

Anthocyanins distribution, transcriptional regulation, epigenetic and post-translational modification in fruits



Liping Sun^a, Jingtian Huo^a, Jieya Liu^a, Jiayi Yu^a, Jialing Zhou^a, Chongde Sun^b, Yue Wang^{b,*}, Feng Leng^{a,*}

^a College of Horticulture and Landscape Architecture, Yangzhou University, Yangzhou 225009, China

^b Laboratory of Fruit Quality Biology/The State Agriculture Ministry Laboratory of Horticultural Plant Growth, Development and Quality Improvement, Zhejiang University, Zijingang Campus, Hangzhou 310058, China

ARTICLE INFO

Keywords:

Fruit
Anthocyanins biosynthesis
Transcriptional regulation
Epigenetic modification
DNA methylation
Post-translational regulation

ABSTRACT

Anthocyanins have indispensable functions in plant resistance, human health, and fruit coloring, which arouse people's favorite. It has been reported that anthocyanins are widely found in fruits, and can be affected by numerous factors. In this review, we systematically summarize anthocyanin functions, classifications, distributions, biosynthesis, decoration, transportation, transcriptional regulation, DNA methylation, and post-translational regulation in fruits.

1. Introduction

Anthocyanins are a type of water-soluble natural pigments that are widely distributed in the tissues of most flowering plants and generally exist in the form of glycosides that give them red, orange, purple, blue, or black colors (Bassolino, Zhang, Schoonbeek, Kiferle, Perata, & Martin, 2013; Xu, Cao, Shi, Chen, Su, & Yang, 2014). With rising incomes and quality of living, people increasingly require higher fruit quality. Anthocyanins can promote fruit coloring to improve fruit quality, resist the damage of ultraviolet rays and the attack of pathogens, and enhance environmental stress resistance (Wang et al., 2010; Qu, Li, Wang, Yu, & Zhu, 2021). Additionally, anthocyanins can aid pollination and seed dispersal (Qu et al., 2021), and be used as a substitute for artificial colorants because of their colors (Ranganath et al., 2018). Studies have also shown that anthocyanins help maintain postharvest quality and extend the shelf life of agricultural products (Qu et al., 2021). For humans, some evidence suggests that anthocyanins are beneficial for human health to protect against diseases such as cancers, coronary heart disease, stroke (Xu et al., 2014), inflammation (Wang et al., 2010), diabetes, cardiovascular disease, neurological disease (Karanjalker, Ravishankar, Shivashankara, & Dinesh, 2018), age-related diseases (Wang et al., 2010) due to their efficacious antioxidant activity and free radical scavenging ability (Cappellini, Marinelli, Toccaceli, Tonelli, &

Petroni, 2021) (Fig. 1). Therefore, we classified and summarized the distribution and content of different anthocyanins in fruits and compared them horizontally, helping people choose anthocyanins-rich fruits more quickly and directly and broadening the channel for natural pigments extraction. Based on understanding anthocyanin biosynthetic pathways and transcriptional regulation can be taken to help plants improve anthocyanin synthesis during growth. We further discuss the findings of epigenetic modifications of anthocyanins in fruits and summarize and prospect them in combination with the biosynthetic pathway of anthocyanins and their transcriptional regulation, which will help to design strategies for obtaining anthocyanin-rich fruits through breeding control and facilitate future bioengineering programs. The data in this review were searched in databases such as the Web of Science using anthocyanins and different fruits as keywords, and papers related to anthocyanins distribution, anabolism, and regulatory modification were mainly selected for review.

2. Classifications and distributions

Anthocyanins are the end-products of the flavonoid pathway, which consist of two aromatic rings connected by three-carbon bridges embedded in oxygen atoms (C6-C3-C6) as their carbon skeleton structure (Tanaka, Sasaki, & Ohmiya, 2008). With the help of mass

* Corresponding authors.

E-mail addresses: julysunlp@163.com (L. Sun), 18252737291@163.com (J. Huo), A2416829519@163.com (J. Liu), yuz_yjy@163.com (J. Yu), zhoujialingjelly@163.com (J. Zhou), adesun2006@zju.edu.cn (C. Sun), fruit@zju.edu.cn (Y. Wang), lengfeng.214@163.com (F. Leng).

spectrometry methods, more anthocyanins have been accurately identified. In fruits, anthocyanins occur as forms of pelargonidin, cyanidin, delphinidin, peonidin, petunidin, and malvidin, which have the same structures on the A and C rings, but with variable numbers of hydroxyl and methoxy groups on their B rings (Liu, Tikunov, Schouten, Marcelis, Visser, & Bovy, 2018). Apart from the different types of anthocyanidins, the structure, quantity, and position of glycosyl or acyl groups can also lead to anthocyanin diversity, which contributes to their diverse colors (Liu et al., 2018) (Fig. 2).

2.1. Pelargonidins

Pelargonidin is one of the primary anthocyanidins, hydroxylated at C4' position of the B ring, and appears orange or red in fruits (Liu et al., 2022b). Different glycosides are generally attached to an oxygen atom at the C3 position of pelargonidin to form pelargonidin-O-glycoside, such as pelargonidin-3-O-glucoside (da Silva, Escribano-Bailón, Alonso, Rivas-Gonzalo, & Santos-Buelga, 2007) and pelargonidin-3-O-rutinoside (Lopes-da-Silva, de Pascual-Teresa, Rivas-Gonzalo, & Santos-Buelga, 2002). Among them, pelargonidin-3-O-glucoside is the common one distributed in fruits, especially rich in strawberries (*Fragaria × ananassa* Duch.), its content can account for about 90 % of the total anthocyanins in the cultivar 'Carisma' (da Silva et al., 2007). Moreover, pelargonidin-3-O-glucoside is also found in red grapes (*Vitis vinifera* L.) (He, He, Pan, & Duan, 2010a), passion fruits (*Passiflora edulis* f. *edulis*) (Shi et al., 2021), and wild berries of *Rubus croceacanthus* and *Rubus sieboldii* (Kubota, Ishikawa, Sugiyama, Fukumoto, Miyagi, & Kumazawa, 2012). While pelargonidin-3-O-rutinoside is frequently found in red berry of *Ruscus aculeatus* L. (Longo & Vasapollo, 2005), tamarillo (*Solanum*

betaceum Cav.) (Vasco, Avila, Ruales, Svanberg, & Kamal-Eldin, 2009), and Andes berry (*Rubus glaucus* Benth.) (Garzon, Riedl, & Schwartz, 2009). In addition, pelargonidins are commonly glycosylated or acylated modifications to accumulate in the form of diglycosides or acetyl glycosides in fruits to increase their stability and water solubility (Tanaka et al., 2008). For example, pelargonidin-3,5-diglucoside in *Syzygium cumini* L. (Nazif, 2007), and pelargonidin-3-*trans-p*-coumaroyl-glucoside in *Ruscus aculeatus* L. (Longo and Vasapollo, 2005). A longitudinal comparison of Fig. 2 shows that pelargonidin has the most straightforward substitution, and its glycosidic substitution structure is also less. The direct reason for this has not yet been reported, but it's worth exploring.

2.2. Cyanidins

Cyanidin is the most common anthocyanidin in nature, which has two hydroxyl groups at C3' and C4' of the B ring (Gu, Wang, Hu, & Hao, 2019). Cyanidins mainly appear red or magenta (Liu et al., 2022b), of which cyanidin-3-O-glucoside is the most widely distributed in fruits. It is especially in berries such as Chinese bayberry (*Myrica rubra* Sieb. and Zucc.) (Zhang et al., 2008) and Andes berry (*Rubus glaucus* Benth.), in which cyanidin-3-O-glucoside can be 82 % and 67 % of total anthocyanin contents respectively (Osorio, Hurtado, Dawid, Hofmann, Heredia-Mir, & Morales, 2012). Cyanidin-3-O-glucoside is also widely distributed in other fruits, like mulberry (*Morus alba* L.) (Chen et al., 2022), black currant (*Ribes nigrum* L.) (Nour, Stampar, Veberic, & Jakopic, 2013), longan (*Dimocarpus longan* Lour.) (Yi et al., 2021), apple (*Malus domestica* Borkh.) (Wojsylo, Oszmianski, & Laskowski, 2008), etc. Excitingly, cyanidin-3-O-glucoside is not only rich in Chinese bayberry,

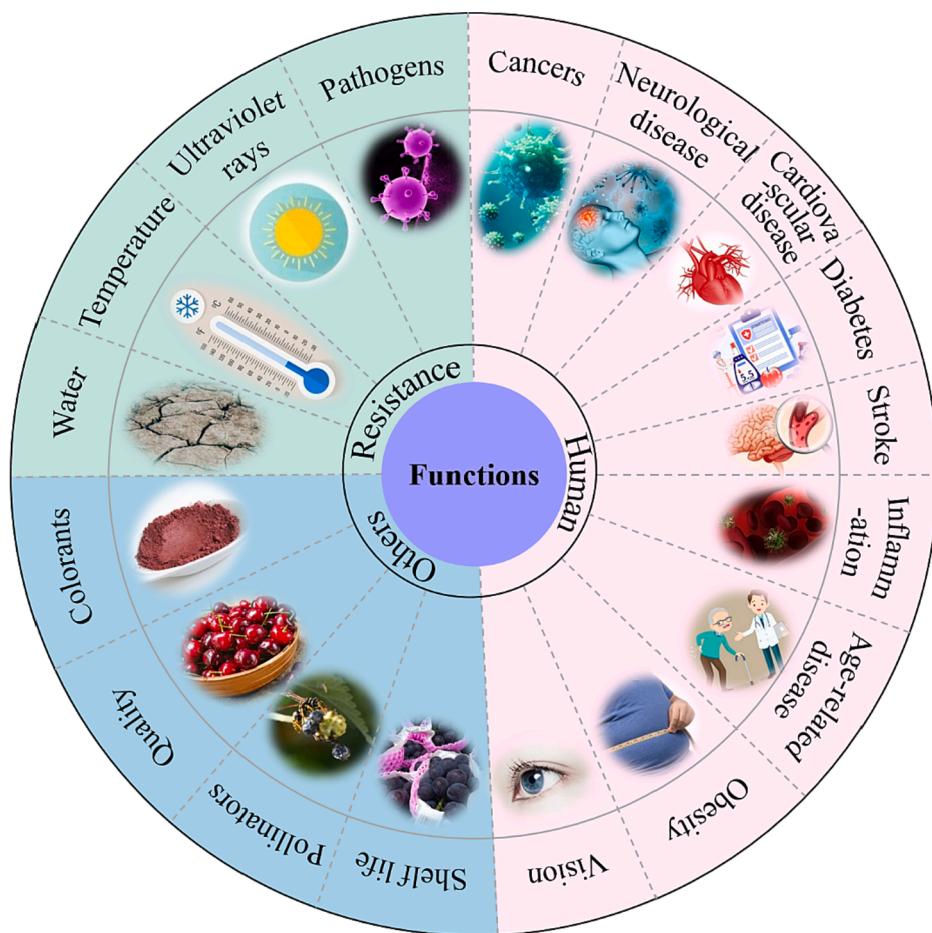


Fig. 1. Anthocyanins functions in fruits.

	Pelargonidin(Pg)	Cyanidin(Cy)	Delphinidin(Dp)	Peonidin(Pn)	Petunidin(Pt)	Malvidin(Mv)
Structure						
Monosaccharide	Pg-3-O-glucoside Pg-3-O-rutinoside	Cy-3-O-glucoside Cy-3-O-galactoside Cyanidin-3-O-rutinoside Cyanidin-3-O-xyloside	Dp-3-O-glucoside Dp-3-O-rutinoside Dp-3-O-galactoside	Pn-3-O-glucoside Pn-3-O-rutinoside Pn-3-O-galactoside	Pt-3-O-glucoside Pt-3-O-rutinoside Pt-3-O-arabinoside	Mv-3-O-glucoside Mv-3-O-galactoside Mv-3-O-arabinoside Mv-3-O-rutinoside
Derivatives	Pg-3,5-diglucoside Pg-3-trans-p-coumaroyl-glucoside	Cy-3-(6"-malonyl)-glucoside Cy-3-(6"-acetyl)-glucoside	Dp-3,5-diglucoside Dp-3-(6"-acetyl)-glucoside Dp-3-(6"-coumaroyl)-glucoside	Pn-3,5-diglucoside Pn-3-(6"-coumaroyl)-glucoside	Pt-3,5-diglucoside Pt-3-(6"-acetyl)-glucoside Pt-3-(6"-coumaroyl)-glucoside	Mv-3-(6"-acetyl)-glucoside Mv-3-(coumaroyl)-5-diglucoside Mv-3-(trans)-coumaroyl-5-diglucoside
Fruit	 Strawberry Passion Andes berry	 Apple Litchi Longan	 Blackberry Tamarillo Pomegranate	 Peach Cheery Apricot	 Blueberry Bilberry Grape	 Cranberry Chagalapoli Chinese wild berry

Fig. 2. Anthocyanins basic skeletal structure, classes, and fruit sources.

but also the only anthocyanin present in it, so Chinese bayberry may be a good source of cyanidin-3-O-glucoside (Chen et al., 2022). Cyanidin-3-O-galactoside is high in apples, the pigment primarily responsible for red coloration in apples (*Malus × domestica* Borkh.) (Dar, Wani, Ahmed, Nazir, Zargar, & Javaid, 2019). Particularly, the content of cyanidin-3-O-galactoside in the cultivar 'Huashuo' is as high as over 5 mg·g⁻¹ at the last color transition stage (Shi et al., 2022), and even accounted for 98 % of the total anthocyanins in the red 'Granny Smith' (Zhang, Wang, Liu, Chen, Yang, & Zhao, 2013). Additionally, cyanidin-3-O-rutinoside is the primary anthocyanins in the litchi pericarp (*Litchi chinensis* Sonn.) (He, Zhou, Zhu, Jiang, & Qu, 2022), and is also abundant in ripe plums (*Prunus domestica* L.) (Usenik, Stampar, & Veberic, 2009), while cyanidin-3-O-xyloside is one of the major anthocyanins in Brazilian 'Restinga' (*Neomitranthes obscura* (DC.) N. Silveira) (Gouvea et al., 2015) and saskatoon (*Amelanchier alnifolia* Nutt.) (Ozga, Saeed, Wismer, & Reinecke, 2007). Cyanidin diglycosides and acetyl glycosides derivatives are less widespread in anthocyanin compared to cyanidin monoglycosides. It has been demonstrated that cyanidin-3-(6"-malonyl)-glucoside is one of the major anthocyanins in red pericarp longan (Yi et al., 2021), as well as in blood orange (*Citrus sinensis*) (Fiore et al., 2005), blackberry and marionberry (Wu & Prior, 2005). Moreover, cyanidin-3-(6"-acetyl)-glucoside is in plum and black plum (Wu et al., 2005).

2.3. Delphinidins

Unlike pelargonidin and cyanidin, delphinidin has three hydroxyl groups at C3', C4', and C5' of the B ring, and contributes to the color violet or blue (Liu et al., 2022b). Delphinidin-3-O-glucoside is the most delphinidin widely distributed in fruits, such as blueberry (*Vaccinium* sp.) (Ma, Meng, Wang, Fan, & Wang, 2022), cherry (*Prunus avium*), and cranberry (*Vaccinium* subg.) (Karaaslan & Yaman, 2016). Delphinidin-3-O-rutinoside is found in tamarillo (Osorio et al., 2012), banana (*Musa* spp. and *Ensete* spp.) (Kitdamrongsont et al., 2008) and black currant (*Ribes nigrum*) (Stany et al., 2019). Delphinidin-3-O-galactoside is present at a relatively widespread in blood-flesh peach (*Prunus persica* (L.) Batsch.) (Tan et al., 2022), chagalapoli (*Ardisia compressa* K.) (Joaquin-Cruz, Duenas, Garcia-Cruz, Salinas-Moreno, Santos-Buelga, & Garcia-Salinas, 2015), and Brazilian 'Restinga' (Gouvea et al., 2015). Among

the delphinidin diglycosides and acetyl glycosides derivatives, the most representative anthocyanins are delphinidin-3,5-diglucoside in pomegranate (*Punica granatum* L.) (Legua, Forner-Giner, Nuncio-Jauregui, & Hernandez, 2016), maqui (*Aristotelia chilensis*) and jambul (*Syzygium cumini*) (Fang, 2015), delphinidin-3-(6"-acetyl)-glucoside in blueberry and concord grape (*Vitis labrusca*) (Li, Wang, Guo, & Wang, 2011), as well as delphinidin-3-(6"-coumaroyl)-glucoside in concord grape and red grape (Li et al., 2011).

2.4. Peonidins

Peonidin is derived from cyanidin by a single O-methylation at the C3' position (Liu et al., 2018), which has a slight reddening effect (Tanaka et al., 2008). Peonidin-3-O-glucoside is the most common peonidin, which is abundantly distributed in blueberries (*Vaccinium ashei*), and their contents differ among different varieties. For example, peonidin-3-O-glucoside is the most common peonidin, which is abundantly distributed in blueberries, especially in 'Crunchie' (highbush cultivar) (Chai et al., 2021). Peonidin-3-O-glucoside is also distributed in many other fruits, such as cornelian cherry (*Cornus mas* L.) (Sengul, Eser, & Ercisli, 2014), grape (*Vitis vinifera* L. cv. Pinot Noir) (Cortell, Halbleib, Gallagher, Righetti, & Kennedy, 2007), and litchi pericarp (He et al., 2022). Peonidin-3-O-rutinoside is mainly distributed in apricot (*Prunus armeniaca* L.) (Bureau, Renard, Reich, Ginies, & Audergon, 2009) and mock strawberry (*Duchesnea indica* Focke.) (Qin, Li, Zhang, Niu, & Ding, 2009). In addition, peonidin-3-O-galactoside is present relatively widespread in American cranberry (*Vaccinium macrocarpon* L.) (Klavins, Kviesis, & Klavins, 2017) and *Myrciaria vexator* (Dastmalchi et al., 2012). Among the diglycosides and acetylglycosides of peonidin in fruits, peonidin-3,5-diglucoside is widely distributed in apples (*Syzygium malaccense*) (Kotepong, Ketsa, & van Doorn, 2011) and grapes (*Vitis vinifera*) (Wang, Race, & Shrikhande, 2003b). While in concord grape and red grape, peonidin-3-(6"-coumaroyl)-glucoside is also discovered (Wu and Prior, 2005).

2.5. Petunidins

Petunidin is derived from delphinidin by a single O-methylation at

the C3' position (Liu et al., 2018). Petunidins are the major sources of dark-colored fruits such as petunidin-3-O-glucoside in grapes (Li et al., 2013), petunidin-3-O-diglucoside in concord grape (Li et al., 2011), and petunidin-3-O-rutinoside in bilberry (*Vaccinium meridionale*) (Fang, 2015). It has been demonstrated that petunidin-3-O-glucoside is the main petunidin derivative, which is one of the main anthocyanins in Chinese wild berries (Li et al., 2011). Unlike the monoglycosides of petunidin, the diglycosides and acylglycosides of petunidin have fewer species and distributions. Small amounts of petunidin 3-(6'-acetyl)-glucoside, petunidin-3,5-diglucoside, and petunidin-3-(6'-coumaroyl)-glucoside are found in concord grape (Wu and Prior, 2005).

2.6. Malvidins

Malvidin is derived from delphinidin by double O-methylation at the C3' and C5' positions (Liu et al., 2018), which is the reddest individual anthocyanidin (He et al., 2010b). Among the monoglycosides of malvidin, the pigment primarily responsible for coloration in grapes is malvidin-3-O-glucoside, which is also the most widely distributed malvidin in other fruits (Fanzone et al., 2015; Wang, Race, & Shrikhande, 2003a). While malvidin-3-O-galactoside has the highest content among the blueberry cultivars (Chai et al., 2021), it also commonly accumulates in cranberry (Wu and Prior, 2005) and chagalapoli of *Ardisia compressa* K. (Joaquin-Cruz et al., 2015). Malvidin-3-O-arabinoside is widely

distributed in many berries, such as blueberries (He et al., 2016), Chinese wild berries (Li et al., 2011), and cranberries (Wu and Prior, 2005). Malvidin-3-O-rutinoside is characterized in fruits of *Liriope platyphylla* (Lee & Choung, 2011), blueberries (*Vaccinium* sp.) (Ma, Meng, Wang, Fan, & Wang, 2022), and grapes (*Vitis vinifera* L.) (Dominguez-Perles, Guedes, Queiroz, Silva, & Barros, 2016). It is worth mentioning that although blueberries contain all the above aglycones except pelargonidin, the content of malvidin is the highest (Chen et al., 2022). In addition, diglycosides and acylglycosides of malvidin are also widely accumulated in various fruits. For instance, malvidin-3-(6'-acetyl)-glucoside is in concord grape, red grape, and blueberry, while malvidin-3-(coumaroyl)-5-diglucoside is in concord grape (Wu and Prior, 2005), kyoho grape, and cabernet sauvignon grape, malvidin-3-(trans)-coumaroyl-5-diglucoside is one of the most abundant anthocyanins in fresh skin of 'kyoho' grape and cabernet sauvignon grape (Li et al., 2013).

The biosynthesis of anthocyanins also varies considerably in fruits. For example, petunidins have a narrower distribution, mainly in berries such as grapes, while cyanidins are more widely distributed in various fruits of the rosaceae family and fruits of the rhododendron and sapotaceae families. Anthocyanins were always identified on the peel of ripe fruits such as cherries, grapes, and a variety of berries, while rarely found in pulp. In addition, we also found that blueberries are one of the richest sources of anthocyanins (Chai et al., 2021). In blueberries, the

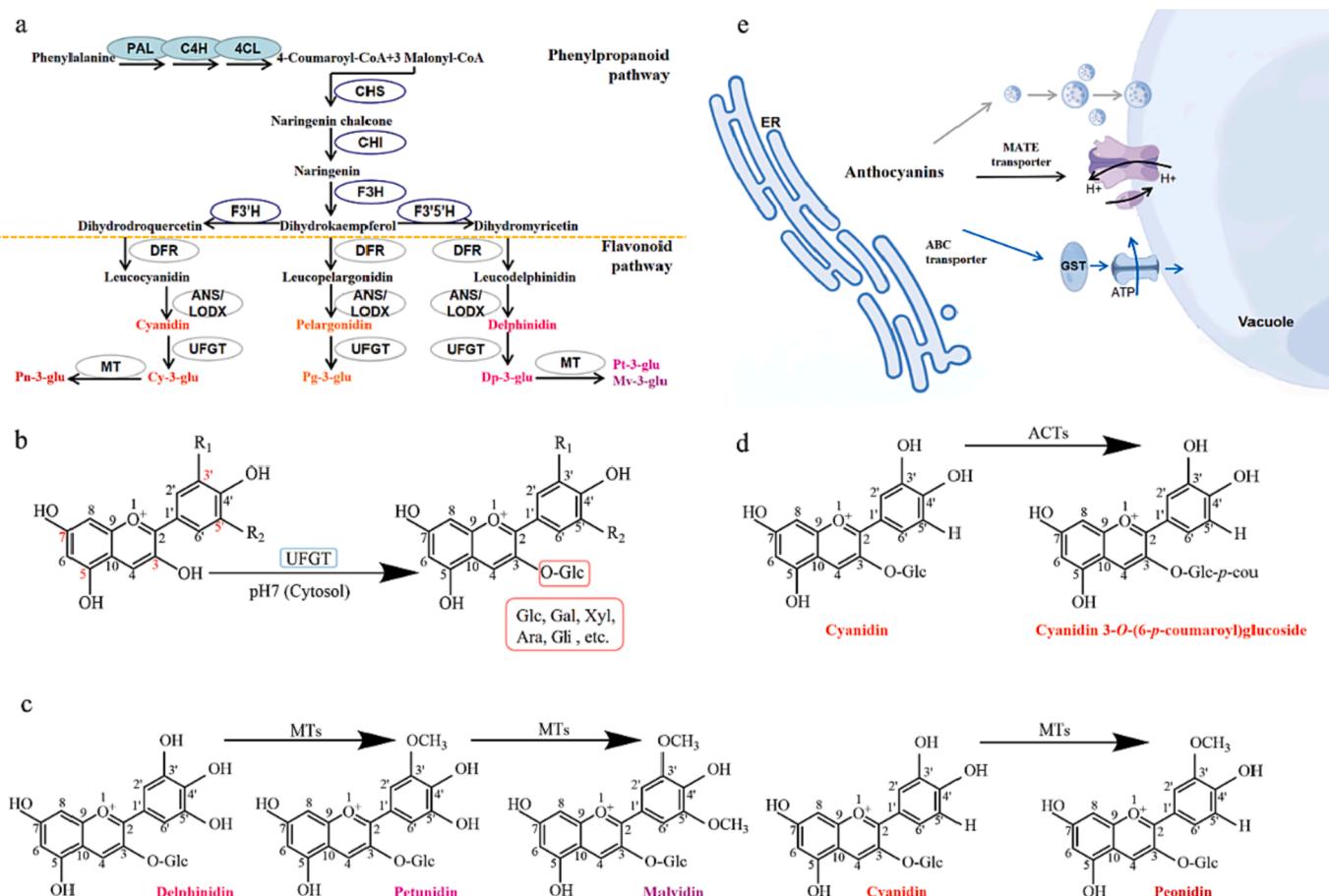


Fig. 3. The mechanistic model of anthocyanin metabolism. (a) Pathway map of anthocyanin biosynthesis. PAL: phenylalanine ammonia-lyase; C4H: cinnamate 4-hydroxylase; 4CL: p-coumaroyl coenzyme A ligase; CHS: chalcone synthase; CHI: chalcone isomerase; F3H: flavanone 3'-hydroxylase; F3'H: flavanone 3'-hydroxylase; F3'5'H: flavanone 3'5'-hydroxylase; DFR: dihydroflavonol 4-reductase; ANS/LDOX: anthocyanidin synthase/Leucoanthocyanidin dioxygenase; UFGT: UDP-glucose: flavonoid 3-O-glucosyltransferase; MT: methyltransferase. (b) Mechanism of glycosylation of anthocyanins. UFGT: UDP-glucose: flavonoid 3-O-glucosyltransferase; Glc: glucoside; Gal: galactoside; Xyl: xyloside; Ara: arabinoside; Gli: glicoside. (c) Methylation mechanism of anthocyanin glycosides. MTs: methyltransferases. (d) Mechanism of acylation of anthocyanin glycosides. ACTs: acyltransferases. (e) Transport mechanism of anthocyanins from endoplasmic reticulum to vacuole. ER: endoplasmic reticulum; MATE: multidrug and toxic compound extrusion; ABC: adenosine triphosphate (ATP)-binding cassette; GST: glutathione S-transferase;

combination of different aglycons and anthocyanins is more diverse, forming more anthocyanin species (Chai et al., 2021; Ma, Meng, Wang, Fan, & Wang, 2022). In addition, the biosynthesis of anthocyanins varies in time. In the pre-harvest ripe fruit, anthocyanins accumulate rapidly at ripening, in non-respiratory climacteric fruit such as grapes and strawberries (da Silva et al., 2007; Li et al., 2013), while in respiratory climacteric fruit such as apples and mangoes, anthocyanins continue to accumulate in the presence of ethylene even after picking (Dar et al., 2019; Ribeiro da Silva et al., 2014).

3. Anthocyanins metabolism

3.1. Biosynthesis of anthocyanins

Based on current knowledge, anthocyanins are the final product of the phenylpropanoid pathway (Fig. 3a), which is catalyzed by phenylalanine ammonia-lyase (PAL), cinnamate 4-hydroxylase (C4H), and *p*-coumaroyl coenzyme A ligase (4CL). Furthermore, one molecule of 4-coumaroyl-CoA combined with three molecules of malonyl-CoA is catalyzed by chalcone synthase (CHS) and chalcone isomerase (CHI) to form naringenin chalcone (Hichri, Barrieu, Bogs, Kappel, Delrot, & Lauvergeat, 2011). Under the catalysis of flavanone 3-hydroxylase (F3H), flavanone 3'-hydroxylase (F3'H), or flavanone 3'5'-hydroxylase (F3'5'H), naringenin converts to different dihydroflavonols, subsequently converts to leucoanthocyanidin by dihydroflavonol 4-reductase (DFR). And anthocyanidin synthase (ANS/LDOX) competes with leucoanthocyanidin reductase (LAR) for the substrate leucoanthocyanidin to form colorless anthocyanins (Jaakola, 2013). Finally, anthocyanidins are glycosylated by glycosyltransferases (GTs) to yield colored anthocyanins. Glycosylation can occur at many check points, the 3-O-position by UDP-glucose: anthocyanidin 3-O-glucosyltransferase (3-GT) is a prerequisite for further modifications, which is one of UDP-glucose: flavonoid 3-O-glucosyltransferase (UFGT) depending on its substrate specificity (Kovinich, Saleem, Arnason, & Miki, 2010). Different types of sugar moieties, such as glucoside, galactoside, glycoside, arabinoside, and xyloside attached to various positions, for instance, hydroxyl groups 3, 5, 7, 3', and 5' position by other corresponding glycosyltransferases to increase the diversity of anthocyanins (Cheng et al., 2014) (Fig. 3b).

3.2. Decoration and transportation

Anthocyanins are further modified by glycosylation, methylation, acylation, and other modifications to increase their stability and water solubility (Cheng et al., 2014; Springob, Nakajima, Yamazaki, & Saito, 2003). Anthocyanins of monoglycosides generate more different monosaccharides under the catalysis of methyltransferases (MTs) as shown in Fig. 3c, cyanidin generates peonidin under the action of MTs while delphinidin generates petunidin and malvidin (Koes, Verweij, & Quattrrochio, 2005). The hydroxyl group of a monosaccharide molecule hemiacetal binds to the hydroxyl group of another monosaccharide molecule to form diglycosides under the action of glycosyltransferases (GTs). Then, diglycosides can be further catalyzed by acyltransferases (ACTs) to form acylated anthocyanins (Fig. 3d). Finally, the synthesized anthocyanins are transported from the endoplasmic reticulum to the vacuole. As shown in Fig. 3e, anthocyanins are transported into the vacuole via vesicles from the endoplasmic reticulum (ER), Golgi apparatus (Golgi), or autophagy. Alternatively, this transport process can be mediated by tonoplast localized transporters by glutathione S-transferase (GST) including the multidrug and toxic compound extrusion (MATE) and the adenosine triphosphate (ATP)-binding cassette (ABC)-transporters (Buhrman, Aravena-Calvo, Zaulich, Hinz, & Laursen, 2022).

4. Transcriptional regulation of anthocyanin metabolism

Normally, anthocyanin metabolism is regulated by a series of

transcription factors, such as MBW protein complex (mainly including MYB, bHLH, and WD40), WRKY, NAC, bZIP, and ERF families, as well as several non-coding RNAs (Fig. 4).

4.1. MYB–bHLH–WD40 (MBW) complex

MYB family is characterized by the highly conserved MYB domain that binds to DNA, which is divided into 1R-MYB, R2R3-MYB, and R3-MYB according to the number of MYB functional domains. R2R3-MYB with two motifs are the most abundant and play crucial roles in regulating the anthocyanins biosynthesis in fruits (Allan, Hellens, & Laing, 2008; Chagne et al., 2013; Jaakola, 2013). The first MYBs isolated from apples were *MdMYB1*, which is involved in promoting anthocyanin biosynthesis in apple peel (Takos, Jaffe, Jacob, Bogs, Robinson, & Walker, 2006). In addition, *MdMYB10*, *MdMYB110a*, *MdMYBA1*, and *MdMYBA* also have positive effects on the transcriptional regulation of anthocyanins in apples (Chagne et al., 2013; Jaakola, 2013). However, *MdMYB28* in apple peel is a balanced transcription factor. In order to prevent anthocyanin excessive accumulation, *MdMYB28* plays a negative regulatory role when its content reaches its peak (Ding et al., 2021). In litchi, it has been suggested that *LcMYB1* activates *LcABF3* (Hu et al., 2019) and *LcGST4* (Hu, Zhao, Lai, Qin, Wang, & Hu, 2016a) to play a critical role in ABA-regulated anthocyanin biosynthesis successively. The patterning and spatial localization of anthocyanins are primarily determined by the activity of R2R3-MYB activators, individual gene family members conferring specific patterns. Polymorphisms of the *VvMYBA* family have been reported to be responsible for variations in anthocyanin content in different grapevine varieties (Kobayashi, Goto-Yamamoto, & Hirochika, 2004). Walker et al. found that both *VvMYBA1* and *VvMYBA2* can switch on the *VvUFGT* promoter and control anthocyanin biosynthesis (2007). And *VvMYBA6.1* and *VvMYBA7* also be verified to activate promoters of UFGT and anthocyanin 3-O-glucoside-6'-O-acyltransferase (3AT), thereby regulating the accumulation of anthocyanins (Matus et al., 2017). Subsequently, more and more MYBs were identified to be involved in the regulation of anthocyanins biosynthesis in other fruits. Such as, in peach, *PpMYB39* plays an important role in anthocyanin biosynthesis by activating *PpDFR* (Khan et al., 2022); in pear, *PbMYB10* and *PbMYB120* can activate and inhibit UFGT promoter activity to regulate anthocyanin biosynthesis, respectively (Bai et al., 2017; Song et al., 2020), and *PbMYB26* activates *PbLAC4-like* leading to anthocyanin degradation (Zhao et al., 2021); in blueberries, *VcMYB1* positively regulates the transcription of *VcDFR*, thereby promoting anthocyanin synthesis (Tang, Chi, Liu, Zhang, & Song, 2021). Conversely, *MaMYB4*, an R2R3-MYB repressor transcription factor, inhibition of anthocyanin accumulation by down-regulation of *MaCHS*, *MaANS*, and *MaDFR* expression in bananas (Deng et al., 2021), mulberry (Li et al., 2020b) and grape (Matus, Aquea, & Arce-Johnson, 2008). Interestingly, *FaMYB1* functions as a transcriptional repressor in anthocyanin biosynthesis in strawberries (Aharoni et al., 2001), but it interacts with *MdERF3* to provide positive feedback for ethylene and anthocyanin biosynthesis in apples (An et al., 2018b).

MBWs commonly combine with bHLHs to form a protein complex that participates in the regulation of anthocyanin biosynthesis. For example, *MdMYB10* to regulate anthocyanin metabolism was dependent on the co-expression of two distinct bHLH apple proteins, *MdbHLH3* and *MdbHLH33* (Espley, Hellens, Putterill, Stevenson, Kutty-Amma, & Allan, 2007), and *MdMYB306-like* protein is required in conjunction with *MdMYB17* and *MdbHLH33*, forms a key regulatory module to fine-tune anthocyanin biosynthesis in apples (Wang et al., 2022c). In currants, *RrMYB10* can interact with *RrbHLH3* to promote the activity of the UFGT promoter and anthocyanin biosynthesis (Starkevic et al., 2020). However, in peaches, *PpMYB10* can not only interact with *PpbHLH3* to regulate anthocyanin accumulation but also interact with *PpbHLH64* to positively regulate anthocyanin biosynthesis after light induction (Rahim, Busatto, & Trainotti, 2014; Tao et al., 2020). In sweet cherry, *PacMYBA* physically interacts with bHLHs to activate promoters of

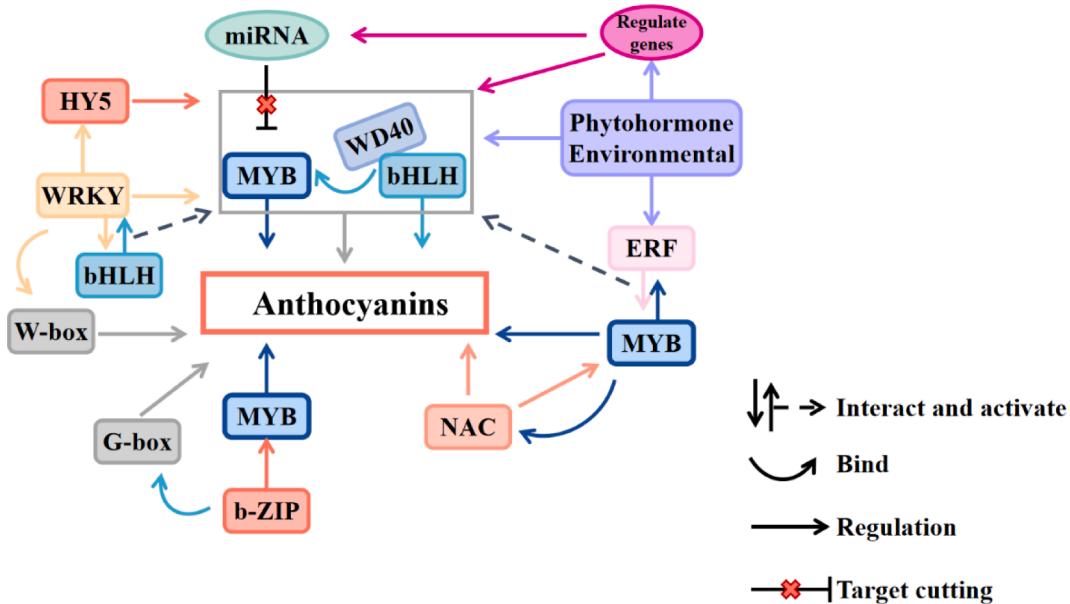


Fig. 4. Transcriptional regulation of anthocyanins in fruits.

PacDFR, *PacANS*, and *PacUFGT* and improve the contents of anthocyanins (Shen et al., 2014).

Additionally, MYBs can also interact with other transcription factors to co-regulate anthocyanin metabolism. For instance, *VmMYBPA1.1* interacts with *VmMYBA1* to regulate the anthocyanin accumulation in bilberries (Lafferty et al., 2022), while *VcMYBPA1.1* could activate *VcMYBA1* and *VcMYBPA2* to promote the contents of anthocyanin and procyanidin respectively in blueberries (Lafferty et al., 2022). In apples, *MdJAZ2* inhibits the recruitment of *MdbHLH3* to the *MdMYB9* and *MdMYB11* promoters, leading to inhibit *MdDFR* expression and anthocyanin accumulation (An et al., 2015); *MdMYB1* stimulates anthocyanin accumulation by binding to the promoter of the *MdWRKY75* (Su et al., 2022); *MdMYB16* and *MdMYB308* promoter activities were inhibited by *MdMYBL1* and *MdHY5*, thus regulating anthocyanin metabolism (Liu et al., 2019b). Furthermore, *PyMYB114* and its partner *PybHLH3* were found to interact with *PyERF3* to coregulate anthocyanin biosynthesis in pears (Yao et al., 2017).

The bHLHs not only play critical roles in the MBW complex but also have independent functions to regulate anthocyanin biosynthesis. For example, *MdbHLH3* interacts directly with and is phosphorylated by a glucose sensor as well as apple hexokinase (*MdHXK1*), to modulate the accumulation of anthocyanin in response to glucose (Hu, Sun, Ma, You, Cheng, & Hao, 2016b). The WD40 protein itself has no catalytic function, but it can reversibly interact with a variety of proteins to provide a platform or link for the assembly of large protein–protein complexes (Xu & Min, 2011). WD40 proteins in the regulatory complex of anthocyanin biosynthesis were first found in Arabidopsis, since which homologs have been characterized from fruit species including apple (Brueggemann, Weisshaar, & Sagasser, 2010), grapevine (Kobayashi et al., 2004), pomegranate (Ben-Simhon et al., 2011), strawberry (Schaart et al., 2013), and Chinese bayberry (Liu, Feng, Zhang, Yin, Xu, & Chen, 2013).

4.2. WRKY

The WRKYS have also been shown to play an important role in anthocyanin transcriptional regulation. In apples, *MdWRKY11* can bind to W-box cis-elements in the promoters of not only the structural gene of *MdUFGT* but also the regulatory gene of *MdMYB10* and *MdMYB11*, as well as can bind to the promoter of *MdHY5* and promote its activity, thereby promoting anthocyanin biosynthesis (Liu et al., 2019c). *MdWRKY72* has two ways to increase anthocyanin biosynthesis that

promotes *MdMYB1* expression indirectly by binding to a W-box element in the *MdHY5* promoter and directly by binding to a W-box element in the *MdMYB1* promoter (Hu et al., 2020). While *MdWRKY40* was identified as a *MdMYB1*-interacting protein, and enhanced *MdMYB1* binding to target genes in response to injury, suggesting that *MdWRKY40* is a key regulator of injury-induced anthocyanin biosynthesis (An, Zhang, You, Bi, Wang, & Hao, 2019). In addition, *PyWRKY26* interacts with *PybHLH3* and could co-target the *PyMYB114* promoter, which resulted in anthocyanin accumulation in red-skinned pear (Li et al., 2020a). Besides, Light-responsive transcription factor *PpWRKY44* promotes the synthesis of anthocyanins in pear (*Pyrus spp*) peel by regulating the expression of *PpMYB10* (Alabd et al., 2022).

4.3. NAC

Regulation of anthocyanin metabolisms by NAC has also been demonstrated in various fruits. For example, overexpression of *MdNAC42* in apple ‘calli’ resulted in the up-regulation of flavonoid pathway genes, including *MdCHS*, *MdCHI*, *MdF3H*, *MdDFR*, *MdANS*, and *MdUFGT*, thereby increasing anthocyanin accumulation (Zhang et al., 2020b). While *MdNAC52* can bind to the promoters of *MdMYB9* and *MdMYB11* to promote the anthocyanins biosynthesis by regulating *MdLAR* in apples (Sun et al., 2019). In blood-fleshed peach, NACs act as a heterodimer with *PpNAC1* to promote anthocyanin accumulation by activating *PpMYB10.1* (Zhou et al., 2015). In litchis, *LcNAC13* interacts with *LcR1MYB1* to antagonistically regulate anthocyanin biosynthesis which accompanies fruit ripening (Jiang et al., 2019).

4.4. ERF

The ERFs affect anthocyanin metabolisms in fruits frequently induced by light and phytohormones. In apples, *MdERF1B* expression was strongly induced by ethylene and jasmonic acid, and combined with *MdMYC2*, *MdJAZ5/10*, and *MdEIL1* to regulate anthocyanin biosynthesis (Wang et al., 2022a). *MdERF78* is involved in anthocyanin accumulation by interacting with *MdMYB1* to enhance the transcriptional ability of *MdMYB1* to *MdDFR*, *MdUFGT*, and *MdGSTF12*, or it activates the expression of *MdF3H* and *MdANS* by binding to its promoter directly (Fang, Zhang, & Wang, 2022). Wang et al. found that during light/dark transitions, *MdERF17* interacts with and is phosphorylated by MAP kinase 4 (*MdMPK4-14G*) to regulate the apple peel coloration (2022b). In

addition, *Pp4ERF24* and *Pp12ERF96* are able to regulate *PpUFGT* expression and anthocyanin biosynthesis via interacting with *PpMYB114* and promoting the interaction between *PpMYB114* and *PpbHLH3* under blue light-induced (Ni et al., 2019).

4.5. b-ZIP

Most reports suggest that bZIP is also involved in the regulation of anthocyanin metabolism in fruits. Such as, *MdbZIP44* enhances *MdMYB1* binding to downstream target gene promoters to increase anthocyanin content in apples (An, Yao, Xu, You, Wang, & Hao, 2018). In blood orange, *CsHY5* is induced by light and directly binds to the G-box within the *CsRuby1* promoter, thus leading to promote anthocyanin accumulation (Huang et al., 2019). Interestingly, in pears, *PybZIPa* binds to tandem G-box motifs in the promoter to activate the expression of *PyUFGT* directly, and the number of G-box motifs affected the process, thus the activation could be amplified by the self-binding of *PybZIPa* to activate its own promoter (Liu et al., 2019a). It has found a negative regulator *VvbZIP36* in grapevine, and knock-out one allele of this gene utilizing the CRISPR/Cas9 technology, thus can significantly promote anthocyanin accumulation (Tu et al., 2022).

4.6. Non-coding RNAs

Recent studies have found that various non-coding RNAs also play pivotal roles in anthocyanin metabolism by targeting mRNAs. For instance, *VvmiR858* targets *VvMYB114* to affect anthocyanin accumulation in grapes (Tirumalai, Swetha, Nair, Pandit, & Shivaprasad, 2019). In kiwifruits, *AcmiR828* and *AamiR858* target *AcMYB110* and *AaMYBC1* respectively, to decrease anthocyanin contents (Li et al., 2020d; Wang et al., 2022e). However, in apples, *mdm-miR828* was found to inhibit anthocyanin production by targeting *MdMYB1* (Zhang et al., 2020a). It was also found that *MdmR7125* mediated the expression of *MdMYB16/MYB1* and affected anthocyanin metabolism (Hu et al., 2021), as well as *MdmR172* inhibits flavonoid biosynthesis by inhibiting *MdMYB10* expression (Ding et al., 2022). A recent study validates a feedback regulatory loop of the *PyPIF5-PymiR156a-PySPL9-PyMYB114/MYB10* module associated with anthocyanin accumulation in red pear during bagging-treated (Liu et al., 2021). Moreover, the *miR156-SPLs* module also coordinates the accumulation of anthocyanins in litchi (Liu, Lai, Hu, Qin, Hu, & Zhao, 2017a) and blueberry (Li et al., 2020c). Additionally, long noncoding RNA *MdLNC499* bridges *MdWRKY1* and *MdERF109* function to regulate light-induced anthocyanin accumulation in apples (Ma et al., 2021). Moreover, *MdLNC610* as a positive regulator to promote *MdACO1* expression and ethylene biosynthesis to participate in the regulation of high-light-induced anthocyanin production (Yu et al., 2022). In mulberries, *mul-miR477* acts as a positive regulator participating in anthocyanin accumulation through the regulatory network of *mul-miR477-Mul-ABCB19AS-Mul-ABCB19* (Dong, Liu, Wang, Dong, Gai, & Ji, 2021).

5. Epigenetic and post-translational modification

Epigenetics (such as DNA methylation, and histone modification) causes heritable changes in gene expression then eventually leads to phenotype changes without changing the genomic DNA sequences (Chachar et al., 2022). Protein post-translational modifications (such as ubiquitination, and phosphorylation) modify existing functional groups or introduce new ones to extend the chemical decoration and properties of the acids (Millar, Heazlewood, Giglione, Holdsworth, Bachmair, & Schulze, 2019). In recent years, epigenetic and protein post-translational modifications also have been shown to play critical roles in the regulation of anthocyanin metabolism.

5.1. DNA methylation

DNA methylation refers to adding a methyl group provided by S-adenosine methionine to the fifth carbon of cytosine (Li, Wang, Zhang, Zhang, & You, 2022). DNA methylation begins with De novo methylation, which is guided by non-coding RNA and is maintained by DNA methyltransferase (MET1, CMT3, CMT2, DRM2) after DNA replication. However, DNA demethylation happens because of the initiation of DNA demethylases or the lack of DNA methyltransferase activity during DNA replication (Kumar & Mohapatra, 2021). In the regulation of anthocyanin metabolism, the methylation of the transcription factors promoter region will inhibit their binding to the structural genes, thereby regulating anthocyanin biosynthesis. For example, DNA methylation of the *MYB1*, *MYB10*, *MYBA1*, and *bHLH74* promoter region, inhibits anthocyanin biosynthesis and results in some fruit varieties a light color (El-Sharkawy, Liang, & Xu, 2015; Jiang et al., 2020; Li, Ning, Mao, Guo, Zhou, & Chen, 2019; Wang et al., 2013; Xia et al., 2021). Meanwhile, DNA methylation inhibitors can block DNA methyltransferase thus promoting transcription factors expressions. Such as DNA methylation inhibitors 5-azacytidine and 5-Aza-2'-deoxycytidine prevent methylation of *PpbHLH3* and *MdMYB1*, thereby affecting anthocyanin metabolism (Ma et al., 2018; Zhu et al., 2020). Moreover, paper bagging reduces DNA methylation in the promoter of the *MdMYB1*, leading to anthocyanin accumulation in different varieties of apples (Bai et al., 2016; Ma et al., 2018). Different from the apple bagging experiment, Liu et al. (2022a) found that after red pear bagging the methylation level of the anthocyanin structural gene *PcUFGT* decreases due to the increase of DNA demethylase level, leading to the accumulation of anthocyanins (Fig. 5a).

5.2. Histone modifications

Histone modifications occur on specific amino acid residues of the histone N-terminal tails and include acetylation, methylation, ubiquitination, and phosphorylation. It has been shown to regulate DNA replication, gene transcription, and chromatin conformation (Chachar et al., 2022; Liu, Wang, Liu, & Xu, 2022c). Histone methylation mainly transfers methyl groups to the lysine residue of histones H3 or H4 by the catalysis of histone methyl transferases (HMTs) (Chachar et al., 2022; Liu et al., 2022c). While histone acetylation is catalyzed by histone acetyltransferase (HAT) and can neutralize the positive charge of the lysine residues to open the chromatin configuration, inhibiting the binding of DNA and histone and resulting in transcriptional activation. Whereas histone deacetylation catalyzed by histone deacetylase (HDA) promotes chromatin condensation and then represses the transcription (Liao, Yang, & Hsieh, 2022). So far, studies on anthocyanin regulation by histone methylation and acetylation have mainly focused on Arabidopsis (Cai et al., 2019; Liao et al., 2022; Nguyen, Jeong, Kang, Yoo, Hong, & Lee, 2015; Wang, Wang, Song, & Zhang, 2016). In fruits, paper bagging treatment activates *MdMYB1* transcription by increasing H3 acetylation, tri-methylation (H3K4me3) and inhibiting DNA methylation of *MdMYB1* to promote anthocyanin accumulation in the 'Mutsu' (Bai et al., 2016). Moreover, also found that *McHDA6*, a histone deacetylase, inhibited *McMYB10* promoter DNA methylation and promoted anthocyanin biosynthesis in the Malus crabapple 'Royalty' (Peng et al., 2020) (Fig. 5b).

5.3. Protein ubiquitination modification

Ubiquitination is a process that ubiquitin binds to the lysine residues of targeted protein and then degrades the protein by the 26S proteasome. It is worth noting that ubiquitin E3 ligase is the key component in the 26S proteasome (Wang, Wang, Chen, Qin, & Tian, 2022d). Generally, protein ubiquitination inhibits anthocyanin accumulation by targeting and degrades MYBs. For instance, ubiquitin E3 ligase MIEL1 and COP1 can ubiquitinate transcription factors (such as *MYB1*,

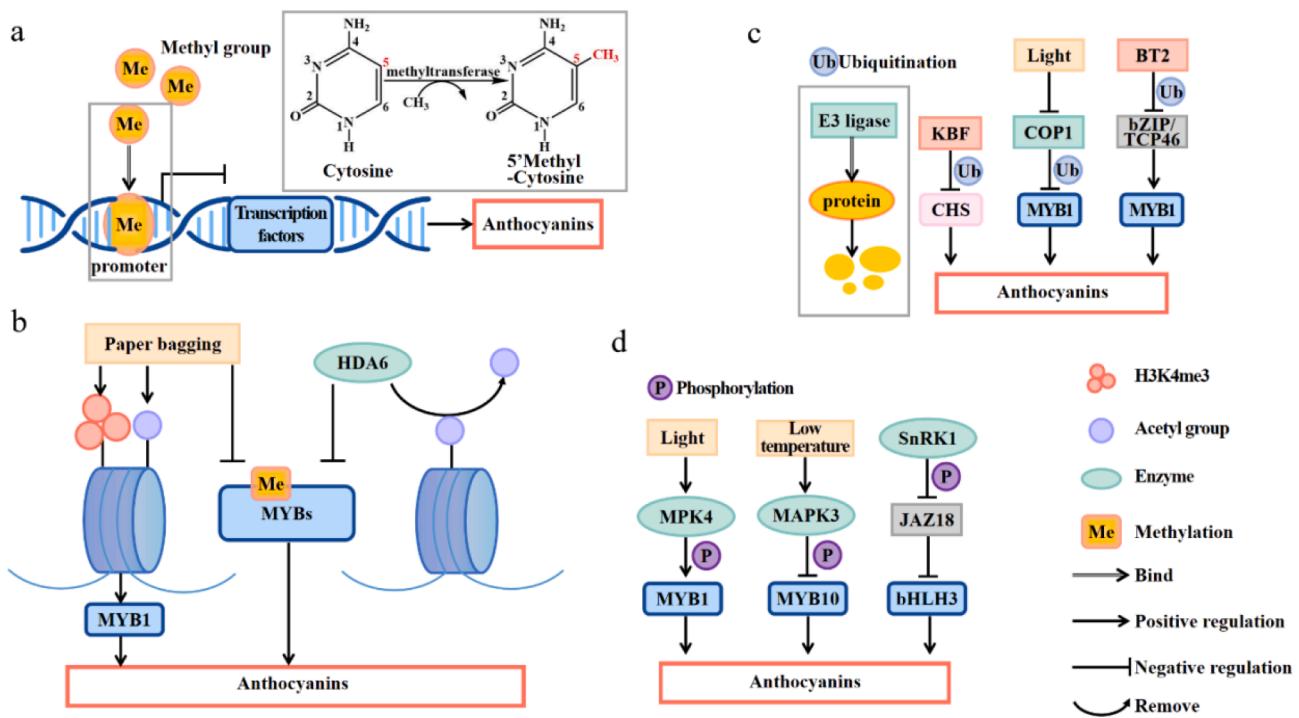


Fig. 5. Epigenetic and post-translational modification. (a) DNA methylation (addition of a methyl group at the fifth carbon of cytosine) occurs in the DNA sequence of transcription factors promoter region. DNA methylation can repress the transcription factors. (b) Regulation model of histone methylation and acetylation. (c) Regulation model of protein ubiquitination. Protein KBF and BT2 possess ubiquitination activity and have function of degradation. The grey box represents the mode of ubiquitination. (d) Regulation model of protein phosphorylation.

MYB308L, or *MYBA*), resulting in anthocyanin accumulation decrease in apples and sweet cherries (An et al., 2017; An et al., 2020; Li et al., 2012; Liang et al., 2020). As a bridge between CUL3 E3 ligase and target proteins, *MdB2T2* has ubiquitination activity to degrades *MdbZIP44* and *MdTCP46*, thus inhibiting *MdMYB1* expression and anthocyanin accumulation in 'Red Delicious' (Wang et al., 2022d). Moreover, *MdB2T2* can directly ubiquitinate *MdMYB9* through 26S proteasome to inhibit anthocyanin accumulation in apples (An et al., 2018a).

Small ubiquitin-related modifier (SUMO) can induce sumoylation which is similar to ubiquitination. Sumoylation hinders the combination of ubiquitin and target proteins to improve the stability of target proteins rather than mediate protein degradation (Zhou et al., 2017). In apples, the small ubiquitin-like modifier E3 ligase *MdSIZ1* sumoylate *MdMYB1*, which also inhibits the binding of ubiquitin and *MdMYB1* and increases *MdMYB1* stability, thereby promoting the anthocyanin biosynthesis (Zhou et al., 2017) (Fig. 5c).

5.4. Protein phosphorylation modification

Protein phosphorylation is a covalent binding of the phosphate group to a hydroxyl group of hydroxyl amino acids by the catalysis of kinases and can change the structure stability, substrate specificity, or protein binding ability of the target proteins (Ajadi et al., 2020). The regulation of protein phosphorylation depends on the kinases. On the one hand, kinase can phosphorylate transcription factors to stabilize them and promote anthocyanin biosynthesis. For example, hexokinase *MdHXK1* phosphorylates *MdBHLH3* at its Ser361 site and stabilizes *MdBHLH3*, promoting anthocyanin biosynthesis in apples (Wang et al., 2022d). Mitogen-activated protein kinases *AtMPK4* activated by light phosphorylates *MdMYB1* to increase their stability, thereby promoting anthocyanin biosynthesis (Li et al., 2016; Wang et al., 2022d). Furthermore, *MdHY5* was phosphorylated by kinases *MdMPK6* and leading to enhance binding of *MdHY5* to its target genes involved in anthocyanin biosynthesis in apples (Xing et al., 2022). On the other

hand, phosphorylation kinase can also negatively regulate anthocyanins. Mitogen-activated protein kinase *FvMAPK3* phosphorylates *FvMYB10* to repress *FvCHI*, or phosphorylates *FvCHS* to promote its proteasome-mediated degradation, thus inhibiting anthocyanin biosynthesis in strawberries under low temperatures (Wang et al., 2022). SNF1-related kinase 1 *MdSnRK1* phosphorylates *MdJAZ18* and degrades it by the 26S proteasome, while *MdJAZ18* inhibits *MdBHLH3*, therefore *MdSnRK1* releases *MdBHLH3* and promotes anthocyanin accumulation in apple (Liu et al., 2017b) (Fig. 5d).

6. Conclusion and prospect

Anthocyanin is one of the most active research areas due to a variety of functions, such as visual attractiveness, nutritional values, medicinal uses, and industrial materials of colored fruits. Anthocyanins are widely distributed and varied in nature, but the main categories and contents of various fruits are different. Extensive research in the past decades have shown that the basic metabolic biosynthetic pathways are conserved in most fruits, and this conservation determines a finite number of basic chemical skeletons, which are then modified by a series of specific enzyme-catalyzed reactions to produce a large number of different secondary metabolites. Their biosynthesis starts with phenylalanine and is catalyzed by a series of enzymes. Different types of anthocyanins are obtained by glycosylation of anthocyanidins by UFGTs, which is a key link in the formation of anthocyanin diversity, and the synthesized anthocyanins are transported to the vacuole for accumulation finally. Therefore, we have summarised the distribution patterns of anthocyanins in terms of class, time, and space by combining their structure, glycoside derivatives, and distribution in fruits with the metabolic pathways of anthocyanins. We generally analyzed and summarized transcriptional regulation models related to mRNAs in gene families such as MYB, bHLH, WD40, WRKY, NAC, bZIP, and ERF during this process. As well as anthocyanins also were affected by epigenetic and protein post-translational modifications. Further research will help to

better understand the diversity of anthocyanins in fruits, and provide more valuable targets for future genetic manipulation, breeding and development and utilization.

With the advent of modern technologies, various regulatory mechanisms involving anthocyanins have been found. At present, studies on the regulation of anthocyanins, especially non-coding RNAs, epigenetic and post-translational modifications are mainly focused on several model plants, showing a trend of rapid increase, and gradually on other plants. Of course, additional anthocyanins regulatory factors and mechanisms in fruits need to be explored, which will become new research lines of horticultural plants in the future. Furthering our understanding of anthocyanins regulatory factors will facilitate accurate regulation of traits by gene editing techniques, thus improving fruit coloring. Synthetic biology has developed rapidly in recent years and has become an important way to solve the problems of source, scale, and sustainable supply of anthocyanins. There are many kinds of anthocyanins, and their structures are complex and diverse. Although anthocyanins have a common precursor synthesis pathway, their stability is not good. Therefore, it is imperative to explore how to extract stable anthocyanins. With the support of modern synthetic biology, the heterologous biosynthesis of anthocyanins has shown great application potential. At the same time, with the large-scale development of metabolomics and genome analysis technologies in horticultural plants and the advent of the post-genome era, more anthocyanin metabolic pathways and post-transcriptional regulation will be analyzed more comprehensively, which will greatly promote anthocyanin The synthesis and extraction of glycosides are developing towards scale and industrialization.

CRediT authorship contribution statement

Liping Sun: Investigation, Formal analysis, Methodology, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Jingtian Huo:** Formal analysis, Methodology, Writing – review & editing. **Jieya Liu:** Methodology, Writing – review & editing. **Jiayi Yu:** Formal analysis, Writing – review & editing. **Jialing Zhou:** Writing – review & editing. **Chongde Sun:** Methodology, Project administration, Writing – review & editing. **Yue Wang:** Project administration, Writing – review & editing. **Feng Leng:** Conceptualization, Funding acquisition, Formal analysis, Methodology, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements:

This work was supported by the Natural Science Foundation of Jiangsu Province (BK20190899); and the Jiangsu Modern Agricultural Industry Single Technology R & D Fund (CX (20) 3173).

References

- Aharoni, A., De Vos, C. H. R., Wein, M., Sun, Z. K., Greco, R., Kroon, A., et al. (2001). The strawberry *FaMYB1* transcription factor suppresses anthocyanin and flavonol accumulation in transgenic tobacco. *Plant Journal*, 28(3), 319–332. <https://doi.org/10.1046/j.1365-313X.2001.01154.x>
- Ajadi, A. A., Cisse, A., Ahmad, S., Yifeng, W., Yazhou, S., Shufan, L., et al. (2020). Protein phosphorylation and phosphoproteome: An overview of rice. *Rice Science*, 27(3), 184–200. <https://doi.org/10.1016/j.rsci.2020.04.003>
- Alabd, A., Ahmad, M., Zhang, X., Gao, Y., Peng, L., Zhang, L., et al. (2022). Light-responsive transcription factor *PpWRKY44* induces anthocyanin accumulation by regulating *PpMYB10* expression in pear. *Horticulture Research*. <https://doi.org/10.1093/hr/uhac199>
- Allan, A. C., Hellens, R. P., & Laing, W. A. (2008). MYB transcription factors that colour our fruit. *Trends in Plant Science*, 13(3), 99–102. <https://doi.org/10.1016/j.tplants.2007.11.012>
- An, J. P., An, X. H., Yao, J. F., Wang, X. N., You, C. X., Wang, X. F., et al. (2018). BTB protein *MdBT2* inhibits anthocyanin and proanthocyanidin biosynthesis by triggering *MdMYB9* degradation in apple. *Tree Physiology*, 38(10), 1578–1587. <https://doi.org/10.1093/treephys/tpy063>
- An, J. P., Wang, X. F., Li, Y. Y., Song, L. Q., Zhao, L. L., You, C. X., et al. (2018). *EIN3-LIKE1, MYB1*, and ETHYLENE RESPONSE FACTOR3 act in a regulatory loop that synergistically modulates ethylene biosynthesis and anthocyanin accumulation. *Plant Physiology*, 178(2), 808–823. <https://doi.org/10.1104/pp.18.00068>
- An, J. P., Wang, X. F., Zhang, X. W., Xu, H. F., Bi, S. Q., You, C. X., et al. (2020). An apple MYB transcription factor regulates cold tolerance and anthocyanin accumulation and undergoes *MIEL1*-mediated degradation. *Plant Biotechnology Journal*, 18(2), 337–353. <https://doi.org/10.1111/pbi.13201>
- An, J. P., Yao, J. F., Xu, R. R., You, C. X., Wang, X. F., & Hao, Y. J. (2018). Apple bZIP transcription factor *MdBZIP44* regulates abscisic acid-promoted anthocyanin accumulation. *Plant Cell and Environment*, 41(11), 2678–2692. <https://doi.org/10.1111/pce.13393>
- An, J. P., Zhang, X. W., You, C. X., Bi, S. Q., Wang, X. F., & Hao, Y. J. (2019). *MdWRKY40* promotes wounding-induced anthocyanin biosynthesis in association with *MdMYB1* and undergoes *MdBT2*-mediated degradation. *New Phytologist*, 224(1), 380–395. <https://doi.org/10.1111/nph.16008>
- An, X. H., Tian, Y., Chen, K. Q., Liu, X. J., Liu, D. D., Xie, X. B., et al. (2015). *MdMYB9* and *MdMYB11* are involved in the regulation of the JA-induced biosynthesis of anthocyanin and proanthocyanidin in apples. *Plant and Cell Physiology*, 56(4), 650–662. <https://doi.org/10.1093/pcp/pcu205>
- Bai, S., Sun, Y., Qian, M., et al. (2017). Transcriptome analysis of bagging-treated red Chinese sand pear peels reveals light-responsive pathway functions in anthocyanin accumulation. *Scientific Reports*, 7(1), 63. <https://doi.org/10.1038/s41598-017-00069-z>
- Bai, S., Tuan, P. A., Saito, T., Honda, C., Hatsuyama, Y., Ito, A., et al. (2016). Epigenetic regulation of *MdMYB1* is associated with paper bagging-induced red pigmentation of apples. *Planta*, 244(3), 573–586. <https://doi.org/10.1007/s00425-016-2524-4>
- Bassolino, L., Zhang, Y., Schoonbeek, H. J., Kiferle, C., Perata, P., & Martin, C. (2013). Accumulation of anthocyanin in tomato skin extends shelf life. *New Phytologist*, 200(3), 650–655. <https://doi.org/10.1111/nph.12524>
- Ben-Simhon, Z., Judeinstein, S., Nadler-Hassar, T., Trainin, T., Bar-Ya'akov, I., Borochov-Neori, H., et al. (2011). A pomegranate (*Punica granatum* L.) WD40-repeat gene is a functional homologue of *Arabidopsis TTG1* and is involved in the regulation of anthocyanin biosynthesis during pomegranate fruit development. *Planta*, 234(5), 865–881. <https://doi.org/10.1007/s00425-011-1438-4>
- Brueggemann, J., Weissaar, B., & Sagasser, M. (2010). A WD40-repeat gene from *Malus x domestica* is a functional homologue of *Arabidopsis thaliana* Transparent testa glabra1. *Plant Cell Reports*, 29(3), 285–294. <https://doi.org/10.1007/s00299-010-0821-0>
- Buhrman, K., Aravena-Calvo, J., Zaulich, C. R., Hinz, K., & Laursen, T. (2022). Anthocyanin vacuolar inclusions: From biosynthesis to storage and possible applications. *Frontiers in Chemistry*, 10. <https://doi.org/10.3389/fchem.2022.913324>
- Bureau, S., Renard, C. M. G. C., Reich, M., Ginies, C., & Audergon, J. M. (2009). Change in anthocyanin concentrations in red apricot fruits during ripening. *LWT-Food Science and Technology*, 42(1), 372–377. <https://doi.org/10.1016/j.lwt.2008.03.010>
- Cai, H., Zhang, M., Chai, M., He, Q., Huang, X., Zhao, L., et al. (2019). Epigenetic regulation of anthocyanin biosynthesis by an antagonistic interaction between H2A.Z and H3K4me3. *New Phytologist*, 221(1), 295–308. <https://doi.org/10.1111/nph.15306>
- Cappellini, F., Marinelli, A., Toccaceli, M., Tonelli, C., & Petroni, K. (2021). Anthocyanins: From mechanisms of regulation in plants to health benefits in foods. *Frontiers in Plant Science*, 12, Article 748049. <https://doi.org/10.3389/fpls.2021.748049>
- Chachar, S., Chachar, M., Riaz, A., Shaikh, A. A., Li, X., Li, X., et al. (2022). Epigenetic modification for horticultural plant improvement comes of age. *Scientia Horticulturae*, 292, Article 110633. <https://doi.org/10.1016/j.scienta.2021.110633>
- Chagne, D., Kui, L. W., Esplay, R. V., Volz, R. K., How, N. M., Rouse, S., et al. (2013). An ancient duplication of apple MYB transcription factors is responsible for novel red fruit-flesh phenotypes. *Plant Physiology*, 161(1), 225–239. <https://doi.org/10.1104/pp.112.206771>
- Chai, Z., Herrera-Balandrano, D. D., Yu, H., Beta, T., Zeng, Q. L., Zhang, X. X., et al. (2021). A comparative analysis on the anthocyanin composition of 74 blueberry cultivars from China. *Journal of Food Composition and Analysis*, 102, Article 104051. <https://doi.org/10.1016/j.jfca.2021.104051>
- Chen, J., Shu, Y., Chen, Y., Ge, Z., Zhang, C., Cao, J., et al. (2022). Evaluation of antioxidant capacity and gut microbiota modulatory effects of different kinds of berries. *Antioxidants*, 11(5). <https://doi.org/10.3390/antiox11051020>
- Cheng, J., Wei, G., Zhou, H., Gu, C., Vimolmangkang, S., Liao, L., et al. (2014). Unraveling the mechanism underlying the glycosylation and methylation of anthocyanins in peach. *Plant Physiology*, 166(2), 1044–1058. <https://doi.org/10.1104/pp.114.246876>
- Cortell, J. M., Halbleib, M., Gallagher, A. V., Righetti, T. L., & Kennedy, J. A. (2007). Influence of vine vigor on grape (*Vitis vinifera* L. cv. Pinot Noir) anthocyanins. 1.

- Anthocyanin concentration and composition in fruit. *Journal of Agricultural and Food Chemistry*, 55(16), 6575–6584. doi: 10.1021/jf070195v.
- da Silva, F. L., Escribano-Bailón, M. T., Alonso, J. J. P., Rivas-Gonzalo, J. C., & Santos-Buelga, C. (2007). Anthocyanin pigments in strawberry. *Lwt-Food Science and Technology*, 40(2), 374–382. <https://doi.org/10.1016/j.lwt.2005.09.018>
- Dar, J. A., Wani, A. A., Ahmed, M., Nazir, R., Zargar, S. M., & Javaid, K. (2019). Peel colour in apple (*Malus x domestica* Borkh.): An economic quality parameter in fruit market. *Scientia Horticulturae*, 244, 50–60. <https://doi.org/10.1016/j.scientia.2018.09.029>
- Dastmalchi, K., Flores, G., Wu, S. B., Ma, C. H., Dabo, A. J., Whalen, K., et al. (2012). Edible Myrciariae vexator fruits: Bioactive phenolics for potential COPD therapy. *Bioorganic & Medicinal Chemistry*, 20(14), 4549–4555. <https://doi.org/10.1016/j.bmc.2012.05.013>
- Deng, G. M., Zhang, S., Yang, Q. S., Gao, H. J., Sheng, O., Bi, F. C., et al. (2021). *MaMYB4*, an R2R3-MYB Repressor Transcription Factor, Negatively Regulates the Biosynthesis of Anthocyanin in Banana. *Frontiers in Plant Science*, 11. <https://doi.org/10.3389/fpls.2020.600704>
- Ding, T. Y., Tomes, S., Gleave, A. P., Zhang, H. T., Dare, A. P., Plunkett, B., et al. (2022). *microRNA172* targets *APETALA2* to regulate flavonoid biosynthesis in apple (*Malus domestica*). *Horticulture Research*, 9. <https://doi.org/10.1093/hr/uhab007>
- Ding, T. Y., Zhang, R. P., Zhang, H. T., Zhou, Z., Liu, C. H., Wu, M. M., et al. (2021). Identification of gene co-expression networks and key genes regulating flavonoid accumulation in apple (*Malus x domestica*) fruit skin. *Plant Science*, 304, Article 110747. <https://doi.org/10.1016/j.plantsci.2020.110747>
- Dominguez-Perles, R., Guedes, A., Queiroz, M., Silva, A. M., & Barros, A. I. R. N. A. (2016). Oxidative stress prevention and anti-apoptosis activity of grape (*Vitis vinifera* L.) stems in human keratinocytes. *Food Research International*, 87, 92–102. <https://doi.org/10.1016/j.foodres.2016.06.030>
- Dong, X., Liu, C., Wang, Y., Dong, Q., Gai, Y., & Ji, X. (2021). MicroRNA Profiling During Mulberry (*Morus alba* L.) Fruit Development and Regulatory Pathway of *miR477* for Anthocyanin Accumulation. *Frontiers in Plant Science*, 12, Article 687364. <https://doi.org/10.3389/fpls.2021.687364>
- El-Sharkawy, I., Liang, D., & Xu, K. (2015). Transcriptome analysis of an apple (*Malus x domestica*) yellow fruit somatic mutation identifies a gene network module highly associated with anthocyanin and epigenetic regulation. *Journal of Experimental Botany*, 66(22), 7359–7376. <https://doi.org/10.1093/jxb/erv433>
- Esplay, R. V., Hellens, R. P., Putterill, J., Stevenson, D. E., Kutty-Amma, S., & Allan, A. C. (2007). Red colouration in apple fruit is due to the activity of the MYB transcription factor, *MdMYB10*. *Plant Journal*, 49(3), 414–427. <https://doi.org/10.1111/j.1365-313X.2006.02964.x>
- Fang, J. (2015). Classification of fruits based on anthocyanin types and relevance to their health effects. *Nutrition*, 31(11–12), 1301–1306. <https://doi.org/10.1016/j.nut.2015.04.015>
- Fang, X., Zhang, L. Z., & Wang, L. J. (2022). The transcription factor *MdERF78* is involved in ALA-induced anthocyanin accumulation in apples. *Frontiers in Plant Science*, 13. <https://doi.org/10.3389/fpls.2022.915197>
- Fanzone, M., Gonzalez-Manzano, S., Perez-Alonso, J., Escribano-Bailón, M. T., Jofre, V., Assof, M., et al. (2015). Evaluation of dihydroquercetin-3-O-glucoside from Malbec grapes as copigment of malvidin-3-O-glucoside. *Food Chemistry*, 175, 166–173. <https://doi.org/10.1016/j.foodchem.2014.11.123>
- Fiore, A., La Fauci, L., Cervellati, R., Guerra, M. C., Speroni, E., Costa, S., et al. (2005). Antioxidant activity of pasteurized and sterilized commercial red orange juices. *Molecular Nutrition & Food Research*, 49(12), 1129–1135. <https://doi.org/10.1002/mnfr.200500139>
- Garzon, G. A., Riedl, K. M., & Schwartz, S. J. (2009). Determination of anthocyanins, total phenolic content, and antioxidant activity in Andes berry (*Rubus glaucus* Benth.). *Journal of Food Science*, 74(3), C227–C232. <https://doi.org/10.1111/j.1750-3841.2009.01092.x>
- Gouveia, A. C. M. S., Melo, A., Santiago, M. C. P. A., Peixoto, F. M., Freitas, V., Godoy, R. L. O., et al. (2015). Identification and quantification of anthocyanins in fruits from *Neomitranthes obscura* (DC.) N. Silveira an endemic specie from Brazil by comparison of chromatographic methodologies. *Food Chemistry*, 185, 277–283. <https://doi.org/10.1016/j.foodchem.2015.02.086>
- Gu, K.-D., Wang, C.-K., Hu, D.-G., & Hao, Y.-J. (2019). How do anthocyanins paint our horticultural products? *Scientia Horticulturae*, 249, 257–262. <https://doi.org/10.1016/j.scienta.2019.01.034>
- He, B., Zhang, L. L., Yue, X. Y., Liang, J., Jiang, J., Gao, X. L., et al. (2016). Optimization of Ultrasound-Assisted Extraction of phenolic compounds and anthocyanins from blueberry (*Vaccinium ashei*) wine pomace. *Food chemistry*, 204, 70–76. <https://doi.org/10.1016/j.foodchem.2016.02.094>
- He, F., Mu, L., Yan, G. L., Liang, N. N., Pan, Q. H., Wang, J., et al. (2010). Biosynthesis of anthocyanins and their regulation in colored grapes. *Molecules*, 15(12), 9057–9091. <https://doi.org/10.3390/molecules15129057>
- He, M. Y., Zhou, Y. J., Zhu, H., Jiang, Y. M., & Qu, H. X. (2022). Metabolome, transcriptome and physiological analyses provide insight into the color transition of litchi pericarp. *Postharvest Biology and Technology*, 192. <https://doi.org/10.1016/j.postharvbio.2022.112031>
- Hichri, I., Barriau, 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>
- Hu, B., Lai, B., Wang, D., Li, J. Q., Chen, L. H., Qin, Y. Q., et al. (2019). Three *LcABFs* are Involved in the Regulation of Chlorophyll Degradation and Anthocyanin Biosynthesis During Fruit Ripening in *Litchi chinensis*. *Plant and Cell Physiology*, 60(2), 448–461. <https://doi.org/10.1093/pcp/pcy219>
- Hu, B., Zhao, J. T., Lai, B. A., Qin, Y. H., Wang, H. C., & Hu, G. B. (2016). *LcGST4* is an anthocyanin-related glutathione S-transferase gene in *Litchi chinensis* Sonn. *Plant Cell Reports*, 35(4), 831–843. <https://doi.org/10.1007/s00299-015-1924-4>
- Hu, J. F., Fang, H. C., Wang, J., Yue, X. X., Su, M. Y., Mao, Z. L., et al. (2020). Ultraviolet B-induced *MdWRKY72* expression promotes anthocyanin synthesis in apple. *Plant Science*, 292. <https://doi.org/10.1016/j.plantsci.2019.110377>
- Hu, Y. J., Cheng, H., Zhang, Y., Zhang, J., Niu, S. Q., Wang, X. S., et al. (2021). The *MdMYB16/MdMYB1-miR7125-MdCCR* module regulates the homeostasis between anthocyanin and lignin biosynthesis during light induction in apple. *New Phytologist*, 231(3), 1105–1122. <https://doi.org/10.1111/nph.17431>
- Huang, D., Yuan, Y., Tang, Z. Z., Huang, Y., Kang, C. Y., Deng, X. X., et al. (2019). Retrotransposon promoter of *Ruby1* controls both light- and cold-induced accumulation of anthocyanins in blood orange. *Plant Cell and Environment*, 42(11), 3092–3104. <https://doi.org/10.1111/pce.13609>
- Jaakola, L. (2013). New insights into the regulation of anthocyanin biosynthesis in fruits. *Trends in Plant Science*, 18(9), 477–483. <https://doi.org/10.1016/j.tplants.2013.06.003>
- Jiang, G. X., Li, Z. W., Song, Y. B., Zhu, H., Lin, S., Huang, R. M., et al. (2019). *LcNAC13* physically interacts with *LcRIMYB1* to coregulate anthocyanin biosynthesis-related genes during litchi fruit ripening. *Biomolecules*, 9(4). <https://doi.org/10.3390/biom9040135>
- Jiang, S., Wang, N., Chen, M., Zhang, R., Sun, Q., Xu, H., et al. (2020). Methylation of *MdMYB1* locus mediated by RdDM pathway regulates anthocyanin biosynthesis in apple. *Plant Biotechnology Journal*, 18(8), 1736–1748. <https://doi.org/10.1111/pbi.13337>
- Joaquin-Cruz, E., Duenas, M., Garcia-Cruz, L., Salinas-Moreno, Y., Santos-Buelga, C., & Garcia-Salinas, C. (2015). Anthocyanin and phenolic characterization, chemical composition and antioxidant activity of chagalapoli (*Ardisia compressa* K.) fruit: A tropical source of natural pigments. *Food Research International*, 70, 151–157. <https://doi.org/10.1016/j.foodres.2015.01.033>
- Karaaslan, N. M., & Yaman, M. (2016). Determination of anthocyanins in cherry and cranberry by high-performance liquid chromatography-electrospray ionization-mass spectrometry. *European Food Research and Technology*, 242(1), 127–135. <https://doi.org/10.1007/s00217-015-2524-9>
- Karanjalkar, G. R., Ravishankar, K. V., Shivashankara, K. S., & Dinesh, M. R. (2018). Influence of Bagging on Color, Anthocyanin and Anthocyanin Biosynthetic Genes in Peel of Red Colored Mango Cv. ‘Lily’. *Erwerbs-obstbau*, 60(4), 281–287. <https://doi.org/10.1007/s10341-018-0371-0>
- Khan, I. A., Rahman, M. U., Sakhi, S., Nawaz, G., Khan, A. A., Ahmad, T., et al. (2022). *PpMYB39* activates *PpDFR* to modulate anthocyanin biosynthesis during peach fruit maturation. *Horticulture*, 8(4). <https://doi.org/10.3390/horticulturae8040332>
- Kitdamrongsonk, K., Pothavorn, P., Swangpol, S., Wongniam, S., Atawongs, K., Svasti, J., et al. (2008). Anthocyanin composition of wild bananas in Thailand. *Journal of Agricultural and Food Chemistry*, 56(22), 10853–10857. <https://doi.org/10.1021/jf8018529>
- Klavins, L., Kviesis, J., & Klavins, M. (2017). Comparison of methods of extraction of phenolic compounds from American cranberry (*Vaccinium macrocarpon* L.) press residues. *Agronomy Research*, 15(Sp. Iss. 2), 1316–1329.
- Kobayashi, S., Goto-Yamamoto, N., & Hirochika, H. (2004). Retrotransposon-induced mutations in grape skin color. *Science*, 304(5673), 982–982. doi: 10.1126/science.1095011.
- Koes, R., Verweij, W., & Quattroccchio, F. (2005). Flavonoids: A colorful model for the regulation and evolution of biochemical pathways. *Trends in Plant Science*, 10(5), 236–242. <https://doi.org/10.1016/j.tplants.2005.03.002>
- Kotepong, P., Ketsa, S., & van Doorn, W. G. (2011). A white mutant of Malay apple fruit (*Syzygium malaccense*) lacks transcript expression and activity for the last enzyme of anthocyanin synthesis, and the normal expression of a MYB transcription factor. *Functional Plant Biology*, 38(1), 75–86. <https://doi.org/10.1071/fpb10164>
- Kovinich, N., Saleem, A., Arnason, J. T., & Miki, B. (2010). Functional characterization of a UDP-glucose: Flavonoid 3-O-glucosyltransferase from the seed coat of black soybean (*Glycine max* (L.) Merr.). *Phytochemistry*, 71(11–12), 1253–1263. <https://doi.org/10.1016/j.phytochem.2010.05.009>
- Kubota, M., Ishikawa, C., Sugiyama, Y., Fukumoto, S., Miyagi, T., & Kumazawa, S. (2012). Anthocyanins from the fruits of *Rubus croceacanthus* and *Rubus sieboldii*, wild berry plants from Okinawa, Japan. *Journal of Food Composition and Analysis*, 28(2), 179–182. <https://doi.org/10.1016/j.jfca.2012.09.002>
- Kumar, S., & Mohapatra, T. (2021). Dynamics of DNA methylation and its functions in plant growth and development. *Frontiers in Plant Science*, 12, Article 596236. <https://doi.org/10.3389/fpls.2021.596236>
- Lafferty, D. J., Esplay, R. V., Deng, C. H., Gunther, C. S., Plunkett, B., Turner, J. L., et al. (2022). Hierarchical regulation of *MYBPA1* by anthocyanin- and proanthocyanidin-related MYB proteins is conserved in *Vaccinium* species. *Journal of Experimental Botany*, 73(5), 1344–1356. <https://doi.org/10.1093/jxb/erab460>
- Lee, J. H., & Choung, M. G. (2011). Identification and characterisation of anthocyanins in the antioxidant activity-containing fraction of *Liriope platyphylla* fruits. *Food Chemistry*, 127(4), 1686–1693. <https://doi.org/10.1016/j.foodchem.2011.02.037>
- Legua, P., Forner-Giner, M. A., Nuncio-Jauregui, N., & Hernandez, F. (2016). Polyphenolic compounds, anthocyanins and antioxidant activity of nineteen pomegranate fruits: A rich source of bioactive compounds. *Journal of Functional Foods*, 23, 628–636. <https://doi.org/10.1016/j.jff.2016.01.043>
- Li, C., Wu, J., Hu, K. D., Wei, S. W., Sun, H. Y., Hu, L. Y., et al. (2020). *PyWRKY26* and *PybHLH3* cotargeted the *PyMYB114* promoter to regulate anthocyanin biosynthesis and transport in red-skinned pears. *Horticulture Research*, 7(1). <https://doi.org/10.1038/s41438-020-0254-z>
- Li, H., Yang, Z., Zeng, Q. W., Wang, S. B., Luo, Y. W., Huang, Y., et al. (2020). Abnormal expression of *bHLH3* disrupts a flavonoid homeostasis network, causing differences

- in pigment composition among mulberry fruits. *Horticulture Research*, 7(1). <https://doi.org/10.1038/s41438-020-0302-8>
- Li, R., Wang, P., Guo, Q., & Wang, Z. Y. (2011). Anthocyanin composition and content of the *Vaccinium uliginosum* berry. *Food chemistry*, 125(1), 116–120. <https://doi.org/10.1016/j.foodchem.2010.08.046>
- Li, S., Wang, W., Gao, J., Yin, K., Wang, R., Wang, C., et al. (2016). *MYB75* phosphorylation by *MPK4* is required for light-induced anthocyanin accumulation in Arabidopsis. *The Plant Cell*, 28(11), 2866–2883. <https://doi.org/10.1105/tpc.16.00130>
- Li, W. F., Ning, G. X., Mao, J., Guo, Z. G., Zhou, Q., & Chen, B. H. (2019). Whole-genome DNA methylation patterns and complex associations with gene expression associated with anthocyanin biosynthesis in apple fruit skin. *Planta*, 250(6), 1833–1847. <https://doi.org/10.1007/s00425-019-03266-4>
- Li, X., Wang, X., Zhang, Y., Zhang, A., & You, C. X. (2022). Regulation of fleshy fruit ripening: From transcription factors to epigenetic modifications. *Horticulture Research*. <https://doi.org/10.1093/hr/uhab013>
- Li, X. Y., Hou, Y. M., Xie, X., Li, H. X., Li, X. D., Zhu, Y., et al. (2020). A blueberry *MIR156a-SPL12* module coordinates the accumulation of chlorophylls and anthocyanins during fruit ripening. *Journal of Experimental Botany*, 71(19), 5976–5989. <https://doi.org/10.1093/jxb/eraa327>
- Li, Y., Ma, R., Xu, Z., Wang, J., Chen, T., Chen, F., et al. (2013). Identification and quantification of anthocyanins in Kyoho grape juice-making pomace, Cabernet Sauvignon grape winemaking pomace and their fresh skin. *Journal of the Science of Food and Agriculture*, 93(6), 1404–1411. <https://doi.org/10.1002/jsfa.5907>
- Li, Y. K., Cui, W., Qi, X. J., Lin, M. M., Qiao, C. K., Zhong, Y. P., et al. (2020). *MicroRNA858* negatively regulates anthocyanin biosynthesis by repressing *AaMYBC1* expression in kiwifruit (*Actinidia arguta*). *Plant Science*, 296, Article 110476. <https://doi.org/10.1016/j.plantsci.2020.110476>
- Li, Y. Y., Mao, K., Zhao, C., Zhao, X. Y., Zhang, H. L., Shu, H. R., et al. (2012). *MdCOP1* ubiquitin E3 ligases interact with *MdMYB1* to regulate light-induced anthocyanin biosynthesis and red fruit coloration in apple. *Plant Physiology*, 160(2), 1011–1022. <https://doi.org/10.1104/pp.112.199703>
- Liang, D., Zhu, T., Deng, Q., Lin, L., Tang, Y., Wang, J., et al. (2020). *PacCOP1* negatively regulates anthocyanin biosynthesis in sweet cherry (*Prunus avium* L.). *Journal of Photochemistry and Photobiology B-biology*, 203, Article 111779. <https://doi.org/10.1016/j.jphotobiol.2020.111779>
- Liao, H. S., Yang, C. C., & Hsieh, M. H. (2022). Nitrogen deficiency- and sucrose-induced anthocyanin biosynthesis is modulated by HISTONE DEACETYLASE15 in Arabidopsis. *Journal of Experimental Botany*, 73(11), 3726–3742. <https://doi.org/10.1093/jxb/erac067>
- Liú, H., Shu, Q., Lin-Wang, K., Allan, A. C., Espley, R. V., Su, J., et al. (2021). The *PyPIF5-PyMIR156a-PySPL9-PyMYB14/MYB10* module regulates light-induced anthocyanin biosynthesis in red pear. *Molecular Horticulture*, 1(1). <https://doi.org/10.1186/s43897-021-00018-5>
- Liú, H., Su, J., Zhu, Y., Yao, G., Allan, A. C., Ampomah-Dwamena, C., et al. (2019). The involvement of *PyZIPa* in light-induced anthocyanin accumulation via the activation of *PyUFGT* through binding to tandem G-boxes in its promoter. *Horticulture Research*, 6(1), 134. <https://doi.org/10.1038/s41438-019-0217-4>
- Liú, H. N., Shu, Q., Lin-Wang, K., Espley, R. V., Allan, A. C., Pei, M. S., et al. (2022). DNA methylation reprogramming provides insights into light-induced anthocyanin biosynthesis in red pear. *Plant Science*, 326, Article 111499. <https://doi.org/10.1016/j.plantsci.2022.111499>
- Liú, R., Lai, B., Hu, B., Qin, Y. H., Hu, G. B., & Zhao, J. T. (2017). Identification of MicroRNAs and their target genes related to the accumulation of anthocyanins in *Litchi chinensis* by high-throughput sequencing and degradome analysis. *Frontiers in Plant Science*, 7. <https://doi.org/10.3389/fpls.2016.02059>
- Liú, W. J., Wang, Y. C., Sun, J. L., Jiang, H. Y., Xu, H. F., Wang, N., et al. (2019). *MdMYBDL1* employed by *MdHY5* increases anthocyanin accumulation via repression of *MdMYB16/308* in apple. *Plant Science*, 283, 32–40. <https://doi.org/10.1016/j.plantsci.2019.01.016>
- Liú, W. J., Wang, Y. C., Yu, L., Jiang, H. Y., Guo, Z. W., Xu, H. F., et al. (2019). *MdWRKY11* participates in anthocyanin accumulation in red-fleshed apples by affecting MYB transcription factors and the photoreponse factor *MdHY5*. *Journal of Agricultural and Food Chemistry*, 67(32), 8783–8793. <https://doi.org/10.1021/acs.jafc.9b02920>
- Liú, X. F., Feng, C., Zhang, M. M., Yin, X. R., Xu, C. J., & Chen, K. S. (2013). The *MrWD40-1* gene of Chinese Bayberry (*Myrica rubra*) interacts with MYB and bHLH to enhance anthocyanin accumulation. *Plant Molecular Biology Reporter*, 31(6), 1474–1484. <https://doi.org/10.1007/s11105-013-0621-0>
- Liú, X. J., An, X. H., Liu, X., Hu, D. G., Wang, X. F., You, C. X., et al. (2017). *MdSnRK1.1* interacts with *MdJAZ18* to regulate sucrose-induced anthocyanin and proanthocyanidin accumulation in apple. *Journal of Experimental Botany*, 68(11), 2977–2990. <https://doi.org/10.1093/jxb/erx150>
- Liú, Y., Qian, J., Li, J., Xing, M., Grierson, D., Sun, C., et al. (2022). Hydroxylation decoration patterns of flavonoids in horticultural crops: Chemistry, bioactivity and biosynthesis. *Horticulture Research*. <https://doi.org/10.1093/hr/uhab068>
- Liú, 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>
- Liú, Y., Wang, J., Liu, B., & Xu, Z. Y. (2022). Dynamic regulation of DNA methylation and histone modifications in response to abiotic stresses in plants. *Journal of Integrative Plant Biology*. <https://doi.org/10.1111/jipb.13368>
- Longo, L., & Vasapollo, G. (2005). Determination of anthocyanins in *Ruscus aculeatus* L. berries. *Journal of Agricultural and Food Chemistry*, 53(2), 475–479. <https://doi.org/10.1021/jf0487250>
- Lopes-da-Silva, F., de Pascual-Teresa, S., Rivas-Gonzalo, J., & Santos-Buelga, C. (2002). Identification of anthocyanin pigments in strawberry (cv Camarosa) by LC using DAD and ESI-MS detection. *European Food Research and Technology*, 214(3), 248–253. <https://doi.org/10.1007/s00217-001-0434-5>
- Ma, C., Jing, C., Chang, B., Yan, J., Liang, B., Liu, L., et al. (2018). The effect of promoter methylation on *MdMYB1* expression determines the level of anthocyanin accumulation in skins of two non-red apple cultivars. *BMC Plant Biology*, 18(1), 108. <https://doi.org/10.1186/s12870-018-1320-7>
- Ma, C., Meng, L., Wang, R., Fan, Y., & Wang, R. (2022). Dynamics of anthocyanin profiles of the fruits of four blueberry (*Vaccinium* sp.) cultivars during different growth stages. *International Journal of Food Properties*, 25(1), 1302–1316. <https://doi.org/10.1080/10942912.2022.2075380>
- Ma, H. Y., Yang, T., Li, Y., Zhang, J., Wu, T., Song, T. T., et al. (2021). The long noncoding RNA *MdLNC499* bridges *MdWRKY1* and *MdERF109* function to regulate early-stage light-induced anthocyanin accumulation in apple fruit. *The Plant Cell*, 33(10), 3309–3330. <https://doi.org/10.1093/plcell/koab188>
- Matus, J. T., Aquea, F., & Arce-Johnson, P. (2008). Analysis of the grape MYB R2R3 subfamily reveals expanded wine quality-related clades and conserved gene structure organization across *Vitis* and *Arabidopsis* genomes. *Bmc Plant Biology*, 8(1), 83. <https://doi.org/10.1186/1471-2229-8-83>
- Matus, J. T., Cavallini, E., Loyola, R., Holl, J., Finezzo, L., Dal Santo, S., et al. (2017). A group of grapevine *MYBA* transcription factors located in chromosome 14 control anthocyanin synthesis in vegetative organs with different specificities compared with the berry color locus. *Plant Journal*, 91(2), 220–236. <https://doi.org/10.1111/tpj.13558>
- Millar, A. H., Heazlewood, J. L., Giglione, C., Holdsworth, M. J., Bachmair, A., & Schulze, W. X. (2019). The Scope, Functions, and Dynamics of Posttranslational Protein Modifications. *Annual Review of Plant Biology*, 70(1), 119–151. <https://doi.org/10.1146/annurev-aplant-050718-100211>
- Nazif, N. M. (2007). The anthocyanin components and cytotoxic activity of *Syzygium cumini* (L.) fruits growing in Egypt. *Natural Product Sciences*, 13(2), 135–139.
- Nguyen, N. H., Jeong, C. Y., Kang, G. H., Yoo, S. D., Hong, S. W., & Lee, H. (2015). *MYBD* employed by *HY5* increases anthocyanin accumulation via repression of *MYBL2* in *Arabidopsis*. *Plant Journal*, 84(6), 1192–1205. <https://doi.org/10.1111/tpj.13077>
- Ni, J. B., Bai, S. L., Zhao, Y., Qian, M. J., Tao, R. Y., Yin, L., et al. (2019). Ethylene response factors *Pp4ERF24* and *Pp12ERF96* regulate blue light-induced anthocyanin biosynthesis in 'Red Zaosu' pear fruits by interacting with *MYB114*. *Plant Molecular Biology*, 99(1–2), 67–78. <https://doi.org/10.1007/s11103-018-0802-1>
- Nour, V., Stampar, F., Veberic, R., & Jakopic, J. (2013). Anthocyanins profile, total phenolics and antioxidant activity of black currant ethanolic extracts as influenced by genotype and ethanol concentration. *Food chemistry*, 141(2), 961–966. <https://doi.org/10.1016/j.foodchem.2013.03.105>
- Osorio, C., Hurtado, N., Dawid, C., Hofmann, T., Heredia-Mir, F. J., & Morales, A. L. (2012). Chemical characterisation of anthocyanins in tamarillo (*Solanum betaceum* Cav.) and Andes berry (*Rubus glaucus* Benth.) fruits. *Food chemistry*, 132(4), 1915–1921. <https://doi.org/10.1016/j.foodchem.2011.12.026>
- Ozga, J. A., Saeed, A., Wismer, W., & Reinecke, D. M. (2007). Characterization of cyanidin- and quercetin-derived flavonoids and other phenolics in mature saskatoon fruits (*Amelanchier alnifolia* Nutt.). *Journal of Agricultural and Food Chemistry*, 55(25), 10414–10424. <https://doi.org/10.1021/jf072949b>
- Peng, Z., Tian, J., Luo, R., Kang, Y., Lu, Y., Hu, Y., et al. (2020). *MiR399d* and epigenetic modification comodulate anthocyanin accumulation in *Malus* leaves suffering from phosphorus deficiency. *Plant, Cell & Environment*, 43(5), 1148–1159. <https://doi.org/10.1111/pce.13697>
- Qin, C. G., Li, Y., Zhang, R. J., Niu, W. N., & Ding, Y. (2009). Separation and elucidation of anthocyanins in the fruit of mockstrawberry (*Duchesnea indica* Focke). *Natural Product Research*, 23(17), 1589–1598. <https://doi.org/10.1080/14786410802496903>
- Qu, S. S., Li, M. M., Wang, G., Yu, W. T., & Zhu, S. J. (2021). Transcriptomic, proteomic and LC-MS analyses reveal anthocyanin biosynthesis during litchi pericarp browning. *Scientia Horticulturae*, 289. <https://doi.org/10.1016/j.scienta.2021.110443>
- Rahim, M. A., Busatto, N., & Trainotti, L. (2014). Regulation of anthocyanin biosynthesis in peach fruits. *Planta*, 240(5), 913–929. <https://doi.org/10.1007/s00425-014-2078-2>
- Ranganath, K. G., Shivashankara, K. S., Roy, T. K., Dinesh, M. R., Geetha, G. A., Pavithra, K. C., et al. (2018). Profiling of anthocyanins and carotenoids in fruit peel of different colored mango cultivars. *Journal of Food Science and Technology*, 55(11), 4566–4577. <https://doi.org/10.1007/s13197-018-3392-7>
- Ribeiro da Silva, L. M., Teixeira do Figueiredo, E. A., Pontes Silva Ricardo, N. M., Pinto Vieira, I. G., de Figueiredo, R. W., Brasil, I. M., & Gomes, C. L. (2014). Quantification of bioactive compounds in pulps and by-products of tropical fruits from Brazil. *Food Chemistry*, 143, 398–404. doi: 10.1016/j.foodchem.2013.08.001
- Schaart, J. G., Dubois, C., De La Fuente, I. R., van Houwelingen, A. M. M. L., de Vos, R. C. H., Jonker, H. H., et al. (2013). Identification and characterization of MYB-bHLH-WD40 regulatory complexes controlling proanthocyanidin biosynthesis in strawberry (*Fragaria x ananassa*) fruits. *New Phytologist*, 197(2), 454–467. <https://doi.org/10.1111/nph.12017>
- Sengul, M., Eser, Z., & Ercisli, S. (2014). Chemical properties and antioxidant capacity of cornelian cherry genotypes grown in Coruh Valley of Turkey. *Acta Scientiarum Polonorum-Hortorum Cultus*, 13(4), 73–82.
- Shen, X. J., Zhao, K., Liu, L. L., Zhang, K. C., Yuan, H. Z., Liao, X., et al. (2014). A role for *PatMYBA* in ABA-regulated anthocyanin biosynthesis in red-colored sweet cherry cv. Hong Deng (*Prunus avium* L.). *Plant and Cell Physiology*, 55(5), 862–880. <https://doi.org/10.1093/pcp/pcu013>

- Shi, C., Liu, L., Wei, Z., Liu, J., Li, M., Yan, Z., et al. (2022). Anthocyanin accumulation and molecular analysis of correlated genes by metabolomics and transcriptomics in sister line apple cultivars. *Life*, 12(8), 1246. <https://doi.org/10.3390/life12081246>
- Shi, M., Ali, M. M., He, Y. Y., Ma, S. F., Rizwan, H. M., Yang, Q., . . . Chen, F. X. (2021). Flavonoids Accumulation in Fruit Peel and Expression Profiling of Related Genes in Purple (*Passiflora edulis f. edulis*) and Yellow (*Passiflora edulis f. flavicarpa*) Passion Fruits. *Plants*, 10(11). doi: 10.3390/plants10112240.
- Song, L. Y., Wang, X. L., Han, W., Qu, Y. Y., Wang, Z. G., Zhai, R., et al. (2020). *PbMYB120* Negatively Regulates Anthocyanin Accumulation in Pear. *International Journal of Molecular Sciences*, 21(4). <https://doi.org/10.3390/ijms21041528>
- Springob, K., Nakajima, J., Yamazaki, M., & Saito, K. (2003). Recent advances in the biosynthesis and accumulation of anthocyanins. *Natural Product Reports*, 20(3), 288–303. <https://doi.org/10.1039/b109542k>
- Stanys, V., Bendokas, V., Rugienius, R., Sasnauskas, A., Frercks, B., Mazeikiene, I., et al. (2019). Management of anthocyanin amount and composition in genus Ribes using interspecific hybridisation. *Scientia Horticulturae*, 247, 123–129. <https://doi.org/10.1016/j.scientia.2018.12.014>
- Starkevic, P., Razanskiene, A., Starkevic, U., Kazanaviciute, V., Denkovskiene, E., Bendokas, V., et al. (2020). Isolation and analysis of anthocyanin pathway genes from ribes genus reveals MYB gene with potent anthocyanin-inducing capabilities. *Plants*, 9(9). <https://doi.org/10.3390/plants9091078>
- Su, M. Y., Zuo, W. F., Wang, Y. C., Liu, W. J., Zhang, Z. Y., Wang, N., et al. (2022). The WRKY transcription factor *MdWRKY75* regulates anthocyanins accumulation in apples (*Malus domestica*). *Functional Plant Biology*, 49(9), 799–809. <https://doi.org/10.1071/Fp21146>
- Sun, Q. G., Jiang, S. H., Zhang, T. L., Xu, H. F., Fang, H. C., Zhang, J., et al. (2019). Apple NAC transcription factor *MdNAC52* regulates biosynthesis of anthocyanin and proanthocyanidin through *MdMYB9* and *MdMYB11*. *Plant Science*, 289. <https://doi.org/10.1016/j.plantsci.2019.110286>
- Takos, A. M., Jaffe, F. W., Jacob, S. R., Bogs, J., Robinson, S. P., & Walker, A. R. (2006). Light-induced expression of a MYB gene regulates anthocyanin biosynthesis in red apples. *Plant Physiology*, 142(3), 1216–1232. <https://doi.org/10.1104/pp.106.088104>
- Tan, S., Miao, Y., Zhou, C., Luo, Y., Lin, Z., Xie, R., et al. (2022). Effects of hot air drying on drying kinetics and anthocyanin degradation of blood-flesh peach. *Foods*, 11(11). <https://doi.org/10.3390/foods11111596>
- Tanaka, Y., Sasaki, N., & Ohmiya, A. (2008). Biosynthesis of plant pigments: Anthocyanins, betalains and carotenoids. *Plant Journal*, 54(4), 733–749. <https://doi.org/10.1111/j.1365-313X.2008.03447.x>
- Tang, Q., Chi, F. M., Liu, H. D., Zhang, H. J., & Song, Y. (2021). Single-molecule real-time and illumina sequencing to analyze transcriptional regulation of flavonoid synthesis in blueberry. *Frontiers in Plant Science*, 12. <https://doi.org/10.3389/fpls.2021.754325>
- Tao, R. Y., Yu, W. J., Gao, Y. H., Ni, J. B., Yin, L., Zhang, X., et al. (2020). Light-induced basic/helix-loop-Helix64 enhances anthocyanin biosynthesis and undergoes constitutive photomorphogenic1-mediated degradation in pear. *Plant Physiology*, 184(4), 1684–1701. <https://doi.org/10.1104/pp.20.01188>
- Tirumalai, V., Swetha, C., Nair, A., Pandit, A., & Shivaprasad, P. V. (2019). *miR828* and *miR858* regulate *VvMYB114* to promote anthocyanin and flavonol accumulation in grapes. *Journal of Experimental Botany*, 70(18), 4775–4792. <https://doi.org/10.1093/jxb/erz264>
- Tu, M., Fang, J., Zhao, R., Liu, X., Yin, W., Wang, Y., et al. (2022). CRISPR/Cas9-mediated mutagenesis of *VvZIP36* promotes anthocyanin accumulation in grapevine (*Vitis vinifera*). *Horticulture Research*. <https://doi.org/10.1093/hr/uahc022>
- Uesenik, V., Stampar, F., & Veberic, R. (2009). Anthocyanins and fruit colour in plums (*Prunus domestica* L.) during ripening. *Food chemistry*, 114(2), 529–534. <https://doi.org/10.1016/j.foodchem.2008.09.083>
- Vasco, C., Avila, J., Ruales, J., Svanberg, U., & Kamal-Eldin, A. (2009). Physical and chemical characteristics of golden-yellow and purple-red varieties of tamarillo fruit (*Solanum betaceum* Cav.). *International Journal of Food Sciences and Nutrition*, 60, 278–288. <https://doi.org/10.1080/09637480903099618>
- Walker, A. R., Lee, E., Bogs, J., McDavid, D. A. J., Thomas, M. R., & Robinson, S. P. (2007). White grapes arose through the mutation of two similar and adjacent regulatory genes. *Plant Journal*, 49(5), 772–785. <https://doi.org/10.1111/j.1365-313X.2006.02997.x>
- Wang, H. B., Race, E. J., & Shrikhande, A. J. (2003a). Anthocyanin transformation in Cabernet Sauvignon wine during aging. *Journal of Agricultural and Food Chemistry*, 51 (27), 7989–7994. <https://doi.org/10.1021/jf034501q>
- Wang, H. B., Race, E. J., & Shrikhande, A. J. (2003b). Characterization of anthocyanins in grape juices by ion trap liquid chromatography-mass spectrometry. *Journal of Agricultural and Food Chemistry*, 51(7), 1839–1844. <https://doi.org/10.1021/jf0260747>
- Wang, S., Li, L. X., Fang, Y., Li, D., Mao, Z. L., Zhu, Z. H., et al. (2022). *MdERF1B-MdMYC2* module integrates ethylene and jasmonic acid to regulate the biosynthesis of anthocyanin in apple. *Horticulture Research*, 9. <https://doi.org/10.1093/hr/uac049>
- Wang, S., Wang, T., Li, Q. Q., Xu, C., Tian, J., Wang, Y., et al. (2022). Phosphorylation of *MdERF17* by *MdMPK4* promotes apple fruit peel degreening during light/dark transitions. *The Plant Cell*, 34(5), 1980–2000. <https://doi.org/10.1093/plcell/koac049>
- Wang, S., Zhang, Z., Li, L. X., Wang, H. B., Zhou, H., Chen, X. S., et al. (2022). Apple *MdMYB306-like* inhibits anthocyanin synthesis by directly interacting with *MdMYB17* and *MdbHLH33*. *Plant Journal*, 110(4), 1021–1034. <https://doi.org/10.1111/tpj.15720>
- Wang, W., Wang, Y., Chen, T., Qin, G., & Tian, S. (2022). Current insights into post-transcriptional regulation of fleshy fruit ripening. *Plant Physiology*. <https://doi.org/10.1093/plphys/kiac483>
- Wang, W. Q., Moss, S. M. A., Zeng, L. H., Espley, R. V., Wang, T. C., Kui, L. W., et al. (2022). The red flesh of kiwifruit is differentially controlled by specific activation-repression systems. *New Phytologist*, 235(2), 630–645. <https://doi.org/10.1111/nph.18122>
- Wang, Y., Wang, Y., Song, Z., & Zhang, H. (2016). Repression of *MYBL2* by Both *microRNA858a* and *HY5* Leads to the Activation of Anthocyanin Biosynthetic Pathway in Arabidopsis. *Molecular Plant*, 9(10), 1395–1405. <https://doi.org/10.1016/j.molp.2016.07.003>
- Wang, Z., Meng, D., Wang, A., Li, T., Jiang, S., Cong, P., et al. (2013). The methylation of the *PcMYB10* promoter is associated with green-skinned sport in Max Red Bartlett pear. *Plant Physiology*, 162(2), 885–896. <https://doi.org/10.1104/pp.113.214700>
- Wojdylo, A., Oszmianski, J., & Laskowski, P. (2008). Polyphenolic compounds and antioxidant activity of new and old apple varieties. *Journal of Agricultural and Food Chemistry*, 56(15), 6520–6530. <https://doi.org/10.1021/jf800510j>
- Wu, X. L., & Prior, R. L. (2005). Systematic identification and characterization of anthocyanins by HPLC-ESI-MS/MS in common foods in the United States: Fruits and berries. *Journal of Agricultural and Food Chemistry*, 53(7), 2589–2599. <https://doi.org/10.1021/jf048068b>
- Xia, H., Shen, Y., Hu, R., Wang, J., Deng, H., Lin, L., et al. (2021). Methylation of *MYBA1* is Associated with the Coloration in “Manicure Finger” Grape Skin. *Journal of Agricultural and Food Chemistry*, 69(51), 15649–15659. <https://doi.org/10.1021/acs.jafc.1c04550>
- Xing, Y., Sun, W., Sun, Y., Li, J., Zhang, J., Wu, T., et al. (2022). *MPK6*-Mediated *HY5* Phosphorylation Regulates Light-Induced Anthocyanin Accumulation in Apple Fruit. *Plant Biotechnology Journal*. <https://doi.org/10.1111/pbi.13941>
- Xu, C., & Min, J. (2011). Structure and function of WD40 domain proteins. *Protein & Cell*, 2(3), 202–214. <https://doi.org/10.1007/s13238-011-1018-1>
- Xu, F., Cao, S., Shi, L., Chen, W., Su, X., & Yang, Z. (2014). Blue light irradiation affects anthocyanin content and enzyme activities involved in postharvest strawberry fruit. *Journal of Agricultural and Food Chemistry*, 62(20), 4778–4783. <https://doi.org/10.1021/jf501120u>
- Yao, G., Ming, M., Allan, A. C., Gu, C., Li, L., Wu, X., et al. (2017). Map-based cloning of the pear gene *MYB114* identifies an interaction with other transcription factors to coordinately regulate fruit anthocyanin biosynthesis. *Plant Journal*, 92(3), 437–451. <https://doi.org/10.1111/tpj.13666>
- Yi, D. B., Zhang, H. N., Lai, B., Liu, L. Q., Pan, X. L., Ma, Z. L., et al. (2021). Integrative Analysis of the Coloring Mechanism of Red Longan Pericarp through Metabolome and Transcriptome Analyses. *Journal of Agricultural and Food Chemistry*, 69(6), 1806–1815. <https://doi.org/10.1021/acs.jafc.0c05023>
- Yu, J., Qiu, K., Sun, W., Yang, T., Wu, T., Song, T., et al. (2022). A long noncoding RNA functions in high-light-induced anthocyanin accumulation in apple by activating ethylene synthesis. *Plant Physiology*, 189(1), 66–83. <https://doi.org/10.1093/plphys/kiac049>
- Zhang, B., Yang, H. J., Yang, Y. Z., Zhu, Z. Z., Li, Y. N., Qu, D., et al. (2020). *mdm-miR828* Participates in the Feedback Loop to Regulate Anthocyanin Accumulation in Apple Peel. *Frontiers in Plant Science*, 11. <https://doi.org/10.3389/fpls.2020.608109>
- Zhang, S. Y., Chen, Y. X., Zhao, L. L., Li, C. Q., Yu, J. Y., Li, T. T., et al. (2020). A novel NAC transcription factor, *MdNAC42*, regulates anthocyanin accumulation in red-fleshed apple by interacting with *MdMYB10*. *Tree Physiology*, 40(3), 413–423. <https://doi.org/10.1093/treephys/tpaa004>
- Zhang, W. S., Li, X., Zheng, J. T., Wang, G. Y., Sun, C. D., Ferguson, I. B., et al. (2008). Bioactive components and antioxidant capacity of Chinese bayberry (*Myrica rubra* Sieb. and Zucc.) fruit in relation to fruit maturity and postharvest storage. *European Food Research and Technology*, 227(4), 1091–1097. <https://doi.org/10.1007/s00217-008-0824-z>
- Zhang, X. J., Wang, L. X., Liu, Y. L., Chen, X. X., Yang, Y. Z., & Zhao, Z. Y. (2013). Differential gene expression analysis of ‘Granny Smith’ apple (*Malus domestica* Borkh.) during fruit skin coloration*. *South African Journal of Botany*, 88, 125–131. <https://doi.org/10.1016/j.sajb.2013.07.009>
- Zhao, G. P., Xiang, F. X., Zhang, S. C., Song, J. X., Li, X. Y., Song, L. Y., et al. (2021). *PbLAC4-like*, activated by *PbMYB26*, related to the degradation of anthocyanin during color fading in pear. *Bmc Plant Biology*, 21(1). <https://doi.org/10.1186/s12870-021-03220-1>
- Zhou, H., Kui, L. W., Wang, H. L., Gu, C., Dare, A. P., Espley, R. V., et al. (2015). Molecular genetics of blood-fleshed peach reveals activation of anthocyanin biosynthesis by NAC transcription factors. *Plant Journal*, 82(1), 105–121. <https://doi.org/10.1111/tpj.12792>
- Zhou, L. J., Li, Y. Y., Zhang, R. F., Zhang, C. L., Xie, X. B., Zhao, C., et al. (2017). The small ubiquitin-like modifier E3 ligase *MdSIZ1* promotes anthocyanin accumulation by sumoylating *MdMYB1* under low-temperature conditions in apple. *Plant Cell and Environment*, 40(10), 2068–2080. <https://doi.org/10.1111/pce.12978>
- Zhu, Y. C., Zhang, B., Allan, A. C., Lin-Wang, K., Zhao, Y., Wang, K., et al. (2020). DNA demethylation is involved in the regulation of temperature-dependent anthocyanin accumulation in peach. *Plant Journal*, 102(5), 965–976. <https://doi.org/10.1111/tpj.14680>