonoid and anthocyanin biosynthetic pathways function under the control of the MYB transcription factor, most of which regulate structural genes at different levels acting specifically depending on the tissue of the plant species. MYB proteins constitute the largest class of modulators of secondary metabolism; this family of proteins is characterized by the presence of a characteristic DNA-binding domain called MYB (Docimo *et al.*, 2016). MYB proteins participate as transcriptional activators or repressors in the regulation of cellular processes; 339 and 230 MYB proteins have been reported in *Arabidopsis thaliana* and rice, respectively (Feller *et al.*, 2011).

Another important genetic element in the pigment pathway is the PAL gene coding for phenylalanine ammonium lyase, which plays an important role in the phenylpropanoid metabolism pathway. The PAL gene is key in phenylpropanoid biosynthesis and is widely distributed in several plant species. It has also been cloned from fungi. In many plant species, the PAL gene is encoded by a polygenic family, that is, for each gene there are several members or alleles; for example, in *Brachypodium distachyon* (8 members), *Populus trichocarpa* (5 members) and *Eucalyptus grandis* (9 members). Recently, four PAL genes were identified, expressed and characterized in *Arabidopsis thaliana* (Li *et al.*, 2019).

The *CHS* gene controls the first committed step of flavonoid biosynthesis. The expression of the *CHS* gene is related to the accumulation of flavonoids and anthocyanins, which generate the colors ranging from red to purple and also determine the antioxidant capacity of fruits and leaves. The function of the *CHS* gene has been studied in many plant species such as soy and dicotyledons such as apple (Wang *et al.*, 2018).

In mango varieties "Amrapali" (green skin color), "Arka Anmol" (yellow skin color) and "Janardhan Pasand" (red skin color), the peels were studied at different ripening stages, analyzing pigments, colors, as well as the gene expression of carotenoids and anthocyanins. The genes studied were *PSY*, *PDS*, *ZDS*, *CHS*, *CHI*, *F3H*, *ANS* and *DFR*. They found that gene expression levels increased as fruit ripening advanced, and the highest expression levels were observed in the red-colored variety (Karanjalker *et al.*, 2018).

Table 3 summarizes a list of multiple genes and gene families associated with pigment production in different species; for example, genes associated with the biosynthetic pathways of carotenoids, flavonoids, anthocyanins, and chlorophylls. Despite this knowledge, further molecular studies are still needed to fully understand the regulation and control of all pigment pathways. For the case of mango, elucidating knowledge is still scarce. In addition to these genes, it has also been found that some SNPs are probably responsible for the differences in fruit pigmentation in some varieties; however, these hypotheses still need to be tested, mainly in Mexican mango germplasm.

Nutritional benefits of pigment consumption

Regardless of the knowledge so far developed in the understanding of the biosynthetic pathways and the genes associated with fruit pigmentation, it is essential to highlight the nutritional contribution of pigments to human health. Below are some examples of the proven benefits of pigments for human health.

Benefits of carotenoids

Interest in carotenoids from a nutritional standpoint has focused primarily on the provitamin A activity of carotenoids that have β-rings, since vitamin A deficiency is a major micronutrient deficiency worldwide. β-carotene is one of the most abundant carotenoids in fruits and vegetables. Carotenoids have an essential role in human nutrition and health, as humans cannot synthesize vitamin A *de novo*, although plant carotenoids such as β-carotene, α-carotene, γ-carotene and β-cryptoxanthin provide the main dietary source of provitamin A (Sharoni *et al.*, 2011).

Table 3. Genes associated with fruit pigmentation.

Gen	Associated metabolic pathway	Accesion number	Specie	Author
Carotenoid pigments				
PSY	Carotenoid	831587	*Arabidopsis thaliana*	(Álvarez *et al*., 2016)
PSY	Carotenoid	103501375	*Cucumis melo*	(Qin *et al*., 2011)
PSY 2	Carotenoid	103443160	*Malus domestica*	(Ampomah-Dwamena *et al*., 2015)
ZDS	Carotenoid	543629	*Solanum lycopersicum*	(McQuinn *et al*., 2020)
PDS	Carotenoid	544073	*Solanum lycopersicum*	(Charles *et al*., 2012)
CRTISO	Carotenoid	101267857	*Solanum lycopersicum*	(Ralley *et al*., 2016)
LCYβ	Carotenoid	544104	*Solanum lycopersicum*	(Ralley *et al*., 2016)
LCY-ε	Carotenoid	544129	*Solanum lycopersicum*	(Charles *et al*., 2012)
Flavonoid and anthocyanin pigments				
PAL1	PFP	KJ461724.1	*Prunus domestica*	(Selvaraj *et al*., 2016)
PAL2	PFP	KJ461725.1	*Prunus domestica*	(Selvaraj *et al*., 2016)
PAL	PFP	EF192469.1	*Vitis vinifera*	(Kobayashi *et al*., 2011)
PAL	PFP	KF956008	*Mangifera indica*	(Hoang *et al*., 2015b)
C4H	PFP	817599	*Arabidopsis thaliana*	(Schilmiller *et al*., 2009)
4CL	PFP	116199772	*Punica granatum*	(Ophir *et al*., 2014)
CHS	PFP	KJ461726.1	*Prunus domestica*	(Selvaraj *et al*., 2016)
CHS1	PFP	KF956020	*Mangifera indica*	(Hoang *et al*., 2015b)
CHS2	PFP	KF956023	*Mangifera indica*	(Hoang *et al*., 2015b)
CHI	PFP	107779699	*Nicotina tabacum*	(Li *et al*., 2019)
F3H	PFP	824287	*Arabidopsis thaliana*	(Owens *et al*., 2008)
DFR	PFP	544150	*Solanum lycopersicum*	(Li *et al*., 2019)
ANS	PFP	107027946	*Sonalum pennellii*	Li *et al*., 2019)
Chlorophyll pigments				
HEMA1	Clorophyll	842198	*Arabidopsis thaliana*	(Ohmiya *et al*., 2014)
HEMD	Clorophyll	817195	*Arabidopsis thaliana*	(Ohmiya *et al*., 2014)
CHLI1	Clorophyll	5716878	*Chlamydomonas reinhardtii*	(Brzezowski *et al*., 2016)
CHLI2	Clorophyll	834633	*Arabidopsis thaliana*	(Huang y Li, 2009)

Beta-carotenes can improve immune function due to their antioxidant capacity and increase lymphocyte proliferation (Maiani *et al*., 2009; Yamaguchi, 2012). The benefits associated with carotenoid intake include enhanced immune system functions and lower risk of developing chronic degenerative diseases, such as age-related muscle degeneration, type 2 diabetes, obesity, certain types of cancer such as breast, cervical, ovarian and colorectal cancers, and cardiovascular disease, among others (Hamer and Chida, 2007; Britton, 2009; Fernández-García *et al*., 2012; Bonet *et al*., 2015; Melo van Lent *et al*., 2016). Carotenoids also attract interest as promoters of cognitive functions (Hammond, 2015), as well as skin photo-protectants and providers of cosmetic benefits (Meléndez-Martínez *et al*., 2018).

Benefits of betalains

Betalains are not well studied compared to other pigments due to their scarcity in nature. In addition to their relevance as colorants, betalains have various effects that promote health benefits, such as antioxidant activity, anti-inflammatory activity, antimicrobial activity, hepatoprotective effects, and chemopreventive and anticancer properties. However, betalains are quite sensitive to heat, pH, light and oxygen (Gengatharan *et al.*, 2015). There are reports that betalains are precursors of vitamins B and C (Rahimi *et al.*, 2019; W.S., 2018). The B vitamins comprise a group of eight water-soluble vitamins that play essential and closely related roles in cellular functioning, acting as coenzymes in a wide range of catabolic and anabolic enzymatic reactions. It is important for the metabolism of proteins, because it helps in the formation of red blood cells in the blood and in the maintenance of the central nervous system. Their effects are particularly prevalent in numerous aspects of brain function, including energy production, DNA/RNA synthesis/repair, genomic and non-genomic methylation, and the synthesis of numerous neurochemicals and signaling molecules (Kennedy, 2016; Fratoni and Brandi, 2015). Vitamin C was first identified in citrus fruits. It is an important vitamin in human health; it is water soluble, necessary for normal growth and development, and it also cannot be synthesized by humans. Its importance lies in the essential factor in the synthesis of collagen, carnitine and norepinephrine (Pacier and Martirosyan, 2015).

Benefits of flavonoids and anthocyanins

Many flavonoids have been reported to have antioxidant activity, free radical scavenging capacity, coronary heart disease prevention, hepatoprotective, anti-inflammatory and anticancer activities, while some flavonoids exhibit potential antiviral activities (Martín *et al.*, 2017). In plants, flavonoids help combat oxidative stress and act as growth regulators. For pharmaceutical purposes, the production of different types of flavonoids has been possible with the help of microbial biotechnology (Pandey, 2013). Anthocyanins are bioactive components of nutraceutical and traditional medicine. They have been used as phyto-pharmaceuticals, appetite stimulants and for the treatment of many other diseases. The potential health benefits of anthocyanins are antioxidant, anti-angiogenesis, anticancer, antidiabetic, visual health improvement, anti-obesity, antimicrobial and neuroprotective effects (Khoo *et al.*, 2017). The vitamins associated with flavonoids and anthocyanins are vitamins C and E.

Vitamin E is a fat-soluble vitamin found in many foods. In the body it acts as an antioxidant, helping to protect cells from damage caused by free radicals. Free radicals are compounds that are formed when the body converts the food we eat into energy. The body also needs vitamin E to boost its immune system so it can fight off invading bacteria and viruses. It is also important in the formation of red blood cells and helps to dilate blood vessels and to prevent blood from clotting within them (Lee and Han, 2018). Therefore, the consumption of fruits containing these pigments is of utmost importance in the human diet and health, since they are a rich source of vitamin precursors that have a positive impact on human health and nutrition.

Benefits of chlorophylls

Chlorophylls are a fat-soluble pigment that gives plants and algae their green color and, together with light, is essential for the photosynthesis process to take place. Chlorophylls have been reported to have antioxidant activity, like anthocyanins, helping to protect cells from free radical damage; they also have anti-inflammatory, anti-cancer, anti-mutagenic and other properties. Positive effects on wound healing have also been reported, and the vitamins associated with chlorophylls are vitamin A, C and E (Zepka *et al.*, 2019; Levent, 2017).

CONCLUSIONS

Morphological, biochemical and genetic studies of pigment diversity establish the basis of scientific knowledge that allows the identification of genes leading to the formation of important compounds with potential benefits for human health. This knowledge represents the basis for future decisions on the agronomic use of mango germplasm in Mexico. However, there is still scarce information in terms of knowledge about the genes and gene families that control all the metabolic pathways involved in the type of pigmentation that mangoes (*M. indica*) express. Therefore, it is necessary to develop research aimed at understanding the elucidation, expression, structure and specific function of these genes, as this could help to understand the possible levels of accumulation and concentration of pigments there are among the different red, yellow, green and other color varieties in the Mexican mango germplasm. Finally, exploring the richness of mango germplasm at the molecular level could be of great benefit to human health; this would allow initiating conservation and propagation programs for the different types of mangoes in the country that could be attractive in national and international markets.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

ACKNOWLEDGMENTS

The authors thank CONACyT project APN-2017-6427 for funding mango (*Mangifera indica* L.) studies at the Instituto de Biociencias UNACH.

REFERENCES

Agati G, Azzarello E, Pollastri S, Tattini M. (2012). Flavonoids as antioxidants in plants: Location and functional significance. *Plant Science*. 196. 67–76. Doi: 10.1016/j.plantsci.2012.07.014

Álvarez D, Voß B, Maass D, Wüst F, Schaub P, Beyer P, Welsch R. (2016). Carotenogenesis is regulated by 5'UTR-mediated translation of phytoene synthase splice variants. *Plant Physiology*. 172 (4). 2314–2326. Doi: 10.1104/pp.16.01262

Ampomah-Dwamena C, Driedonks N, Lewis D, Shumskaya M, Chen X, Wurtzel E T, Espley R V, Allan A. C. (2015). The Phytoene synthase gene family of apple (*Malus × domestica*) and its role in controlling fruit carotenoid content. *BMC Plant Biology* 15 (185). 1–14. Doi: 10.1186/s12870-015-0573-7

Arscott, S. A., Tanumihardjo S.A. (2010). Carrots of Many Phytochemicals Acting as a Functional Food. *Comprehensive Reviews in Food Science and Food Safety*. 9 (2). 223:239. Doi: 10.1111/j.1541-4337.2009.00103.x

Brzezowski P, Sharifi M. N., Dent R. M., Morhard M. K., Niyogi K. K., Grimm B. (2016). Mg chelatase in chlorophyll synthesis and retrograde signaling in *Chlamydomonas reinhardtii*: CHLI2 cannot substitute for CHLI1. *Journal of Experimental Botany* 67: 3925–3938.

Castillejo, C., Waurich, V., Wagner, H., Ramos, R., Oiza, N., Muñoz, P., Triviño, J. C., Caruana, J., Liu, Z., Cobo, N., Hardigan, M.A., Knapp, S., Vallarino, J. G., Osorio, S., Martín-Pizarro, C., Pose, D., Toivainen, T., Hytonen, T., Oh, Y., Amaya I. (2020). Allelic Variation of MYB10 is the Major Force Controlling Natural Variation of Skin and Flesh Color in Strawberry (*Fragaria* spp.) fruit. *The Plant Cell* 32 (12). 3723-3749. Doi: 10.1105/tpc.20.00474

Charles, A., Supinya, D., David, L., Paul, S., Richard, K., Andrew, C. (2012). Metabolic and gene expression analysis of apple (*Malus × domestica*) carotenogenesis. *Journal of Experimental Botany*. 63 (12). 4497-4511. Doi: 10.1093/jxb/ers134

Chaudhary, N., Nijhawan, A., Khurana, J. P., Khurana, P. (2010). Carotenoid biosynthesis genes in rice: Structural analysis, genome-wide expression profiling and phylogenetic analysis. *Molecular Genetics and Genomics*. 283. 13–33. Doi: 10.1007/s00438-009-0495-x

Clotault, J., Peltier, D., Berruyer R, Thomas M, Briard M, Geoffriau E. 2008. Expression of carotenoid biosynthesis genes during carrot root development. *Journal of Experimental Botany* 59: 3563–3573. https://doi.org/10.1093/jxb/ern210

Colunga Biancatelli R M L, Berrill M, Catravas J D, Marik P E. 2020. Quercetin and Vitamin C: An Experimental, Synergistic Therapy for the Prevention and Treatment of SARS-CoV-2 Related Disease (COVID-19). *Frontiers in Immunology* 1: 1–11. https://doi.org/10.3389/fimmu.2020.01451

Dibari B, Murat F, Chosson A, Gautier V, Poncet C, Lecomte P, Mercier I, Bergès H, Pont C, Blanco A, Salse J. 2012. Deciphering the genomic structure, function and evolution of carotenogenesis related phytoene synthases in grasses. *BMC Genomics* 13: 221. https://doi.org/10.1186/1471-2164-13-221

Docimo T, Francese G, Ruggiero A, Batelli G, De Palma M, Bassolino L, Toppino L, Rotino G L, Mennella G, Tucci M. 2016. Phenylpropanoids accumulation in eggplant fruit: Characterization of biosynthetic genes and regulation by a MYB transcription factor. *Frontiers in Plant Science* 6: 1–18. https://doi.org/10.3389/fpls.2015.01233

Evans E A. 2008. Recent Trends in World and U.S. Mango Production, Trade, and Consumption. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 107: 106–111.

Falcone Ferreyra M L, Rius S P, Casati P. 2012. Flavonoids: Biosynthesis, biological functions, and biotechnological applications. *Frontiers in Plant Science* 3: 1–15. https://doi.org/10.3389/fpls.2012.00222

Fantini E, Falcone G, Frusciante S, Giliberto L, Giuliano G. 2013. Dissection of tomato lycopene biosynthesis through virus-induced gene silencing. *Plant Physiology*, 163: 986–998. https://doi.org/10.1104/pp.113.224733

Feller A, MacHemer K, Braun E L, Grotewold E. 2011. Evolutionary and comparative analysis of MYB and bHLH plant transcription factors. *Plant Journal* 66: 94–116. https://doi.org/10.1111/j.1365-313X.2010.04459.x

Fernández-García E, Carvajal-Lérida I, Jarén-Galán M, Garrido-Fernández J, Pérez-Gálvez A, Hornero-Méndez D. 2012. Carotenoids bioavailability from foods: From plant pigments to efficient biological activities. *Food Research International* 46: 438–450. https://doi.org/10.1016/j.foodres.2011.06.007

Fratoni V, Brandi M L. 2015. B vitamins, Homocysteine and bone health. *Nutrients* 7: 2176. https://doi.org/10.3390/nu7042176

Britton G, F K. 2009. Carotenoids. *Carotenoids in Food* 25: 45–66.

Galvéz-López D, Adriano-Anaya M L, Villareal-Treviño C, Mayek-Pérez N, Salvador-Figueroa M. 2007a. Diversidad Isoenzimática De Mangos Criollos De Chiapas, México. *Revista Chapingo Serie Horticultura XIII*(1): 71–76. https://doi.org/10.5154/r.rchsh.2005.04.028

Gálvez López D, Salvador Figueroa M, Mayek Pérez N. 2007b. Diversidad morfológica del fruto en germoplasma nativo de mango *Mangifera indica* L. (Anacardiaccac) nativo de Chiapas, México. *Cuadernos de Biodiversidad* 24: 10–19. https://doi.org/10.14198/cdbio.2007.24.02

Gandía-Herrero F, García-Carmona F. 2013. Biosynthesis of betalains: Yellow and violet plant pigments. *Trends in Plant Science* 18(6): 334–343. https://doi.org/10.1016/j.tplants.2013.01.003

García-Morales S, Gómez-Merino F C, Trejo-Téllez L I, Herrera-Cabrera É B. 2013. Factores de transcripción involucrados en respuestas moleculares de las plantas al estrés osmótico. *Revista Fitotecnia Mexicana* 36(2): 105–115.

Gengatharan A, Dykes G A, Choo W S. 2015. Betalains: Natural plant pigments with potential application in functional foods. *Lwt* 64(2): 645–649. https://doi.org/10.1016/j.lwt.2015.06.052

Groenenboom M, Gomez-Roldan V, Stigter H, Astola L, van Daelen R, Beekwilder J, Bovy A, Hall R, Molenaar J. 2013. The Flavonoid Pathway in Tomato Seedlings: Transcript Abundance and the Modeling of Metabolite Dynamics. *PLoS ONE* 8(7): 1–11. https://doi.org/10.1371/journal.pone.0068960

Guedes A C, Amaro H M, Sousa-Pinto I, Malcata F X. 2019. Algal spent biomass A pool of applications. *Biofuels from Algae* 2: 397–433.

Hamer M, Chida Y. 2007. Intake of fruit, vegetables, and antioxidants and risk of type 2 diabetes: Systematic review and meta-analysis. *Journal of Hypertension* 25(12): 2361–2369. https://doi.org/10.1097/HJH.0b013e3282efc214

Hammond B. 2015. Dietary Carotenoids and the Nervous System. *Foods* 4(4): 698–701. https://doi.org/10.3390/foods4040698

Hichri I, Barrieu F, Bogs J, Kappel C, Delrot S, Lauvergeat V. 2011. Recent advances in the transcriptional regulation of the flavonoid biosynthetic pathway. *Journal of Experimental Botany* 62(8): 2465–2483. https://doi.org/10.1093/jxb/erq442

Hoang Van LT, Innes D J, Shaw P N, Monteith G R, Gidley M J, Dietzgen R G. 2015a. Sequence diversity and differential expression of major phenylpropanoid-flavonoid biosynthetic genes among three mango varieties. *BMC Genomics* 16(1): 1–12.

Hoang Van Le Thu, Pierson J T, Curry M C, Shaw P N, Dietzgen R G, Gidley M J, Roberts-Thomson S J, Monteith G R. 2015b. Polyphenolic contents and the effects of methanol extracts from mango varieties on breast cancer cells. *Food Science and Biotechnology* 24(1): 265–271. https://doi.org/10.1007/s10068-015-0035-x

Huang Y S, Li H M. 2009. Arabidopsis CHLI2 Can Substitute for CHLI1. *Plant Physiology* 150(2): 636–645.

Karanjalker G R, Ravishankar K V, Shivashankara K S, Dinesh M R, Roy T K, Sudhakar Rao D V. 2018. A Study on the Expression of Genes Involved in Carotenoids and Anthocyanins During Ripening in Fruit Peel of Green, Yellow, and Red Colored Mango Cultivars. *Applied Biochemistry and Biotechnology* 184(1): 140–154. https://doi.org/10.1007/s12010-017-2529-x

Kayesh E, Shangguan L, Korir N K, Sun X, Bilkish N, Zhang Y, Han J, Song C, Cheng Z M, Fang J. 2013. Fruit skin color and the role of anthocyanin. *Acta Physiologiae Plantarum*, 35(10): 2879–2890. https://doi.org/10.1007/s11738-013-1332-8

Kennedy D O. 2016. B vitamins and the brain: Mechanisms, dose and efficacy A review. *Nutrients* 8(2): 68-97. https://doi.org/10.3390/nu8020068

Khoo H E, Azlan A, Tang S T, Lim S M. 2017. Anthocyanidins and anthocyanins: Colored pigments as food, pharmaceutical ingredients, and the potential health benefits. *Food and Nutrition Research* 61(1): 136-157. https://doi.org/10.1080/16546628.2017.1361779

Kobayashi H, Takase H, Suzuki Y, Tanzawa F, Takata R, Fujita K, Kohno M, Mochizuki M, Suzuki S, Konno, T. 2011. Environmental stress enhances biosynthesis of flavor precursors, S-3-(hexan-1-ol)-glutathione and S-3-(hexan-1-ol)-L-cysteine, in grapevine through glutathione S-transferase activation. *Journal of Experimental Botany* 62(3): 1325–1336. https://doi.org/10.1093/jxb/erq376

Lee G Y, Han S N. 2018. The role of vitamin E in immunity. *Nutrients* 10(11): 1–18. https://doi.org/10.3390/nu10111614

Levent, A. 2017. Chlorophyll: Structural properties, health benefits and its occurrence in Virgin olive oils. *Academic Food Journal* 9(2): 26-32.

Leong S Y, Oey I. 2012. Effects of processing on anthocyanins, carotenoids and vitamin C in summer fruits and vegetables. *Food Chemistry* 133(4): 1577–1587. https://doi.org/10.1016/j.foodchem.2012.02.052

Li G, Wang H, Cheng X, Su X, Zhao Y, Jiang T, Jin Q, Lin Y, Cai Y. 2019. Comparative genomic analysis of the PAL genes in five Rosaceae species and functional identification of Chinese white pear. *PeerJ* 2019(12). https://doi.org/10.7717/peerj.8064

Li L, Yuan H. 2013. Chromoplast biogenesis and carotenoid accumulation. *Archives of Biochemistry and Biophysics* 539(2): 102–109. https://doi.org/10.1016/j.abb.2013.07.002

Li Z, Vickrey T L, McNally M G, Sato S J, Clemente T E, Mower J P. 2019. Assessing anthocyanin biosynthesis in solanaceae as a model pathway for secondary metabolism. *Genes* 10(8): 559-574. https://doi.org/10.3390/genes10080559

Liang M, Su X, Yang Z, Deng H, Yang Z, Liang R, Huang J. 2020. Carotenoid composition and expression of carotenogenic genes in the peel and pulp of commercial mango fruit cultivars. *Scientia Horticulturae* 263: 109072.

Liu Y, Tikunov Y, Schouten R E, Marcelis L F M, Visser R G F, Bovy A. 2018. Anthocyanin biosynthesis and degradation mechanisms in Solanaceous vegetables: A review. *Frontiers in Chemistry* 6:52. https://doi.org/10.3389/fchem.2018.00052

Luisa, B.M., Canas, J. A., Ribot, J., Palou, A. (2015). Carotenoids and their conversion products in the control of adipocyte function, adiposity and obesity. *Archives of Biochemistry and Biophysics*. 572. 112–125. Doi: 10.1016/j.abb.2015.02.022

Maiani, G., Castón, M.J.P., Catasta, G., Toti, E., Cambrodón, I.G., Bysted, A., Granado-Lorencio, F., Olmedilla-Alonso, B., Knuthsen, P., Valoti, M., Böhm, V., Mayer-Miebach, E., Behsnilian, D., Schlemmer, U. (2009). Carotenoids: Actual knowledge on food sources, intakes, stability and bioavailability and their protective role in humans. *Molecular Nutrition and Food Research*. 53. 194–218. Doi: 10.1002/mnfr.200800053

Maldonado-Celis, M.E., Yahia, E.M., Bedoya, R., Landázuri, P., Loango, N., Aguillón, J., Restrepo, B., Guerrero Ospina, J .C. (2019). Chemical Composition of Mango (*Mangifera indica* L.) Fruit: Nutritional and Phytochemical Compounds. *Frontiers in Plant Science*. 10. 1–21. Doi: 10.3389/fpls.2019.01073

Martín, J., Kuskoski, E.M., Navas, M.J., Asuero, A.G. (2017). Antioxidant Capacity of Anthocyanin Pigments. Flavonoids. *Biosynthesis to Human Health*. 11. 205-219. Doi: 10.5772/67718

Martinelli, F., Tonutt,i P. (2012). Flavonoid metabolism and gene expression in developing olive (*Olea europaea* L.) fruit. *Plant Biosystems*. 146. 164–170. Doi: 10.1080/11263504.2012.681320

McQuinn, R.P., Gapper, N.E., Gray, A.G., Zhong, S., Tohge, T., Fei, Z., Fernie, A.R, Giovannoni, J.J. (2020). Manipulation of ZDS in tomato exposes carotenoid- and ABA-specific effects on fruit development and ripening. *Plant Biotechnology Journal*. 18 (11). 2210–2224. Doi: 10.1111/pbi.13377

Meléndez-Martínez, A.J., Mapelli-Brahm, P., Stinco, C.M. (2018). The colourless carotenoids phytoene and phytofluene: From dietary sources to their usefulness for the functional foods and nutricosmetics industries. *Journal of Food Composition and Analysis*. 67. 91–103. 103. Doi: 10.1016/j.jfca.2018.01.002

Melo van-Lent, D., Leermakers, E.T.M., Darweesh, S.K.L., Moreira, E.M., Tielemans, M.J., Muka, T., Vitezova, A., Chowdhury, R., Bramer, W.M., Brusselle, G.G., Felix, J.F., Kiefte-de Jong, J.C., Franco, O.H. (2016). The effects of lutein on respiratory health across the life course: A systematic review. *Clinical Nutrition ESPEN*. 13. 1-7. Doi: 10.1016/j.clnesp.2016.02.096

Mitra, S.K. (2016). Mango production in the world Present situation and future prospect. *Acta Horticulturae* 1111: 287–296. Doi: 10.17660/ActaHortic.2016.1111.41

Ohmiya, A., Hirashima, M., Yagi, M., Tanase, K., Yamamizo, C. (2014). Identification of genes associated with chlorophyll accumulation in flower petals. *PLoS ONE*. 9(12). 1–16.

Ophir, R., Sherman, A., Rubinstein, M., Eshed, R., Schwager, M.S., Harel-Beja, R., Bar-Ya'akov I., Holland, D. (2014). Single-nucleotide polymorphism markers from de-novo assembly of the pomegranate transcriptome reveal germplasm genetic diversity. *PLoS ONE* 9(2): e88998. Doi: 10.1371/journal.pone.0088998

Owens, D.K., Crosby, K.C., Runac, J., Howard ,B.A., Winkel, B.S.J. (2008). Biochemical and genetic characterization of Arabidopsis flavanone 3'-hydroxylase. *Plant Physiology and Biochemistry* 46(10): 833–843. https://doi.org/10.1016/j.plaphy.2008.06.004

Pacier, C., Martirosyanm, D.M. (2015). Vitamin C: Optimal dosages, supplementation and use in disease prevention. *Functional Foods in Health and Disease* 5(3). 89–107. Doi: 10.31989/ffhd.v5i3.174

Pandey, S.K., & Pandey, A K. (2013). Chemistry and Biological Activities of Flavonoids: An Overview. *The Scientific World Journal*. 58(4).145–148. Doi: 10.1155/2013/162750

Perera, C.O., Yen, G.M. (2007). Functional properties of carotenoids in human health. *International Journal of Food Properties*. 10 (2). 201–230. Doi: 10.1080/10942910601045271

Polturak, G., Aharoni, A. (2018). "La Vie en Rose": Biosynthesis, Sources, and Applications of Betalain Pigments. *Molecular Plant*, 11(1): 7–22. Doi: 10.1016/j.molp.2017.10.008

Qin, X., Coku, A., Inoue, K., Tian, L. (2011). Expression, subcellular localization, and cis-regulatory structure of duplicated phytoene synthase genes in melon (*Cucumis melo* L.). *Planta*. 234.(4). 737–748. Doi: 10.1007/s00425-011-1442-8

Rahimi, P., Abedimanesh, S., Mesbah-Namin, S.A., Ostadrahimi, A. (2019). Betalains, the nature-inspired pigments, in health and diseases. *Critical Reviews in Food Science and Nutrition*. 59(18). 2949–2978. Doi: 10.1080/10408398.2018.1479830

Ralley, L., Schuch, W., Fraser, P.D., Bramley , P.M. (2016). Genetic modification of tomato with the tobacco lycopene '-cyclase gene produces high '-carotene and lycopene fruit. *Zeitschrift Fur Naturforschung Section C Journal of Biosciences*. 71 (9–10). 295–301. Doi: 10.1515/znc-2016-0102

Rinaldo, D., Mbéguié-A-Mbéguié, D., Fils-Lycaon, B. (2010). Advances on polyphenols and their metabolism in sub-tropical and tropical fruits. *Trends in Food Science and Technology*. 21(12). 599–606. Doi: 10.1016/j.tifs.2010.09.002

Rodríguez-Villalón, A., Gas, E., Rodríguez-Concepción, M. (2009). Phytoene synthase activity controls the biosynthesis of carotenoids and the supply of their metabolic precursors in dark-grown Arabidopsis seedlings. *Plant Journal*. 60(3). 424–435. Doi: 10.1111/j.1365-313X.2009.03966.x

Saito, K., Yonekura-Sakakibara, K., Nakabayashi, R., Higashi, Y., Yamazaki, M., Tohge, T., Fernie, A.R. (2013). The flavonoid biosynthetic pathway in Arabidopsis: Structural and genetic diversity. *Plant Physiology and Biochemistry*. 72. 21–34. Doi: 10.1016/j.plaphy.2013.02.001

Schilmiller, A.L., Stout, J., Weng ,J.K., Humphreys, J., Ruegger, M.O., Chapple, C. (2009). Mutations in the cinnamate 4-hydroxylase gene impact metabolism, growth and development in Arabidopsis. *Plant Journal*. 60(5). 771–782. Doi: 10.1111/j.1365-313X.2009.03996.x

Selvaraj, D., Sherif, S., Pak Dek, M.S., Paliyath, G., El-Sharkawy, I., Subramanian, J. (2016). Identification and characterization of genes involved in the fruit color development of European plum. *Journal of the American Society for Horticultural Science*. 141(5). 467–474. Doi: 10.21273/JASHS03617-16

Sharoni, Y., Linnewiel-hermoni, K., Khanin, M., Salman, H., Veprik, A., Danilenko, M., Levy, J. (2011). Carotenoids and apocarotenoids in cellular signaling related to cancer : A review. *Molecular Nutrition Food Research*. 56 (2). 259-269. Doi: 10.1002/mnfr.201100311

SIAP. 2017. Márgenes de comercialización Mango Ataulfo. Disponible en. https://www.gob.mx/cms/uploads/attachment/file/240992/Mango_ataulfo_Junio_2017.pdf

SIAP. 2020. Avance de siembras y cosechas, resumen nacional por estado. Disponible en: Disponible en: http://infosiap.siap.gob.mx:8080/agricola_siap_gobmx/ResumenDelegacion.do

SNICS. 2020. Catálogo Nacional de Variedades Vegetales. Disponible en: https://www.gob.mx/snics/acciones-y-programas/catalogo-nacional-de-variedades-vegetales-239452.pdf.

Sivankalyani, V., Feygenberg, O., Diskin, S., Wright, B., Alkan, N. (2016). Increased anthocyanin and flavonoids in mango fruit peel are associated with cold and pathogen resistance. *Postharvest Biology and Technology*. 111. 132–139. Doi: 10.1016/j.postharvbio.2015.08.001

Srivastava, S., Somasagara, R.R, Hegde, M., Nishana, M., Tadi, S.K., Srivastava, M., Choudhary, B., Raghavan, S.C. (2016). Quercetin, a natural flavonoid interacts with DNA, arrests cell cycle and causes tumor regression by activating mitochondrial pathway of apoptosis. *Scientific Reports*. 6. 1–13. Doi: 10.1038/srep24049

Stahl, W., Sies, H. (2005). Bioactivity and protective effects of natural carotenoids. *Biochimica et Biophysica Acta Molecular Basis of Disease*. 1740(2): 101–107. Doi: 10.1016/j.bbadis.2004.12.006

Subburaj S, Lee K, Jeon Y, Tu L, Son G, Choi S B, Lim Y P, McGregor C, Lee G J. 2019. Whole genome resequencing of watermelons to identify single nucleotide polymorphisms related to flesh color and lycopene content. *PLoS ONE*. 14(10). 1–22. Doi: 10.1371/journal.pone.0223441

Sudhakar, P., Latha, P., Reddy, P.V. (2016). Phenotyping Crop Plants for Physiological and Biochemical Traits. In: Sudhakar, P., Latha, P. Chapter 15 - Plant pigments. Academic Press, London, UK. pp. 107-115. Doi: 10.1016/b978-0-12-804073-7.00015-6

Sudheeran, P.K., Feygenberg, O., Maurer, D., Alkan, N. (2018). Improved cold tolerance of mango fruit with enhanced anthocyanin and flavonoid contents. *Molecules* 23(7). Doi: 10.3390/molecules23071832

Vogt, T. (2010). Phenylpropanoid biosynthesis. *Molecular Plant* 3(1): 2–20. Doi: 10.1093/mp/ssp106

Choo, W.S. (2018) Betalains: Application in Functional Foods. In: Mérillon JM., Ramawat K. (eds) Bioactive Molecules in Food. Reference Series in Phytochemistry. Springer, Cham. Doi: 10.1007/978-3-319-54528-8_38-1

Wang, Z., Yu, Q., Shen, W., El Mohtar, C.A., Zhao, X., Gmitter, F.G. (2018). Functional study of CHS gene family members in citrus revealed a novel CHS gene affecting the production of flavonoids. *BMC Plant Biology* 18(1): 1–13. Doi: 10.1186/s12870-018-1418-y

Yamaguchi, M. (2012). Role of carotenoid β-cryptoxanthin in bone homeostasis. *Journal of Biomedical Science*. 19(1): 36. Doi: 10.1186/1423-0127-19-36

Yanjie, X., Daokun, X.W.C. (2012). Mutation of Arabidopsis HY1 causes UV-C hypersensitivity by imparing carotenoid and flavonoid biosynthesis and the down-regulation of antioxidant defence. *Journal of Experimental Botany* 63(10): 3869–3884. Doi: 10.1093/jxb/errs301738

Yao, D., Wang, Y., Li, Q., Ouyang, X., Li, Y., Wang, C., Ding, L., Hou, L., Luo, M., Xiao, Y. (2018). Specific Upregulation of a Cotton Phytoene Synthase Gene Produces Golden Cottonseeds with Enhanced Provitamin A. *Scientific Reports* 8(1): 1–8. Doi: 10.1038/s41598-018-19866-1

Yonekura-Sakakibara, K., Tohge, T., Matsuda, F., Nakabayashi, R., Takayama, H., Niida, R., Watanabe-Takahashi, A., Inouem E., Saito, K. (2008). Comprehensive flavonol profiling and transcriptome coexpression analysis leading to decoding gene-metabolite correlations in Arabidopsis. *Plant Cell*. 20(8): 2160–2176. Doi:10.1105/tpc.108.058040

Yuan H, Zhang J, Nageswaran D, Li L. 2015a. Carotenoid metabolism and regulation in horticultural crops. *Horticulture Research* 2:15036. https://doi.org/10.1038/hortres.2015.36

Yuan Y, Qin S, Chen S, Yang Z, Huang L, Shuai L. 2015b. Flavonoids and Antioxidative Enzymes in Temperature-Challenged Roots of *Scutellaria baicalensis* Georgi. *Zeitschrift Für Naturforschung C* 67: 77–85. https://doi.org/10.1515/znc-2012-1-210