



# Colorful hues: insight into the mechanisms of anthocyanin pigmentation in fruit

Yun Zhao,<sup>1,2</sup> Juanli Sun,<sup>1,3</sup> Sylvia Cheronon,<sup>1,3</sup> Jian-Ping An,<sup>1</sup> Andrew C. Allan<sup>4,5</sup> and Yuepeng Han<sup>1,2,\*</sup>

- 1 CAS Key Laboratory of Plant Germplasm Enhancement and Specialty Agriculture, Wuhan Botanical Garden, The Innovative Academy of Seed Design of Chinese Academy of Sciences, Wuhan 430074, China
- 2 Hubei Hongshan Laboratory, Wuhan, 430070, China
- 3 University of Chinese Academy of Sciences, 19A Yuquanlu, Beijing 100049, China
- 4 The New Zealand Institute for Plant & Food Research Ltd, Mt Albert Research Centre, Private Bag, Auckland 92169, New Zealand
- 5 School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

\*Author for correspondence: [yphan@wbcas.cn](mailto:yphan@wbcas.cn) (Y.H.)

The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (<https://academic.oup.com/plphys/pages/General-Instructions>) is Yuepeng Han ([yphan@wbcas.cn](mailto:yphan@wbcas.cn)).

## Abstract

Anthocyanin is a vital indicator for both fruit nutritional and commercial value. Anthocyanin accumulation is a surprisingly complicated process mediated by multiple networks associated with genetic, developmental, hormonal, and environmental factors. Transcriptional regulation along with epigenetic regulation constitutes the dominant molecular framework for anthocyanin biosynthesis. Here, we focus on current knowledge on regulatory mechanisms of anthocyanin accumulation, with emphasis on the latest progress in transcriptional and epigenetic regulation and the crosstalk between various signaling pathways. We present an emerging picture of how various internal and external stimuli control anthocyanin biosynthesis. Additionally, we discuss the synergistic or antagonistic effect of developmental, hormonal and environmental cues on anthocyanin accumulation in fruit.

## Introduction

Fruit consumption as part of the daily diet has many health benefits and may extend “health-span”. While color plays a crucial role in fruit appearance and acceptability, there is also a growing awareness of the nutritional value of highly colored fruit. Anthocyanins are the most prevalent water-soluble fruit pigments. They endow fruit with a variety of colors, ranging from red to purple and blue, which serve to attract seed dispersers and to protect against various biotic and abiotic stresses (Landi et al. 2015). In addition to their pigmentation, anthocyanins have the ability to act as free radical scavengers, thereby protecting living organisms from oxidative damage (Bendokas et al. 2020). Fruit and their processed by-products are important contributors to anthocyanin intake in our daily life. Currently, fruit-based anthocyanins have been widely used as a dietary supplement in the food and pharmaceutical

industry (Albuquerque et al. 2021). Therefore, the development of anthocyanin-enriched fruit is becoming an important goal in fruit breeding programs.

Efforts to enhance anthocyanin contents require a thorough understanding of how anthocyanins are synthesized during fruit development and the factors affecting their synthesis and degradation. Anthocyanins are the glycosylated forms of anthocyanidins sharing the C6-C3-C6 general skeletal backbone in which the two phenolic C6 rings are linked by a heterocyclic ring. Anthocyanins can be distinguished by their hydroxylation and methoxylation degree and pattern. To date, more than 20 naturally occurring anthocyanidins have been identified, and the most common types of anthocyanidins in fruit are cyanidin, delphinidin, peonidin, pelargonidin, petunidin, and malvidin (Jaakola 2013). Anthocyanins belong to the group of flavonoids synthesized via the phenylpropanoid pathway (Hichri et al. 2011). Anthocyanin

### ADVANCES BOX

- The activator–repressor system is essential for anthocyanin homeostasis and temporal–spatial distribution in fruit.
- A series of studies have demonstrated the crucial role of epigenetic regulation in anthocyanin biosynthesis in fruit.
- The crucial roles of developmental, hormonal, and environmental cues and their crosstalk in fruit anthocyanin accumulation have been uncovered.
- Different hormones frequently interact with each other to synergistically or antagonistically regulate anthocyanin biosynthesis in fruit.
- Anthocyanin vacuolar transport and degradation are crucial for anthocyanin accumulation in fruit.

accumulation is controlled by the highly conserved myeloblastosis-basic helix-loop-helix-WD40 repeat protein [MYB-bHLH-WDR, (MBW)] complex at the transcription level (Xu et al. 2015; Allan and Espley 2018).

In fruit, the molecular mechanism of anthocyanin biosynthesis has been intensely studied. Numerous anthocyanin activators and repressors have been identified to regulate the homeostasis and temporal–spatial pattern of anthocyanin pigmentation. Genetic studies have demonstrated aberrant anthocyanin pigmentation in a variety of plant species due to loss-of-function mutations in anthocyanin biosynthetic genes, such as *F3H* encoding flavonoid 3-hydroxylase (Maloney et al. 2014) and *DFR* encoding dihydroflavonol 4-reductase (Wang et al. 2022a), and in anthocyanin transporter genes such as *GST* encoding glutathione *S*-transferase (Lu et al. 2021). However, natural genetic variations in anthocyanin regulators particularly anthocyanin-activating MYB transcription factors (TFs) are major contributors to fruit color variation (Castillejo et al. 2020; Jiu et al. 2021). Alternative splicing in an R2R3-MYB TF SIAN2like is responsible for anthocyanin-free phenotype in cultivated tomato (*Solanum lycopersicum*) (Colanero et al. 2019). Allelic variations in an MYB TF Ruby that are caused by single-nucleotide mutations, DNA fragment deletions, and insertions of transposable elements contribute to the diversity of anthocyanin pigmentation in *Citrus* species (Butelli et al. 2012, 2017; Huang et al. 2018). Likewise, in apple (*Malus × domestica*), the natural variation in fruit anthocyanin pigmentation can be attributed to the difference in activity of MdMYB1 and MdMYB110 due to the insertions of transposable elements (Chagné et al. 2013; Zhang et al. 2019) and minisatellite (Espley et al. 2009).

Apart from genetic factors, a myriad of developmental, hormonal, and environmental signals have been reported to affect anthocyanin accumulation. However, the molecular basis behind the crosstalk of multiple signaling pathways in

anthocyanin regulation is less understood. Additionally, fresh insights have been gained into anthocyanin vacuolar transport and degradation (Fang et al. 2015; Zhao 2015; Zipor et al. 2015; Kallam et al. 2017). In this review, we focus on the regulatory mechanism of various internal and external stimuli on anthocyanin accumulation, as well as networks associated with the orchestration of transcriptional and epigenetic regulation.

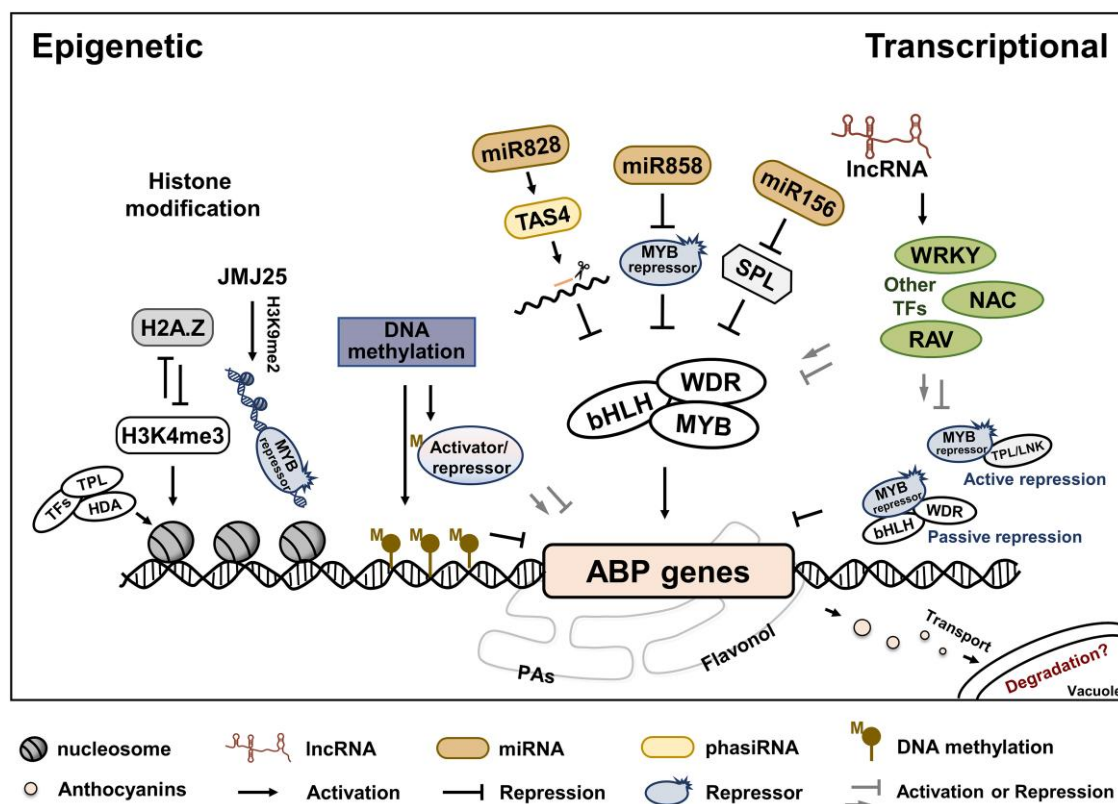
### Developmental cues

In most fruit, anthocyanin pigmentation occurs at the onset of ripening and is thus used as a ready-to-eat indicator. A vast array of efforts have been conducted to uncover the mechanism underlying developmental-induced anthocyanin accumulation over the past decades. These results show that anthocyanin accumulation is organized in a multifaceted hierarchical manner associated with transcriptional and epigenetic regulation.

### Transcriptional regulation

The MBW complex plays an essential role in the regulation of anthocyanin accumulation at the transcriptional level, with MYB TF as the core regulator and others as “reinforcement” members (Liu et al. 2015; Xu et al. 2015; Sun et al. 2020). However, loss-of-function mutants often point to the bHLH partner; for example, bHLH3 has been found to play an important role in anthocyanin accumulation in mulberry (*Morus alba*) fruit as the disruption of its expression is associated with pale colored fruit (Li et al. 2020a). The finding of MYB10 putative orthologs promoting fruit coloration in various rosaceous fruit species implies a conserved network of anthocyanin-activating MYBs in the regulation of anthocyanin accumulation (Lin-Wang et al. 2010; Albert et al. 2014; Medina-Puche et al. 2014). In particular fruit species, multiple MYB members, such as *VmMYBA1*, *VmMYBPA1.1*, and *VmMYBPA2.2* in bilberry (*Vaccinium myrtillus*), co-regulate anthocyanin pigmentation (Karppinen et al. 2021), whereas in other species, a single MYB activator such as *FaMYB63* in strawberry (*Fragaria × ananassa*) simultaneously mediates the accumulation of anthocyanins and other secondary metabolites like eugenol (Wang et al. 2022b). This indicates functional redundancy and diversification of anthocyanin-related MYBs after duplication (Huang et al. 2018). Additionally, redirection of metabolic flux towards proanthocyanidins (PAs) biosynthesis has a negative impact on anthocyanin accumulation (Han et al. 2012). However, in bilberry (*Vaccinium myrtillus*), the PAs-related MYB activator *VmMYBPA1.1* that is upregulated by anthocyanin-activating *VmMYBA1* during later ripening stages acts as a positive regulator of anthocyanin accumulation (Lafferty et al. 2022).

Reports detailing TFs, such as NAC, WRKY, and RELATED TO ABI3/VP1 (RAV), have demonstrated that these function as both positive and negative regulators of anthocyanin accumulation during the process of fruit ripening (Amato et al. 2019; Zhang et al. 2020; Martín-Pizarro et al. 2021) (Fig. 1).



**Figure 1.** A simplified model of the transcriptional and epigenetic regulation on anthocyanin biosynthesis. The transcription of structural genes in anthocyanin biosynthesis pathway is regulated by the MYB-bHLH-WDR (MBW) complex. MYB repressors negatively regulate anthocyanin biosynthesis through active and passive repression. Other TFs such as NAC, WRKY, and RELATED TO ABI3/VP1 (RAV) participate in the coordinated regulation of anthocyanin accumulation by modulating the activity of the MBW complex. The modes of epigenetic regulation in anthocyanin biosynthesis are categorized as follows: histone modification, DNA methylation, and noncoding RNAs. ABP, anthocyanin biosynthesis pathway; H2A.Z, histone H2 variant; H3K4me3, trimethylation of lysine 4 on histone H3; H3K9me2, dimethylation of lysine 9 on histone H3; HDA, histone deacetylase; JMJ25, H3K9 demethylase 25; SPL, SQUAMOSA PROMOTER BINDING PROTEIN-LIKE; TPL, TOPLESS co-repressor. Created by PowerPoint and Figdraw (<https://www.figdraw.com>).

In red-fleshed peach (*Prunus persica*), a NAC TF termed BLOOD interacts with a positive ripening regulator PpNAC1 to activate the transcription of *PpMYB10.1*, which provides a connection between fruit development and anthocyanin accumulation (Zhou et al. 2015; Lü et al. 2018). Similarly, a link between the putative ripening-related MADS-box TF VmTDR4 and anthocyanin-related VmMYB1/2 is reported in bilberry (Jaakola et al. 2010). In red-skinned pear (*Pyrus communis*), PyWRKY26 forms a heterodimer with PybHLH3 to activate transcription of *PyMYB114* (Li et al. 2020b), which subsequently interacts with ethylene response factor PyERF3 to induce the expression of anthocyanin structural genes (Yao et al. 2017).

In addition to anthocyanin-activating MYBs, a great number of anthocyanin-repressing MYBs have been identified that regulate the homeostasis and temporal-spatial pattern of anthocyanin pigmentation (LaFountain and Yuan 2021). MYB repressors can be divided into two types, R3-MYB and R2R3-MYB, which contain one and two repeats, respectively, in the DNA-binding domain. The studied MYB repressors have the conserved motif of (D/E)LX<sub>2</sub>(R/K)<sub>3</sub>LX<sub>6</sub>LX<sub>3</sub>R for

interaction with bHLH in the R3-MYB domain, which enables them to act as passive repressors by competing with MYB activators for binding to bHLHs. Apart from this passive repression function, MYB repressors can have active repression function due to repression motifs in the C-terminal, such as C1 (IsrGIDPx<sup>T</sup><sub>N</sub>HR), C2 (pdLNL<sup>D</sup><sub>E</sub>L), and TLLLFR (Cavallini et al. 2015; Ma and Constabel 2019; Zhou et al. 2019). The C1 and C2 motifs are conserved in studied R2R3-MYB repressors, but the TLLLFR motif is only present in some MYB repressors. The C2 motif, also known as ethylene-responsive element binding factor-associated amphiphilic repression (EAR), confers an active repressive function of MYB repressors as it is essential for interaction with co-repressors such as NIGHT LIGHT-INDUCIBLE AND CLOCKREGULATED1/2 (LNK1/2) and TOPLESS (TPL) (Zhou et al. 2017; Plant et al. 2021). However, the mechanisms of C1- and TLLLFR-mediated repression are still unknown. Interestingly, transcription of MYB repressors could be activated by MYB activators, which instigates a fine-tuning negative feedback loop to balance anthocyanin accumulation (Zhou et al. 2019; Yan et al. 2020) (Fig. 1). A

R3-MYB repressor termed RED TONGUE (RTO) is shown to move between cells and inhibits the function of the R2R3-MYB activator NECTAR GUIDE ANTHOCYANIN (NEGAN), resulting in spotted or striped pigmentation patterns in monkeyflower (*Mimulus lewisii*) (Ding et al. 2020). It is worthy to investigate whether this activator–repressor system is involved in the formation of dispersed spots or stripes in anthocyanin pigmentation in fruit.

### Epigenetic regulation

Increasing evidence indicates the involvement of epigenetic modifications in anthocyanin pigmentation in fruit, such as DNA methylation, histone modification, and noncoding RNAs. Hypermethylation of the promoter region in *MdMYB10* is associated with striped patterns of anthocyanin pigmentation in apple fruit (Talias et al. 2011). Abnormal hypermethylation of the *MYB10* promoter can even cause a loss of anthocyanins in fruit skin as reported in a yellow-skinned sport in apple (Wang et al. 2013) and a green-skinned sport in pear (El-Sharkawy et al. 2015). Methylation of the *MYB10* locus has been shown to be mediated by a regulator of RNA-directed DNA methylation (RdDM), Argonaute 4 (AGO4) in apple (Jiang et al. 2020). In *Arabidopsis thaliana*, trimethylation of lysine 4 in histone H3 (H3K4me3) is required for promotion of the transcription of anthocyanin biosynthetic genes, but its function is inhibited by a conserved histone H2 variant H2A.Z (Cai et al. 2019). A histone H3K9 demethylase gene *PtrJMJ25* epigenetically modulates anthocyanin biosynthesis by mediating H3K9me2 demethylation and DNA hypomethylation in *PtrMYB182* locus in poplar (*Populus trichocarpa*) (Fan et al. 2018) (Fig. 1).

MicroRNAs (miRNAs) are small noncoding endogenous RNAs that play an important role in fruit anthocyanin accumulation. SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL) TFs targeted by miR156 inhibit anthocyanin biosynthesis through destabilizing the MBW complex (Gou et al. 2011). During the process of fruit ripening, miR156 is activated to silence SPL TFs, resulting in anthocyanin pigmentation (Li et al. 2022). The miR156-SPL module involved in anthocyanin accumulation in fruit may be conserved across plant species (He et al. 2022). Moreover, miR828 and miR858 target anthocyanin-related MYB activators and repressors, thereby participating in the regulation of anthocyanin accumulation in fruit. Both miR828 and miR858 promote anthocyanin accumulation in grape (*Vitis vinifera*) through inhibiting the anthocyanin-related repressor *VvMYB114* (Tirumalai et al. 2019). By contrast, miR858 downregulates anthocyanin accumulation in tomato by inhibiting the expression of *SIMYB7-like* (Jia et al. 2015). Similarly, miR858 negatively regulates PAs accumulation in the peel of apple fruit by targeting *MdMYB9/11/12* (Zhang et al. 2022). In kiwifruit (*Actinidia chinensis*), miR828 inhibits anthocyanin accumulation by targeting the noncoding TRANSCRIPTING SILENCING GENE 4 (TAS4) transcript to generate a phased secondary

siRNAs (phasiRNAs) *AcTAS4-D4(-)* which further silences *AcMYB110* (Wang et al. 2022c). Anthocyanin-related *MdMYB1* (an allele of *MdMYB10*) can also play a role in lignin biosynthesis in apple fruit via activating *miR7125* that can silence the lignin biosynthesis gene *cinnamoyl-coenzyme A reductase* (*MdCCR*), thereby regulating the balance between anthocyanin and lignin metabolism (Hu et al. 2021).

Long noncoding RNAs (lncRNAs) also have been shown to play important roles in anthocyanin accumulation in fruit (Bai et al. 2019a) (Fig. 1). In strawberry, a lncRNA, FRUIT RIPENING-RELATED LONG INTERGENIC RNA (FRILAIR), functions as a noncanonical target mimic of miR397 to enhance the transcript level of *LAC11a* encoding a putative laccase-11-like protein, resulting in anthocyanin pigmentation during fruit ripening (Tang et al. 2021). In apple, the lncRNAs *MdLNC610* and *MdLNC499* participate in the regulation of light-induced anthocyanin accumulation by activating ethylene synthesis or the expression of *MdERF109*, respectively (Ma et al. 2021; Yu et al. 2022).

### Environmental factors

Anthocyanin biosynthesis is influenced by various environmental factors. Due to their sessile nature, plants have evolved an efficient system to produce anthocyanins as a protective mechanism against environmental stressors. Here, we focus on the influence of light and temperature on anthocyanin biosynthesis.

#### Light

Anthocyanin accumulation is profoundly influenced by light conditions including quality, duration, and intensity (Henry-Kirk et al. 2018). Molecular mechanisms underlying light-controlled anthocyanin accumulation, including photoreceptors and light signal transduction, have been intensively investigated. The light signaling component, ELONGATED HYPOCOTYL5 (HY5, a bZIP TF), acts as the master regulator of light-induced anthocyanin accumulation (Gangappa and Botto 2016). In *Arabidopsis*, HY5 positively regulates anthocyanin accumulation through activating expression of *PRODUCTION OF ANTHOCYANIN PIGMENT 1* (*PAP1*) and anthocyanin biosynthesis pathway (ABP) genes as well as miR858a which targets the anthocyanin repressor *MYB2* or via restraining the transcription of *MYB2* by epigenetic histone modifications (Wang et al. 2016). In rosaceous fruits, HY5 has shown to promote anthocyanin accumulation through activating expression of *MYB10* homologues and ABP genes (Tao et al. 2018; Zhao et al. 2022). Since HY5 lacks the transactivation domain, it requires the B-box-containing proteins (BBXs) as essential partners for HY5-dependent regulation of anthocyanin accumulation (Bai et al. 2019b; Bursch et al. 2020; Li et al. 2021). Under dark conditions, CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1) physically interacts with nuclear-localized HY5, MYBs, and bHLHs activators, triggering their ubiquitination and subsequent

proteasome-mediated degradation (Li et al. 2012; Tao et al. 2020). Upon light exposure, COP1 is re-located into the cytoplasm, leading to stabilization of HY5 and other anthocyanin activators. Thus, COP1 functions as a repressor of anthocyanin accumulation in the dark by destabilizing anthocyanin-activating regulators, and this appears to be highly conserved across plant species (Wang et al. 2021a). Notably, in addition to COP1, an apple BTB-BACK-TAZ domain protein MdbT2 has been reported to participate in the ubiquitination and degradation of MdbBX22 in the dark (An et al. 2019). Under light conditions, mitogen-activated protein kinase 4 (MPK4) mediates phosphorylation of anthocyanin-activating MYBs to increase their stability, leading to increase in anthocyanin accumulation (Li et al. 2016; Yang et al. 2021a).

Despite the key role of light in anthocyanin accumulation, light-independent anthocyanin pigmentation does exist in fruit. For example, some peach cultivars produce anthocyanins in the flesh around the stone that is controlled by a single locus of *Cs* on linkage group 3 (Dirlewanger et al. 2004). A similar case exists for some kiwifruit cultivars that display anthocyanin pigmentation in the inner pericarp (Liu et al. 2018). The mechanism underlying anthocyanin pigmentation in the inner pericarp where light levels should be relatively low remains to be determined for a number of fruit species.

### Temperature

Temperature is an important environmental factor affecting anthocyanin pigmentation in plants, with high temperatures restraining and low temperatures eliciting anthocyanin accumulation (Gouot et al. 2019). The reasons for high temperature-induced repression of anthocyanin biosynthesis may involve the nuclear import of COP1 (Park et al. 2017) and the redirection of the phenylpropanoid pathway flux from the anthocyanin branch to the chlorogenic acid or lignin biosynthesis branches (Liu et al. 2019). High temperature also induces MYB repressors of anthocyanin accumulation in apple (Lin-Wang et al. 2011), potato (*Solanum tuberosum*) (Liu et al. 2019), and Arabidopsis (Rowan et al. 2009). Besides its role in impairing anthocyanin biosynthesis, high temperature promotes anthocyanin degradation in fruit due to the increased peroxidase activity (Movahed et al. 2016). Exogenous peroxidase inhibitors are able to counteract the negative impact of high temperature on anthocyanin accumulation in fruit (Niu et al. 2017). Therefore, decreased biosynthesis and increased catabolism may both contribute to the low levels of anthocyanin in fruit when grown at elevated temperatures.

In contrast, low temperatures trigger the export of COP1 from the nucleus, which stabilizes HY5 to enhance anthocyanin accumulation in Arabidopsis (Catalá et al. 2011). In apple, the small ubiquitin-like modifier (SUMO) E3 ligase SAP AND MIZ1 DOMAIN-CONTAINING LIGASE1 (MdSIZ1) senses low temperature and promotes anthocyanin accumulation through activating the sumoylation of MdMYB1 (Jiang et al. 2022). Cold stress can induce DNA demethylation and

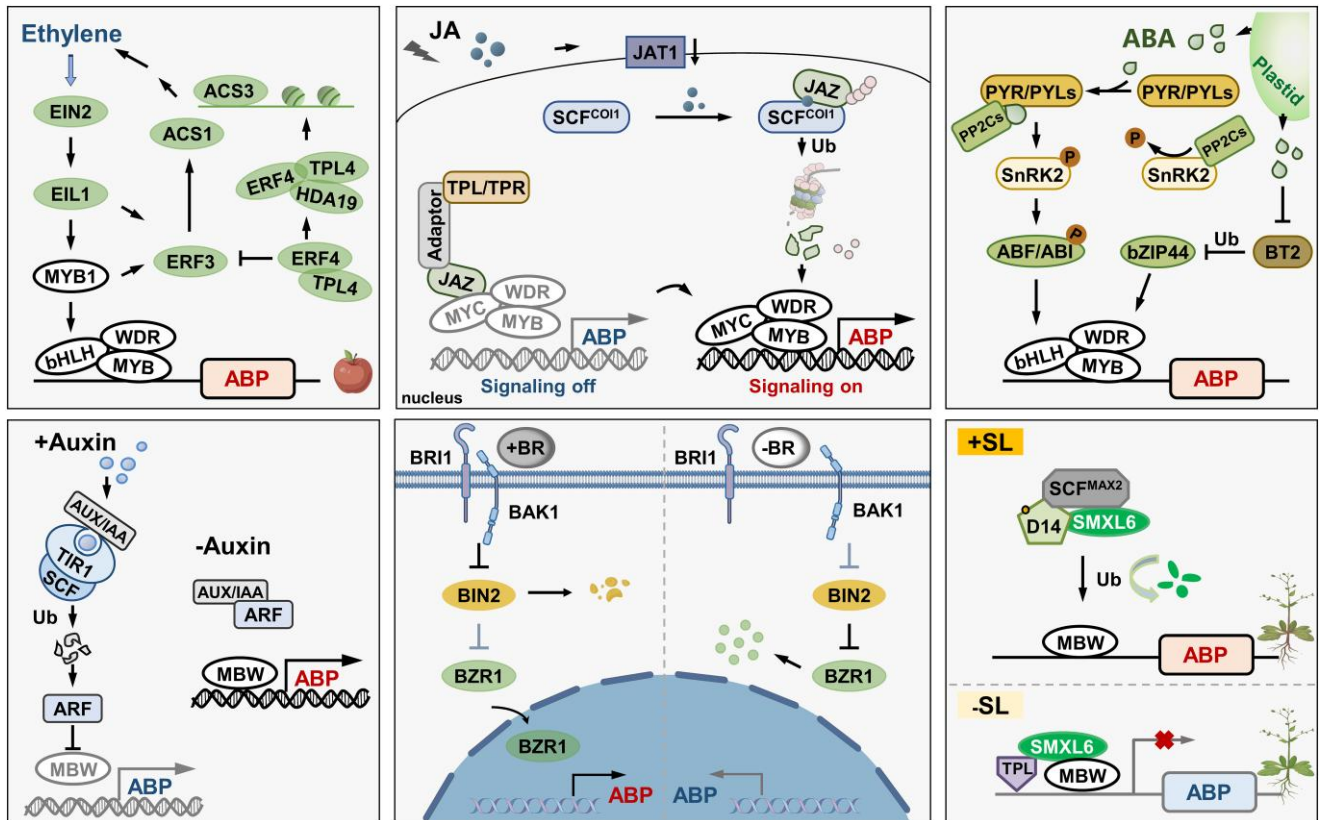
upregulation of the ABP genes, thereby leading to an increased accumulation of anthocyanins in sweet orange (*Citrus sinensis*) and peach fruit (Sicilia et al. 2020; Zhu et al. 2020). Notably, prefoldins are found to act as a brake to ensure proper levels of anthocyanins with the progression of cold acclimation by mediating the ubiquitination and subsequent degradation of HY5 in Arabidopsis (Perea-Resa et al. 2017). However, low temperature inhibits anthocyanin accumulation in strawberry fruit through stimulating MITOGEN-ACTIVATED PROTEIN KINASE 3 (FvMAPK3)-mediated phosphorylation of FvMYB10 to reduce its transcriptional activity and as well as enhancing the proteasome-mediated degradation of chalcone synthase1 (FvCHS1) (Mao et al. 2022).

In addition to the G-box motif for HY5 binding, *cis*-acting elements for cold acclimation have been found in the promoters of anthocyanin-activating MYBs in fruit crops. In apple, the cold-induced bHLH MdbHLH3 binds to the MYC binding motif in the *MdMYB1* promoter to activate anthocyanin accumulation under cold stress (Xie et al. 2012). Moreover, the insertion of a retrotransposon containing a cold acclimation transcription factor dehydration responsive element binding protein/C-repeat binding factor (DREB/CBF) binding motif upstream of *MdMYB1* likely contributes to apple fruit coloration under low temperatures (Zhang et al. 2019). Likewise, the insertion of a retrotransposon containing a low temperature-responsive (LTR) element upstream of *Ruby* is responsible for the fruit-specific, cold-dependent accumulation of anthocyanins in blood oranges (Butelli et al. 2012). Additionally, a LTR *cis*-acting element for MdbHLH3 binding has been identified in the promoter of *MdbBX20*, the interacting partner of MdHY5 (Fang et al. 2019). Therefore, it appears that BBX, MYB, and bHLH TFs act as integrators of light and low temperature signals in the regulation of anthocyanin pigmentation in fruit (Huang et al. 2019).

## Plant hormones

### Ethylene

During fruit ripening, anthocyanin accumulation is often accompanied by ethylene release. The positive influence of ethylene on fruit coloration has been implicated in various fruit crops, such as grape (Wang et al. 2022d), plum (*Prunus salicina*) (Farcuh et al. 2022), and mango (*Mangifera indica*) (Chen et al. 2022a). In apple, upon ethylene treatment, the key component of ethylene signaling *ETHYLENE-INSENSITIVE3 LIKE1* (*MdEIL1*) induces transcription of *MdMYB1* that further activates *MdERF3*, thereby forming a regulatory feedback loop controlling anthocyanin pigmentation and ethylene production (An et al. 2018a) (Fig. 2). Ethylene-induced anthocyanin accumulation can be fine-tuned by a regulatory module containing *MdEIL1*, *MdMYB1*, and the *MdMYB17* repressor in apple (Wang et al. 2022e). In addition to the role in directly activating anthocyanin-related regulators, *MdbHLH3* can indirectly regulate anthocyanin pigmentation through participating



**Figure 2.** The regulatory network of hormone signaling pathways in anthocyanin accumulation. Simplified models for ethylene, jasmonate (JA), abscisic acid (ABA), auxin, brassinosteroid (BR) and strigolactone (SL) are shown. The signaling mechanisms for these six hormones mostly contain a Skp1/Cullin/F-box (SCF) E3 ubiquitin ligase complex to trigger the ubiquitination and degradation of target proteins via 26S proteasome. Icons indicate the example system in which these genes are characterized, as follows: ethylene, apple; SL, Arabidopsis. Created by PowerPoint and Figdraw (<https://www.figdraw.com>).

in ethylene biosynthesis in apple (Hu et al. 2019). MdERF4 participates in the regulation of anthocyanin pigmentation through forming a complex with MdTPL and histone deacetylase MdHDA19 to suppress ethylene production in apple (Hu et al. 2022) (Fig. 2). However, the epigenetic mechanism by which ethylene participates in the regulation of fruit coloration remains unclear.

Notably, the effect of ethylene on anthocyanin biosynthesis differs between plant species. In Arabidopsis, ethylene inhibits anthocyanin accumulation through inhibiting the expression of the anthocyanin activator *PAP1* and stimulating the expression of anthocyanin repressor *MYB2* (Jeong et al. 2010). In pear, *PpERF105* activates the expression of anthocyanin repressor *PpMYB140* to impede the appearance of red coloration (Ni et al. 2021).

### Abscisic acid

Abscisic acid (ABA) has a positive role in modulating anthocyanin accumulation in a variety of fruits. Exogenous application of ABA stimulates the expression of anthocyanin-activating MYBs, leading to anthocyanin pigmentation in fruit (Lai et al. 2014; Shen et al. 2014;

Kadomura-Ishikawa et al. 2015; Oh et al. 2018). In contrast, inhibition of the expression of a 9-*cis*-epoxycarotenoid dioxygenase gene *FaNCED1*, the key gene for ABA synthesis, reduces ABA levels and anthocyanin content in strawberry (Jia et al. 2011). As an essential hub in the ABA signaling pathway, abscisic acid-insensitive 5 (MdABI5, a bZIP TF) promotes anthocyanin accumulation through activating *MdbHLH3* and strengthening the interaction between MdMYB1 and *MdbHLH3* in apple (An et al. 2021a). Furthermore, ABA inhibits MdBT2-mediated ubiquitination degradation of the ABA-responsive TF *MdbZIP44*, which subsequently cooperates with MdMYB1 to activate anthocyanin accumulation (An et al. 2018b) (Fig. 2). Additionally, miRNAs may serve as important regulators that assist ABA in regulating target genes involved in anthocyanin pigmentation in fruit (Li et al. 2019).

### Jasmonate

Jasmonate (JA) is a class of lipid-derived phytohormones that acts as an important regulator of plant secondary metabolism (Oblessuc et al. 2020). Exogenous application of JA causes an increase in anthocyanin accumulation in a number of

fruits, but the degree of increase varies with their concentration and stereoisomeric form (Wang et al. 2021b). In Arabidopsis, F-box protein CORONATINE INSENSITIVE1 (COI1) recruits jasmonate-ZIM domain proteins (JAZs) for ubiquitination and degradation by the SCF<sup>COI1</sup>-26S proteasome pathway in response to JA signals (Thines et al. 2007). The JA-triggered degradation of JAZ proteins abolishes the interactions of JAZ proteins with MYB and bHLH TFs, allowing the formation of the MBW complex that subsequently activates anthocyanin accumulation (Qi et al. 2011) (Fig. 2). The interference of JAZ proteins with the formation of the MBW complex is also involved in the regulation of JA-induced anthocyanin accumulation in fruit (Wang et al. 2019; Chen et al. 2022b). Moreover, an EAR motif-containing adaptor protein (ECAP) aids JAZ recruitment of the transcriptional co-repressor, TOPLESS-RELATED 2 (TPR2), resulting in an enhancement of transcriptional repression activities (Li et al. 2020d). In apple, a telomere-binding protein (MdTRB1) acts as positive regulator of anthocyanin accumulation via interacting with MdMYB9 to enhance the MdMYB9-activated transcription of the ABP genes (An et al. 2021b). The JA signaling repressor MdJAZ1 interferes with the formation of the MdTRB1-MdMYB9 complex to fine-tune JA-mediated anthocyanin accumulation.

### Auxin

Auxin is of pivotal importance in plant growth and development (Matthes et al. 2019). Emerging evidences reveal the inhibitory effect of exogenous auxin application on the regulation of anthocyanin accumulation in apple, grape, and red raspberry (*Rubus idaeus*) (Ji et al. 2015; Jia et al. 2017; Moro et al. 2017). In red-fleshed apple callus, low auxin levels facilitate the complex formation of auxin/indole-3-acetic acid (Aux/IAA) repressor MdIAA121 and auxin response factor MdARF13. Under high auxin concentrations, MdIAA121 is degraded to release MdARF13, which represses transcription of anthocyanin biosynthetic gene *MdDFR* via directly binding to auxin-responsive elements (AuxREs) in the promoter (Wang et al. 2018) (Fig. 2). Overall, the molecular mechanism underlying the role of auxin in fruit pigmentation remains to be determined.

### Brassinosteroid

Brassinosteroid (BR) is a class of steroidal hormones that affect fruit quality (Ji et al. 2021). A series of important BR signaling components, from the cell surface receptors BRASSINOSTEROID INSENSITIVE1 (BRI1) and BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) to the key nuclear-localized TFs BRASSINAZOLE RESISTANT1 (BZR1) and BRI1 EMS SUPPRESSOR1 (BES1), have been identified in Arabidopsis (Kim and Russinova 2020) (Fig. 2). There seems to be a lack of consensus opinion on the effect of BR on anthocyanin biosynthesis. Studies have shown that exogenous BR treatment promotes anthocyanin accumulation in Arabidopsis, grape, and strawberry (Peng et al. 2011; Vergara et al. 2020; Zahedipour-Sheshglani and Asghari

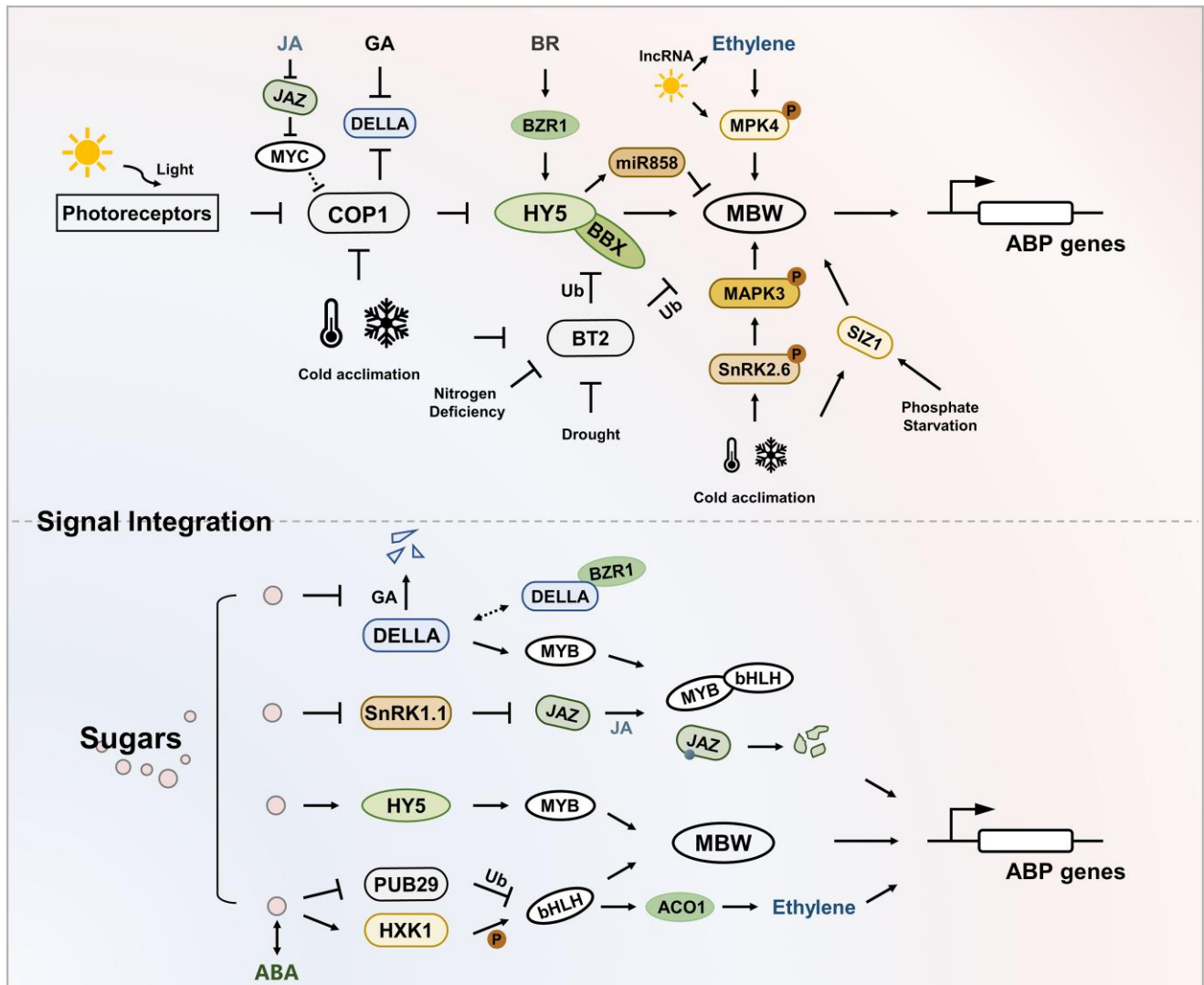
2020). However, in the seedlings and calli of red-fleshed apple, exogenous BR treatment inhibits anthocyanin pigmentation by activating the *MdBEH2.2* (a BZR1/BES1 family TF) and *MdMYB60*, both of which act as negative regulators of the ABP genes (Wang et al. 2021c). A recent study also reveals that overexpression of *MdBZR1*, an important component of the BR signaling pathway, represses anthocyanin biosynthesis in “Yinv” apple fruit peel (Wang et al. 2023). Therefore, further studies are needed to clarify the molecular mechanism by which the BR signal mediates anthocyanin pigmentation in fruit.

### Strigolactone

Strigolactone (SL), a carotenoid-derived endogenous plant hormone, is established to positively impact anthocyanin biosynthesis (Mashiguchi et al. 2021). In Arabidopsis, SL signaling is transduced by the DWARF14 (D14) receptor to form a D14-SCF<sup>MAX2</sup>-SMXLs complex, triggering the ubiquitin-mediated degradation of SL signaling inhibitor SUPPRESSOR OF MAX2-LIKE6 (AtSMXL6) which functions as a repressor of the anthocyanin-related regulator (Seto et al. 2019; Tang and Chu 2020) (Fig. 2). Intriguingly, AtSMXL6 serves dual functions as a typical repressor and an autoregulated transcription factor to maintain the homeostasis of SL signal transduction via a negative feedback loop (Wang et al. 2022). Several studies have preliminarily explored the role of SL in fruit anthocyanin pigmentation (Liu et al. 2022). In grape, exogenous SL treatment promotes fruit coloration by inducing transcription of anthocyanin biosynthetic genes (Ju et al. 2022). However, the molecular basis of SL in regulating anthocyanin accumulation in fruit remains to be investigated.

### Interplay among multiple hormones

Phytohormones act synergistically or antagonistically to regulate various processes of growth and development in plants. For instance, JA does not work independently but operate in a complex signaling network combined with other phytohormone signaling pathways (Fenn and Giovannoni 2021). In Arabidopsis, JA-activated bHLHs attenuate the repression of ethylene-stabilized TFs ETHYLENE-INSENSITIVE3 (EIN3)/EIL1 on the transcriptional activity of the MBW complex, resulting in crosstalk between JA and ethylene to regulate anthocyanin biosynthesis (Song et al. 2022). Similarly, the ABA receptor PYRABACTIN RESISTANCE1-LIKE (PYL4) whose expression is regulated by JA impacts anthocyanin accumulation (Lackman et al. 2011; Yu et al. 2021). The finding that the DELLA protein in the gibberellin (GA) signaling pathway sequesters the JAZ repressor of the MBW complex indicates a crosstalk between JA and GA signals in the regulation of anthocyanin accumulation (Xie et al. 2016). Moreover, BR enhances JA-induced anthocyanin accumulation in Arabidopsis seedlings, but the related mechanism remains to be determined (Peng et al. 2011). In addition, coordinated regulation of distinct hormones on fruit coloration has been revealed.



**Figure 3.** Schematic diagram of light–hormone and sugar–hormone interactions in anthocyanin accumulation. Anthocyanin biosynthesis is coordinately regulated by developmental cues, hormones, and environmental factors. The diverse signals converge and drive synergy or attenuation effects on anthocyanin accumulation. Light, sugar, and hormones are key factors affecting anthocyanin biosynthesis. Light-responsive anthocyanin accumulation occurs mainly through the COP1–HY5 module, which also displays as an essential hub at the interface between light and hormones. Sugar signal regulates anthocyanin biosynthesis by activating the transcription of the MYB–bHLH–WDR (MBW) complex. The crosstalk between sugar and hormones signaling in anthocyanin biosynthesis is implicated. Created by PowerPoint.

Exogenous SL has been found to affect ABA-induced anthocyanin biosynthesis in grape berries (Ferrero et al. 2018). *MdERF1B*, whose expression is upregulated by JA, acts as an integrator of ethylene and JA signals to synergistically regulate anthocyanin biosynthesis in apple (Wang et al. 2022f).

### Crosstalk between developmental, hormonal, and environmental cues

The light signaling TF components are known to interact with TFs of hormone signaling pathways to regulate photomorphogenesis in Arabidopsis. A well-studied signaling hub is the COP1–HY5 module that serves as the interface between

light and hormones (Fig. 3). COP1 destabilizes the JA-related TFs MYC2/3/4 under the shade conditions to facilitate reallocation of resources from defense to growth (Chico et al. 2014). The COP1-targeted destabilization of DELLA proteins that are negative elements in the GA signaling pathway is relevant for growth responses to shade and warm temperature (Blanco-Touriñán et al. 2020). Moreover, BRASSINOSTEROID-INSENSITIVE 2 (BIN2) and BZR1 in BR pathway interact with key components of light signaling pathway to mediate hypocotyl elongation, cell elongation, and cotyledon opening (Kim et al. 2014; Li and He 2016; Li et al. 2020e). In Arabidopsis, UV-B irradiation inhibits the transcription of BR-induced *BES1* that represses flavonol-activating MYBs, allocating energy to flavonoid biosynthesis



(Liang et al. 2020). Under light conditions, exogenous 24-epibrassinolide (EBR) promotes anthocyanin accumulation in grape pericarp, indicating a crosstalk between light and BR signals in anthocyanin regulation (Zhou et al. 2018; Yang et al. 2021b). However, it remains to be determined if induction of anthocyanin accumulation by the combined treatment of light and EBR is related to the inhibition of anthocyanin repressors. On the contrary, the integration of light and BR signals shows an antagonistic effect on the regulation of anthocyanin accumulation in apple (Wang et al. 2023). Additionally, ABA signal transduction is involved in anthocyanin accumulation in bilberry fruit under red light treatment (Samkumar et al. 2021). Likewise, the transcription of *MdHYS* can be induced by ABA treatment in apple (An et al. 2017), and an additive effect on anthocyanin accumulation in strawberry exists between light and ABA (Kadomura-Ishikawa et al. 2015). Thus, the ABA signal is essential for fine-tuning fruit coloration by interacting with light. As mentioned previously, lncRNAs *MdLNC610* and *MdLNC499* participate in light-induced anthocyanin accumulation through activating ethylene production (Ma et al. 2021; Yu et al. 2022), which expands the possibility that noncoding RNAs integrate hormone signals to regulate anthocyanin pigmentation in fruit.

The crosstalk between sugar and hormone signaling is involved in multiple fundamental biological processes, such as circadian clock (Wang et al. 2020d), inflorescence growth (Goetz et al. 2021), bud outgrowth (Bertheloot et al. 2020), and male fertility (Wu et al. 2022). As precursors for glycosyl derivatives, soluble sugars are crucial for anthocyanin biosynthesis. A recent study shows an association between the amounts of UDP-glucose and UDP-galactose substrates and anthocyanin content (Xu et al. 2020). The crosstalk between sugar and hormone signaling in anthocyanin biosynthesis has been initially established in Arabidopsis. Sugar transporter *SUC1* serves as an integrator for sugar, light, and ethylene signals, and its suppression by ethylene inhibits sucrose-induced anthocyanin accumulation under light conditions to fine-tune anthocyanin homeostasis (Jeong et al. 2010). Sucrose also blocks GA-mediated degradation of DELLA proteins, thereby activating *PAP1* to promote anthocyanin biosynthesis (Li et al. 2014) (Fig. 3). In apple, exogenous glucose activates hexokinase *MdHXX1* that phosphorylates and stabilizes *MdbHLH3* and inhibits ubiquitin E3 ligase *MdPUB29* that ubiquitinates and degrades *MdbHLH3*, to promote anthocyanin accumulation (Hu et al. 2016a; Hu et al. 2019) (Fig. 3). The glucose-induced accumulation of anthocyanins in apple is in contrast to a previous report where sugar-induced anthocyanin accumulation has been shown to be sucrose-specific in Arabidopsis (Solfanelli et al. 2006). The ABA-stress-ripening (ASR) TF integrates ABA and sugar signals to mediate fruit coloration in strawberry (Jia et al. 2016). A conserved energy sensor SNF1-related kinase 1 (*MdSnRK1.1*) interacts with the JA signaling repressor *MdJAZ18* to stimulate proteasome-mediated JAZ degradation, allowing *MdbHLH3* to promote anthocyanin biosynthesis in apple (Liu et al. 2017).

## Perspectives

Anthocyanin accumulation is controlled by developmental, environmental, and hormonal cues, and their concerted action in fruit pigmentation is a challenge for future research. After synthesis in the cytosolic surface of the endoplasmic reticulum (ER), anthocyanins are transported into the vacuole for storage. Loss-of-function mutations or upregulation of GST-type anthocyanin transporters can alter fruit coloration, suggesting that the transport of anthocyanins from the ER to the vacuole is a crucial step for anthocyanin pigmentation (Gao et al. 2020; Zhao et al. 2020). Additionally, there is evidence supporting the existence of anthocyanin turnover and degradation in fruit (Movahed et al. 2016). Hence, anthocyanin homeostasis is a dynamic balance mediated by biosynthesis, transport, and degradation. With the ongoing rapid development of new technologies, deciphering the mystery of anthocyanin transport and degradation in response to internal and external signals becomes more certain. This has the potential for enabling the improvement of anthocyanin content in fruit.

As a conspicuous aspect of fruit ripening, anthocyanin pigmentation is normally accompanied by chlorophyll breakdown. A miR156a-SPL12 module is found to coordinate the chlorophyll and anthocyanin accumulation during fruit ripening in blueberry (*Vaccinium corymbosum*) (Li et al. 2020c). However, it is not yet elucidated whether anthocyanin accumulation and chlorophyll degradation are

### OUTSTANDING QUESTIONS BOX

- How conserved is the activator–repressor system across fruit species? Does the negative feedback loop between MYB activators and repressors balance anthocyanin accumulation independently or synergistically with other repressors?
- What is the regulatory mechanism underlying anthocyanin transport and degradation? How do internal and external stimuli coordinately regulate transport and degradation to maintain anthocyanin homeostasis?
- How does epigenetic regulation integrate developmental, hormonal, and environmental signaling pathways to regulate anthocyanin accumulation?
- Are there core regulators that simultaneously regulate the accumulation of anthocyanin and other pigments?
- How does anthocyanin biosynthesis affect the accumulation of metabolites associated with fruit taste?
- What are the exact mechanisms underpinning the unique spatial–temporal pigmentation patterns in fruit?

simultaneously mediated by internal and external signals. The co-regulation of anthocyanin and other compounds has recently become an active research topic (Wang et al. 2022g). In apple, MdMYB1 acts as a positive regulator of both anthocyanin and malate accumulation (Hu et al. 2016b), and overexpression of MdMYB6 in red-flesh callus results in increased hexose content and decreased anthocyanin accumulation (Xu et al. 2020). Thus, it would be interesting to investigate whether and how anthocyanin accumulation affects fruit taste and/or other quality traits. Despite the substantial progress in the regulatory mechanism of anthocyanin pigmentation in fruit over the past decades, many areas still need to be explored (see “Outstanding questions”). A comprehensive insight into the mechanism of anthocyanin accumulation is essential for development of anthocyanin-rich and tasteful fruit through breeding and environmental management.

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## Author contributions

Y.H. conceived and designed the original article. Y.Z. wrote the manuscript with help from J.S., S.C., and J.-P.A.; Y.H. and A.A. revised the manuscript. All authors reviewed and edited the manuscript.

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## Data availability

All data supporting the findings of this study are available within the article.

## References

- Albert NW, Davies KM, Lewis DH, Zhang H, Montefiori M, Brendolise C, Boase MR, Ngo H, Jameson PE, Schwinn KE. A conserved network of transcriptional activators and repressors regulates anthocyanin pigmentation in eudicots. *Plant Cell*. 2014;26(3):962–980. <https://doi.org/10.1105/tpc.113.122069>
- Albuquerque B, Oliveira M, Barros L, Ferreira I. Could fruits be a reliable source of food colorants? Pros and cons of these natural additives. *Crit Rev Food Sci Nutr*. 2021;61(5):805–835. <https://doi.org/10.1080/10408398.2020.1746904>
- Allan AC, Espley RV. MYBs drive novel consumer traits in fruits and vegetables. *Trends Plant Sci*. 2018;23(8):693–705. <https://doi.org/10.1016/j.tplants.2018.06.001>
- Amato A, Cavallini E, Walker AR, Pezzotti M, Bliet M, Quattrocchio F, Koes R, Ruperti B, Bertini E, Zenoni S, et al. The MYB5-driven MBW complex recruits a WRKY factor to enhance the expression of targets involved in vacuolar hyper-acidification and trafficking in grapevine. *Plant J*. 2019;99(6):1220–1241. <https://doi.org/10.1111/tbj.14419>
- An JP, Qu FJ, Yao JF, Wang XN, You CX, Wang XF, Hao YJ. The bZIP transcription factor MdHY5 regulates anthocyanin accumulation and nitrate assimilation in apple. *Hortic Res*. 2017;4(1):17023. <https://doi.org/10.1038/hortres.2017.23>
- An JP, Wang XF, Li YY, Song LQ, Zhao LL, You CX, Hao YJ. EIN3-LIKE1, MYB1, and ETHYLENE RESPONSE FACTOR3 act in a regulatory loop that synergistically modulates ethylene biosynthesis and anthocyanin accumulation. *Plant Physiol*. 2018a;178(2):808–823. <https://doi.org/10.1104/pp.18.00068>
- An JP, Wang XF, Zhang XW, Bi SQ, You CX, Hao YJ. MdBBX22 regulates UV-B-induced anthocyanin biosynthesis through regulating the function of MdHY5 and is targeted by MdbT2 for 26S proteasome-mediated degradation. *Plant Biotechnol J*. 2019;17(12):2231–2233. <https://doi.org/10.1111/pbi.13196>
- An JP, Xu RR, Liu X, Zhang JC, Wang XF, You CX, Hao YJ. Jasmonate induces biosynthesis of anthocyanin and proanthocyanidin in apple by mediating the JAZ1-TRB1-MYB9 complex. *Plant J*. 2021b;106(5):1414–1430. <https://doi.org/10.1111/tbj.15245>
- An JP, Yao JF, Xu RR, You CX, Wang XF, Hao YJ. Apple bZIP transcription factor MdbZIP44 regulates abscisic acid-promoted anthocyanin accumulation. *Plant Cell Environ*. 2018b;41(11):2678–2692. <https://doi.org/10.1111/pce.13393>
- An JP, Zhang XW, Liu YJ, Wang XF, You CX, Hao YJ. ABI5 regulates ABA-induced anthocyanin biosynthesis by modulating the MYB1-bHLH3 complex in apple. *J Exp Bot*. 2021a;72(4):1460–1472. <https://doi.org/10.1093/jxb/eraa525>
- Bai L, Chen Q, Jiang L, Lin Y, Ye Y, Liu P, Wang X, Tang H. Comparative transcriptome analysis uncovers the regulatory functions of long noncoding RNAs in fruit development and color changes of *Fragaria pentaphylla*. *Hortic Res*. 2019a;6(1):42. <https://doi.org/10.1038/s41438-019-0128-4>
- Bai S, Tao R, Tang Y, Yin L, Ma Y, Ni J, Yan X, Yang Q, Wu Z, Zeng Y, et al. BBX16, a B-box protein, positively regulates light-induced anthocyanin accumulation by activating MYB10 in red pear. *Plant Biotechnol J*. 2019b;17(10):1985–1997. <https://doi.org/10.1111/pbi.13114>
- Bendokas V, Skemiene K, Trumbeckaite S, Stanys V, Passamonti S, Borutaite V, Liobikas J. Anthocyanins: from plant pigments to health benefits at mitochondrial level. *Crit Rev Food Sci Nutr*. 2020;60(19):3352–3365. <https://doi.org/10.1080/10408398.2019.1687421>
- Bertheloot J, Barbier F, Boudon F, Perez-Garcia MD, Péron T, Citerne S, Dun E, Beveridge C, Godin C, Sakr S. Sugar availability suppresses the auxin-induced strigolactone pathway to promote bud outgrowth. *New Phytol*. 2020;225(2):866–879. <https://doi.org/10.1111/nph.16201>
- Blanco-Touriñán N, Legris M, Minguet EG, Costigliolo-Rojas C, Nohales MA, Iniesto E, García-León M, Pacín M, Heucken N, Blomeier T, et al. COP1 destabilizes DELLA proteins in *Arabidopsis*. *Proc Natl Acad Sci USA*. 2020;117(24):13792–13799. <https://doi.org/10.1073/pnas.1907969117>
- Bursch K, Toledo-Ortiz G, Pireyre M, Lohr M, Braatz C, Johansson H. Identification of BBX proteins as rate-limiting cofactors of HY5. *Nat Plants*. 2020;6(8):921–928. <https://doi.org/10.1038/s41477-020-0725-0>

- Butelli E, Garcia-Lor A, Licciardello C, Las Casas G, Hill L, Recupero GR, Keremane ML, Ramadugu C, Krueger R, Xu Q, et al.** Changes in anthocyanin production during domestication of *Citrus*. *Plant Physiol*. 2017;**173**(4):2225–2242. <https://doi.org/10.1104/pp.16.01701>
- Butelli E, Licciardello C, Zhang Y, Liu J, Mackay S, Bailey P, Reforgiato-Recupero G, Martin C.** Retrotransposons control fruit-specific, cold-dependent accumulation of anthocyanins in blood oranges. *Plant Cell*. 2012;**24**(3):1242–1255. <https://doi.org/10.1105/tpc.111.095232>
- Cai H, Zhang M, Chai M, He Q, Huang X, Zhao L, Qin Y.** Epigenetic regulation of anthocyanin biosynthesis by an antagonistic interaction between H2A.Z and H3K4me3. *New Phytol*. 2019;**221**(1):295–308. <https://doi.org/10.1111/nph.15306>
- Castillejo C, Waurich V, Wagner H, Ramos R, Oiza N, Muñoz P, Triviño JC, Caruana J, Liu Z, Cobo N, et al.** Allelic variation of MYB10 is the major force controlling natural variation in skin and flesh color in strawberry (*Fragaria* spp.) fruit. *Plant Cell*. 2020;**32**(12):3723–3749. <https://doi.org/10.1105/tpc.20.00474>
- Catalá R, Medina J, Salinas J.** Integration of low temperature and light signaling during cold acclimation response in *Arabidopsis*. *Proc Natl Acad Sci USA*. 2011;**108**(39):16475–16480. <https://doi.org/10.1073/pnas.1107161108>
- Cavallini E, Matus JT, Finezzo L, Zenoni S, Loyola R, Guzzo F, Schlechter R, Ageorges A, Arce-Johnson P, Tornielli GB.** The phenylpropanoid pathway is controlled at different branches by a set of R2R3-MYB C2 repressors in grapevine. *Plant Physiol*. 2015;**167**(4):1448–1470. <https://doi.org/10.1104/pp.114.256172>
- Chagné D, Lin-Wang K, Espley RV, Volz RK, How NM, Rouse S, Brendolise C, Carlisle CM, Kumar S, De Silva N, et al.** An ancient duplication of apple MYB transcription factors is responsible for novel red fruit-flesh phenotypes. *Plant Physiol*. 2013;**161**(1):225–239. <https://doi.org/10.1104/pp.112.206771>
- Chen M, Gu H, Wang L, Shao Y, Li R, Li W.** Exogenous ethylene promotes peel color transformation by regulating the degradation of chlorophyll and synthesis of anthocyanin in postharvest mango fruit. *Front Nutr*. 2022a;**9**:11542. <https://doi.org/10.3389/fnut.2022.911542>
- Chen Y, Kim P, Kong L, Wang X, Tan W, Liu X, Chen Y, Yang J, Chen B, Song Y, et al.** A dual-function transcription factor, SJJAF13, promotes anthocyanin biosynthesis in tomato. *J Exp Bot*. 2022b;**73**(16):5559–5580. <https://doi.org/10.1093/jxb/erac209>
- Chico JM, Fernández-Barbero G, Chini A, Fernández-Calvo P, Díez-Díaz M, Solano R.** Repression of jasmonate-dependent defenses by shade involves differential regulation of protein stability of MYC transcription factors and their JAZ repressors in *Arabidopsis*. *Plant Cell*. 2014;**26**(5):1967–1980. <https://doi.org/10.1105/tpc.114.125047>
- Colanero S, Tagliani A, Perata P, Gonzali S.** Alternative splicing in the anthocyanin fruit gene encoding an R2R3 MYB transcription factor affects anthocyanin biosynthesis in tomato fruits. *Plant Commun*. 2019;**1**(1):100006. <https://doi.org/10.1016/j.xplc.2019.100006>
- Ding B, Patterson EL, Holalu SV, Li J, Johnson GA, Stanley LE, Greenlee AB, Peng F, Bradshaw HD, Blinov ML, et al.** Two MYB proteins in a self-organizing activator-inhibitor system produce spotted pigmentation patterns. *Curr Biol*. 2020;**30**(5):802–814. <https://doi.org/10.1016/j.cub.2019.12.067>
- Dirlewanger E, Graziano E, Joobeur T, Garriga-Caldere F, Cosson P, Howad W, Arus P.** Comparative mapping and marker-assisted selection in Rosaceae fruit crops. *Proc Natl Acad Sci USA*. 2004;**101**(26):9891–9896. <https://doi.org/10.1073/pnas.0307937101>
- El-Sharkawy I, Liang D, Xu K.** Transcriptome analysis of an apple yellow fruit somatic mutation identifies a gene network module highly associated with anthocyanin and epigenetic regulation. *J Exp Bot*. 2015;**66**(22):7359–7376. <https://doi.org/10.1093/jxb/erv433>
- Espley RV, Brendolise C, Chagné D, Kutty-Amma S, Green S, Volz R, Putterill J, Schouten HJ, Gardiner SE, Hellens RP, et al.** Multiple repeats of a promoter segment causes transcription factor autoregulation in red apples. *Plant Cell*. 2009;**21**(1):168–183. <https://doi.org/10.1105/tpc.108.059329>
- Fan D, Wang X, Tang X, Ye X, Ren S, Wang D, Luo K.** Histone H3K9 demethylase JM25 epigenetically modulates anthocyanin biosynthesis in poplar. *Plant J*. 2018;**96**(6):1121–1136. <https://doi.org/10.1111/tpl.14092>
- Fang H, Dong Y, Yue X, Hu J, Jiang S, Xu H, Wang Y, Su M, Zhang J, Zhang Z, et al.** The B-box zinc finger protein MdBBX20 integrates anthocyanin accumulation in response to ultraviolet radiation and low temperature. *Plant Cell Environ*. 2019;**42**(7):2090–2104. <https://doi.org/10.1111/pce.13552>
- Fang F, Zhang XL, Luo HH, Zhou JJ, Gong YH, Li WJ, Shi ZW, He Q, Wu Q, Li L, et al.** An intracellular laccase is responsible for epicatechin-mediated anthocyanin degradation in litchi fruit pericarp. *Plant Physiol*. 2015;**169**(4):2391–2408. <https://doi.org/10.1104/pp.15.00359>
- Farcuh M, Tajima H, Lerno LA, Blumwald E.** Changes in ethylene and sugar metabolism regulate flavonoid composition in climacteric and non-climacteric plums during postharvest storage. *Food Chem*. 2022;**4**:100075. <https://doi.org/10.1016/j.fochms.2022.100075>
- Fenn MA, Giovannoni JJ.** Phytohormones in fruit development and maturation. *Plant J*. 2021;**105**(2):446–458. <https://doi.org/10.1111/tpl.15112>
- Ferrero M, Pagliarani C, Novák O, Ferrandino A, Cardinale F, Visentin I, Schubert A.** Exogenous strigolactone interacts with abscisic acid-mediated accumulation of anthocyanins in grapevine berries. *J Exp Bot*. 2018;**69**(9):2391–2401. <https://doi.org/10.1093/jxb/ery033>
- Gangappa SN, Botto JF.** The multifaceted roles of HY5 in plant growth and development. *Mol Plant*. 2016;**9**(10):1353–1365. <https://doi.org/10.1016/j.molp.2016.07.002>
- Gao Q, Luo H, Li Y, Liu Z, Kang C.** Genetic modulation of RAP alters fruit coloration in both wild and cultivated strawberry. *Plant Biotechnol J*. 2020;**18**(7):1550–1561. <https://doi.org/10.1111/pbi.13317>
- Goetz M, Rabinovich M, Smith HM.** The role of auxin and sugar signaling in dominance inhibition of inflorescence growth by fruit load. *Plant Physiol*. 2021;**187**(3):1189–1201. <https://doi.org/10.1093/plphys/kiab237>
- Gou JY, Felippes FF, Liu CJ, Weigel D, Wang JW.** Negative regulation of anthocyanin biosynthesis in *Arabidopsis* by a miR156-targeted SPL transcription factor. *Plant Cell*. 2011;**23**(4):1512–1522. <https://doi.org/10.1105/tpc.111.084525>
- Guout JC, Smith JP, Holzapfel BP, Walker AR, Barril C.** Grape berry flavonoids: a review of their biochemical responses to high and extreme high temperatures. *J Exp Bot*. 2019;**70**(2):397–423. <https://doi.org/10.1093/jxb/ery392>
- Han Y, Vimolmangkang S, Soria-Guerra RE, Korban SS.** Introduction of apple ANR genes into tobacco inhibits expression of both *CHI* and *DFR* genes in flowers, leading to loss of anthocyanin. *J Exp Bot*. 2012;**63**(7):2437–2447. <https://doi.org/10.1093/jxb/err415>
- He M, Kong X, Jiang Y, Qu H, Zhu H.** MicroRNAs: emerging regulators in horticultural crops. *Trends Plant Sci*. 2022;**27**(9):936–951. <https://doi.org/10.1016/j.tplants.2022.03.011>
- Henry-Kirk RA, Plunkett B, Hall M, McGhie T, Allan AC, Wargent JJ, Espley RV.** Solar UV light regulates flavonoid metabolism in apple. *Plant Cell Environ*. 2018;**41**(3):675–688. <https://doi.org/10.1111/pce.13125>
- Hichri I, Barriue F, Bogs J, Kappel C, Delrot S, Lauvergeat V.** Recent advances in the transcriptional regulation of the flavonoid biosynthetic pathway. *J Exp Bot*. 2011;**62**(8):2465–2483. <https://doi.org/10.1093/jxb/erq442>
- Hu Y, Cheng H, Zhang Y, Zhang J, Niu S, Wang X, Li W, Zhang J, Yao Y.** The MdMYB16/MdMYB1-miR7125-MdCCR module regulates the homeostasis between anthocyanin and lignin biosynthesis during light induction in apple. *New Phytol*. 2021;**231**(3):1105–1122. <https://doi.org/10.1111/nph.17431>

- Hu Y, Han Z, Wang T, Li H, Li Q, Wang S, Tian J, Wang Y, Zhang X, Xu X, et al.** Ethylene response factor MdERF4 and histone deacetylase MdHDA19 suppress apple fruit ripening through histone deacetylation of ripening-related genes. *Plant Physiol.* 2022;**188**(4):2166–2181. <https://doi.org/10.1093/plphys/kiac016>
- Hu DG, Sun CH, Ma QJ, You CX, Cheng L, Hao YJ.** MdMYB1 regulates anthocyanin and malate accumulation by directly facilitating their transport into vacuoles in apples. *Plant Physiol.* 2016b;**170**(3):1315–1330. <https://doi.org/10.1104/pp.15.01333>
- Hu DG, Sun CH, Zhang QY, An JP, You CX, Hao YJ.** Glucose sensor MdHXK1 phosphorylates and stabilizes MdbHLH3 to promote anthocyanin biosynthesis in apple. *PLoS Genet.* 2016a;**12**(8):e1006273. <https://doi.org/10.1371/journal.pgen.1006273>
- Hu DG, Yu JQ, Han PL, Xie XB, Sun CH, Zhang QY, Wang JH, Hao YJ.** The regulatory module MdPUB29-MdbHLH3 connects ethylene biosynthesis with fruit quality in apple. *New Phytol.* 2019;**221**(4):1966–1982. <https://doi.org/10.1111/nph.15511>
- Huang D, Wang X, Tang Z, Yuan Y, Xu Y, He J, Jiang X, Peng SA, Li L, Butelli E, et al.** Subfunctionalization of the *Ruby2-Ruby1* gene cluster during the domestication of citrus. *Nat Plants.* 2018;**4**(11):930–941. <https://doi.org/10.1038/s41477-018-0287-6>
- Huang D, Yuan Y, Tang Z, Huang Y, Kang C, Deng X, Xu Q.** Retrotransposon promoter of *Ruby1* controls both light- and cold-induced accumulation of anthocyanins in blood orange. *Plant Cell Environ.* 2019;**42**(11):3092–3104. <https://doi.org/10.1111/pce.13609>
- Jaakola L.** New insights into the regulation of anthocyanin biosynthesis in fruits. *Trends Plant Sci.* 2013;**18**(9):477–483. <https://doi.org/10.1016/j.tplants.2013.06.003>
- Jaakola L, Poole M, Jones MO, Kämäräinen-Karppinen T, Koskimäki JJ, Hohtola A, Häggman H, Fraser PD, Manning K, King GJ, et al.** A SQUAMOSA MADS box gene involved in the regulation of anthocyanin accumulation in bilberry fruits. *Plant Physiol.* 2010;**153**(4):1619–1629. <https://doi.org/10.1104/pp.110.158279>
- Jeong SW, Das PK, Jeoung SC, Song JY, Lee HK, Kim YK, Kim WJ, Park YI, Yoo SD, Choi SB, et al.** Ethylene suppression of sugar-induced anthocyanin pigmentation in *Arabidopsis*. *Plant Physiol.* 2010;**154**(3):1514–1531. <https://doi.org/10.1104/pp.110.161869>
- Jia HF, Chai YM, Li CL, Lu D, Luo JJ, Qin L, Shen YY.** Abscisic acid plays an important role in the regulation of strawberry fruit ripening. *Plant Physiol.* 2011;**157**(1):188–199. <https://doi.org/10.1104/pp.111.177311>
- Jia H, Jiu S, Zhang C, Wang C, Tariq P, Liu Z, Wang B, Cui L, Fang J.** Abscisic acid and sucrose regulate tomato and strawberry fruit ripening through the abscisic acid-stress-ripening transcription factor. *Plant Biotechnol J.* 2016;**14**(10):2045–2065. <https://doi.org/10.1111/pbi.12563>
- Ji Y, Qu Y, Jiang Z, Yan J, Chu J, Xu M, Su X, Yuan H, Wang A.** The mechanism for brassinosteroids suppressing climacteric fruit ripening. *Plant Physiol.* 2021;**185**(4):1875–1893. <https://doi.org/10.1093/plphys/kiab013>
- Jia X, Shen J, Liu H, Li F, Ding N, Gao C, Pattanaik S, Patra B, Li R, Yuan L.** Small tandem target mimic-mediated blockage of microRNA858 induces anthocyanin accumulation in tomato. *Planta.* 2015;**242**(1):283–293. <https://doi.org/10.1007/s00425-015-2305-5>
- Jia HF, Xie ZQ, Wang C, Shangguan LF, Qian N, Cui MJ, Liu ZJ, Zheng T, Wang MQ, Fang JG.** Abscisic acid, sucrose, and auxin coordinately regulate berry ripening process of the Fujiminori grape. *Funct Integr Genomics.* 2017;**17**(4):441–457. <https://doi.org/10.1007/s10142-017-0546-z>
- Ji XH, Zhang R, Wang N, Yang L, Chen XS.** Transcriptome profiling reveals auxin suppressed anthocyanin biosynthesis in red-fleshed apple callus (*Malus sieversii* f. *niedzwetzkyana*). *Plant Cell Tissue Organ Cult.* 2015;**123**(2):389–404. <https://doi.org/10.1007/s11240-015-0843-y>
- Jiang S, Wang N, Chen M, Zhang R, Sun Q, Xu H, Zhang Z, Wang Y, Sui X, Wang S, et al.** Methylation of MdMYB1 locus mediated by RdDM pathway regulates anthocyanin biosynthesis in apple. *Plant Biotechnol J.* 2020;**18**(8):1736–1748. <https://doi.org/10.1111/pbi.13337>
- Jiang H, Zhou LJ, Gao HN, Wang XF, Li ZW, Li YY.** The transcription factor MdMYB2 influences cold tolerance and anthocyanin accumulation by activating SUMO E3 ligase MdSIZ1 in apple. *Plant Physiol.* 2022;**189**(4):2044–2060. <https://doi.org/10.1093/plphys/kiac211>
- Jiu S, Guan L, Leng X, Zhang K, Haider MS, Yu X, Zhu X, Zheng T, Ge M, Wang C, et al.** The role of VvMYBA2r and VvMYBA2w alleles of the MYBA2 locus in the regulation of anthocyanin biosynthesis for molecular breeding of grape (*Vitis* spp.) skin coloration. *Plant Biotechnol J.* 2021;**19**(6):1216–1239. <https://doi.org/10.1111/pbi.13543>
- Ju Y, Liu B, Xu X, Wu J, Sun W, Fang Y.** Targeted metabolomic and transcript level analysis reveals the effects of exogenous strigolactone and methyl jasmonate on grape quality. *Sci Hortic.* 2022;**299**:111009. <https://doi.org/10.1016/j.scienta.2022.111009>
- Kadomura-Ishikawa Y, Miyawaki K, Takahashi A, Masuda T, Noji S.** Light and abscisic acid independently regulated FaMYB10 in *Fragaria × ananassa* fruit. *Planta.* 2015;**241**(4):953–965. <https://doi.org/10.1007/s00425-014-2228-6>
- Kallam K, Appelhagen I, Luo J, Albert N, Zhang H, Deroles S, Hill L, Findlay K, Andersen M, Davies K, et al.** Aromatic decoration determines the formation of anthocyanic vacuolar inclusions. *Curr Biol.* 2017;**27**(7):945–957. <https://doi.org/10.1016/j.cub.2017.02.027>
- Karppinen K, Lafferty DJ, Albert NW, Mikkola N, McGhie T, Allan AC, Afzal BM, Häggman H, Espley RV, Jaakola L.** MYBA And MYBPA transcription factors co-regulate anthocyanin biosynthesis in blue-coloured berries. *New Phytol.* 2021;**232**(3):1350–1367. <https://doi.org/10.1111/nph.17669>
- Kim B, Jeong YJ, Corvalán C, Fujioka S, Cho S, Park T, Choe S.** Darkness and gulliver2/phyB mutation decrease the abundance of phosphorylated BZR1 to activate brassinosteroid signaling in *Arabidopsis*. *Plant J.* 2014;**77**(5):737–747. <https://doi.org/10.1111/tj.12423>
- Kim EJ, Russinova E.** Brassinosteroid signalling. *Curr Biol.* 2020;**30**(7):R294–R298. <https://doi.org/10.1016/j.cub.2020.02.011>
- Lackman P, González-Guzmán M, Tilleman S, Carqueijeiro I, Pérez AC, Moses T, Seo M, Kanno Y, Häkkinen ST, Van Montagu MC, et al.** Jasmonate signaling involves the abscisic acid receptor PYL4 to regulate metabolic reprogramming in *Arabidopsis* and tobacco. *Proc Natl Acad Sci USA.* 2011;**108**(14):5891–5896. <https://doi.org/10.1073/pnas.1103010108>
- Lafferty DJ, Espley RV, Deng CH, Günther CS, Plunkett B, Turner JL, Jaakola L, Karppinen K, Allan AC, Albert NW.** Hierarchical regulation of MYBPA1 by anthocyanin- and proanthocyanidin-related MYB proteins is conserved in Vaccinium species. *J Exp Bot.* 2022;**73**(5):1344–1356. <https://doi.org/10.1093/jxb/erab460>
- LaFountain AM, Yuan YW.** Repressors of anthocyanin biosynthesis. *New Phytol.* 2021;**231**(3):933–949. <https://doi.org/10.1111/nph.17397>
- Lai B, Li XJ, Hu B, Qin YH, Huang XM, Wang HC, Hu GB.** LcMYB1 is a key determinant of differential anthocyanin accumulation among genotypes, tissues, developmental phases and ABA and light stimuli in *Litchi chinensis*. *PLoS One.* 2014;**9**(1):e86293. <https://doi.org/10.1371/journal.pone.0086293>
- Landi M, Tattini M, Gould KS.** Multiple functional roles of anthocyanins in plant-environment interactions. *Environ Exp Bot.* 2015;**119**:4–17. <https://doi.org/10.1016/j.envexpbot.2015.05.012>
- Li QF, He JX.** BZR1 Interacts with HY5 to mediate brassinosteroid- and light-regulated cotyledon opening in *Arabidopsis* in darkness. *Mol Plant.* 2016;**9**(1):113–125. <https://doi.org/10.1016/j.molp.2015.08.014>
- Li X, Hou Y, Xie X, Li H, Li X, Zhu Y, Zhai L, Zhang C, Bian S.** A blueberry MIR156a-SPL12 module coordinates the accumulation of chlorophylls and anthocyanins during fruit ripening. *J Exp Bot.* 2020c;**71**(19):5976–5989. <https://doi.org/10.1093/jxb/eraa327>

- Li YY, Mao K, Zhao C, Zhao XY, Zhang HL, Shu HR, Hao YJ. MdCOP1 ubiquitin E3 ligases interact with MdMYB1 to regulate light-induced anthocyanin biosynthesis and red fruit coloration in apple. *Plant Physiol.* 2012;160(2):1011–1022. <https://doi.org/10.1104/pp.112.199703>
- Li D, Mou W, Xia R, Li L, Zawora C, Ying T, Mao L, Liu Z, Luo Z. Integrated analysis of high-throughput sequencing data shows abscisic acid-responsive genes and miRNAs in strawberry receptacle fruit ripening. *Hortic Res.* 2019;6(1):26. <https://doi.org/10.1038/s41438-018-0100-8>
- Li C, Pei J, Yan X, Cui X, Tsuruta M, Liu Y, Lian C. A poplar B-box protein PtrBBX23 modulates the accumulation of anthocyanins and proanthocyanidins in response to high light. *Plant Cell Environ.* 2021;44(9):3015–3033. <https://doi.org/10.1111/pce.14127>
- Li C, Shi L, Wang Y, Li W, Chen B, Zhu L, Fu Y. *Arabidopsis* ECAP is a new adaptor protein that connects JAZ repressors with the TPR2 co-repressor to suppress jasmonate-responsive anthocyanin accumulation. *Mol Plant.* 2020d;13(2):246–265. <https://doi.org/10.1016/j.molp.2019.10.014>
- Li J, Terzaghi W, Gong Y, Li C, Ling JJ, Fan Y, Qin N, Gong X, Zhu D, Deng XW. Modulation of BIN2 kinase activity by HY5 controls hypocotyl elongation in the light. *Nat Commun.* 2020e;11(1):1592. <https://doi.org/10.1038/s41467-020-15394-7>
- Li Y, Van den Ende W, Rolland F. Sucrose induction of anthocyanin biosynthesis is mediated by DELLA. *Mol Plant.* 2014;7(3):570–572. <https://doi.org/10.1093/mp/sst161>
- Li S, Wang W, Gao J, Yin K, Wang R, Wang C, Petersen M, Mundy J, Qiu JL. MYB75 phosphorylation by MPK4 is required for light-induced anthocyanin accumulation in *Arabidopsis*. *Plant Cell.* 2016;28(11):2866–2883. <https://doi.org/10.1105/tpc.16.00130>
- Li C, Wu J, Hu KD, Wei SW, Sun HY, Hu LY, Han Z, Yao GF, Zhang H. PyWRKY26 and PylHLH3 cotargeted the PyMYB114 promoter to regulate anthocyanin biosynthesis and transport in red-skinned pears. *Hortic Res.* 2020b;7(1):37. <https://doi.org/10.1038/s41438-020-0254-z>
- Li H, Yang Z, Zeng Q, Wang S, Luo Y, Huang Y, Xin Y, He N. Abnormal expression of bHLH3 disrupts a flavonoid homeostasis network, causing differences in pigment composition among mulberry fruits. *Hortic Res.* 2020a;7(1):83. <https://doi.org/10.1038/s41438-020-0302-8>
- Liang T, Shi C, Peng Y, Tan H, Xin P, Yang Y, Wang F, Li X, Chu J, Huang J, et al. Brassinosteroid-activated BRI1-EMS-SUPPRESSOR 1 inhibits flavonoid biosynthesis and coordinates growth and UV-B stress responses in plants. *Plant Cell.* 2020;32(10):3224–3239. <https://doi.org/10.1105/tpc.20.00048>
- Lin-Wang K, Bolitho K, Grafton K, Kortstee A, Karunairetnam S, McGhie TK, Espley RV, Hellens RP, Allan AC. An R2R3 MYB transcription factor associated with regulation of the anthocyanin biosynthetic pathway in *Rosaceae*. *BMC Plant Biol.* 2010;10(1):50. <https://doi.org/10.1186/1471-2229-10-50>
- Lin-Wang K, Micheletti D, Palmer J, Volz R, Lozano L, Espley R, Hellens RP, Chagnè D, Rowan DD, Troglio M, et al. High temperature reduces apple fruit colour via modulation of the anthocyanin regulatory complex. *Plant Cell Environ.* 2011;34(7):1176–1190. <https://doi.org/10.1111/j.1365-3040.2011.02316.x>
- Liu XJ, An XH, Liu X, Hu DG, Wang XF, You CX, Hao YJ. MdSnRK1.1 interacts with MdJAZ18 to regulate sucrose-induced anthocyanin and proanthocyanidin accumulation in apple. *J Exp Bot.* 2017;68(11):2977–2990. <https://doi.org/10.1093/jxb/erx150>
- Liu Y, Lin-Wang K, Espley RV, Wang L, Li Y, Liu Z, Zhou P, Zeng L, Zhang X, Zhang J, et al. StMYB44 negatively regulates anthocyanin biosynthesis at high temperatures in tuber flesh of potato. *J Exp Bot.* 2019;70(15):3809–3824. <https://doi.org/10.1093/jxb/erz194>
- Liu J, Osbourn A, Ma P. MYB transcription factors as regulators of phenylpropanoid metabolism in plants. *Mol Plant.* 2015;8(5):689–708. <https://doi.org/10.1016/j.molp.2015.03.012>
- Liu B, Zhang Y, Wang S, Wang W, Xu X, Wu J, Fang Y, Ju Y. Effects of strigolactone and abscisic acid on the quality and antioxidant activity of grapes (*Vitis vinifera* L.) and wines. *Food Chem X.* 2022;16:100496. <https://doi.org/10.1016/j.fochx.2022.100496>
- Liu Y, Zhou B, Qi Y, Liu C, Liu Z, Ren X. Biochemical and functional characterization of AcJFGT3a, a galactosyltransferase involved in anthocyanin biosynthesis in the red-fleshed kiwifruit (*Actinidia chinensis*). *Physiol Plant.* 2018;162(4):409–426. <https://doi.org/10.1111/ppl.12655>
- Lu Z, Cao H, Pan L, Niu L, Wei B, Cui G, Wang L, Yao JL, Zeng W, Wang Z. Two loss-of-function alleles of the glutathione S-transferase (GST) gene cause anthocyanin deficiency in flower and fruit skin of peach (*Prunus persica*). *Plant J.* 2021;107(5):1320–1331. <https://doi.org/10.1111/tpj.15312>
- Lü P, Yu S, Zhu N, Chen YR, Zhou B, Pan Y, Tzeng D, Fabi JP, Argyris J, Garcia-Mas J, et al. Genome encode analyses reveal the basis of convergent evolution of fleshy fruit ripening. *Nat Plants.* 2018;4(10):784–791. <https://doi.org/10.1038/s41477-018-0249-z>
- Ma D, Constabel CP. MYB repressors as regulators of phenylpropanoid metabolism in plants. *Trends Plant Sci.* 2019;24(3):275–289. <https://doi.org/10.1016/j.tplants.2018.12.003>
- Ma H, Yang T, Li Y, Zhang J, Wu T, Song T, Yao Y, Tian J. The long noncoding RNA MdLNC499 bridges MdWRKY1 and MdERF109 function to regulate early-stage light-induced anthocyanin accumulation in apple fruit. *Plant Cell.* 2021;33(10):3309–3330. <https://doi.org/10.1093/plcell/koab188>
- Maloney GS, DiNapoli KT, Muday GK. The anthocyanin reduced tomato mutant demonstrates the role of flavonols in tomato lateral root and root hair development. *Plant Physiol.* 2014;166(2):614–631. <https://doi.org/10.1104/pp.114.240507>
- Mao W, Han Y, Chen Y, Sun M, Feng Q, Li L, Liu L, Zhang K, Wei L, Han Z, et al. Low temperature inhibits anthocyanin accumulation in strawberry fruit by activating FvMAPK3-induced phosphorylation of FvMYB10 and degradation of chalcone synthase 1. *Plant Cell.* 2022;34(4):1226–1249. <https://doi.org/10.1093/plcell/koac006>
- Martín-Pizarro C, Vallarino JG, Osorio S, Meco V, Urrutia M, Pillet J, Casañal A, Merchante C, Amaya I, Willmitzer L, et al. The NAC transcription factor FaRIF controls fruit ripening in strawberry. *Plant Cell.* 2021;33(5):1574–1593. <https://doi.org/10.1093/plcell/koab070>
- Mashiguchi K, Seto Y, Yamaguchi S. Strigolactone biosynthesis, transport and perception. *Plant J.* 2021;105(2):335–350. <https://doi.org/10.1111/tpj.15059>
- Matthes MS, Best NB, Robil JM, Malcomber S, Gallavotti A, McSteen P. Auxin evodevo: conservation and diversification of genes regulating auxin biosynthesis, transport, and signaling. *Mol Plant.* 2019;12(3):298–320. <https://doi.org/10.1016/j.molp.2018.12.012>
- Medina-Puche L, Cumplido-Laso G, Amil-Ruiz F, Hoffmann T, Ring L, Rodríguez-Franco A, Caballero JL, Schwab W, Muñoz-Blanco J, Blanco-Portales R. MYB10 plays a major role in the regulation of flavonoid/phenylpropanoid metabolism during ripening of *Fragaria × ananassa* fruits. *J Exp Bot.* 2014;65(2):401–417. <https://doi.org/10.1093/jxb/ert377>
- Moro L, Hassimotto N, Purgatto E. Postharvest auxin and methyl jasmonate effect on anthocyanin biosynthesis in red raspberry (*Rubus idaeus* L.). *J Plant Growth Regul.* 2017;36(3):773–782. <https://doi.org/10.1007/s00344-017-9682-x>
- Movahed N, Pastore C, Cellini A, Allegro G, Valentini G, Zenoni S, Cavallini E, D'Inca E, Tornielli GB, Filippetti I. The grapevine VviPrx31 peroxidase as a candidate gene involved in anthocyanin degradation in ripening berries under high temperature. *J Plant Res.* 2016;129(3):513–526. <https://doi.org/10.1007/s10265-016-0786-3>
- Ni J, Premathilake AT, Gao Y, Yu W, Tao R, Teng Y, Bai S. Ethylene-activated PpERF105 induces the expression of the repressor-type R2R3-MYB gene PpMYB140 to inhibit anthocyanin biosynthesis in red pear fruit. *Plant J.* 2021;105(1):167–181. <https://doi.org/10.1111/tpj.15049>
- Niu J, Zhang G, Zhang W, Goltsev V, Sun S, Wang J, Li P, Ma F. Anthocyanin concentration depends on the counterbalance between its synthesis and degradation in plum fruit at high temperature. *Sci Rep.* 2017;7(1):7684. <https://doi.org/10.1038/s41598-017-07896-0>

- Oblessuc PR, Obulareddy N, DeMott L, Mاتيوللي CC, Thompson BK, Melotto M.** JAZ4 is involved in plant defense, growth, and development in *Arabidopsis*. *Plant J.* 2020;**101**(2):371–383. <https://doi.org/10.1111/tpj.14548>
- Oh HD, Yu DJ, Chung SW, Chea S, Lee HJ.** Abscisic acid stimulates anthocyanin accumulation in 'jersey' highbush blueberry fruits during ripening. *Food Chem.* 2018;**244**:403–407. <https://doi.org/10.1016/j.foodchem.2017.10.051>
- Park YJ, Lee HJ, Ha JH, Kim JY, Park CM.** COP1 conveys warm temperature information to hypocotyl thermomorphogenesis. *New Phytol.* 2017;**215**(1):269–280. <https://doi.org/10.1111/nph.14581>
- Peng Z, Han C, Yuan L, Zhang K, Huang H, Ren C.** Brassinosteroid enhances jasmonate-induced anthocyanin accumulation in *Arabidopsis* seedlings. *J Integr Plant Biol.* 2011;**53**(8):632–640. <https://doi.org/10.1111/j.1744-7909.2011.01042.x>
- Perea-Resa C, Rodríguez-Milla MA, Iniesto E, Rubio V, Salinas J.** Prefoldins negatively regulate cold acclimation in *Arabidopsis thaliana* by promoting nuclear proteasome-mediated HY5 degradation. *Mol Plant.* 2017;**10**(6):791–804. <https://doi.org/10.1016/j.molp.2017.03.012>
- Plant AR, Larrieu A, Causier B.** Repressor for hire! the vital roles of TOPLESS-mediated transcriptional repression in plants. *New Phytol.* 2021;**231**(3):963–973. <https://doi.org/10.1111/nph.17428>
- Qi T, Song S, Ren Q, Wu D, Huang H, Chen Y, Fan M, Peng W, Ren C, Xie D.** The jasmonate-ZIM-domain proteins interact with the WD-repeat/bHLH/MYB complexes to regulate jasmonate-mediated anthocyanin accumulation and trichome initiation in *Arabidopsis thaliana*. *Plant Cell.* 2011;**23**(5):1795–1814. <https://doi.org/10.1105/tpc.111.083261>
- Rowan DD, Cao M, Lin-Wang K, Cooney JM, Jensen DJ, Austin PT, Hunt MB, Norling C, Hellens RP, Schaffer RJ, et al.** Environmental regulation of leaf colour in red 35S:AP1 *Arabidopsis thaliana*. *New Phytol.* 2009;**182**(1):102–115. <https://doi.org/10.1111/j.1469-8137.2008.02737.x>
- Samkumar A, Jones D, Karppinen K, Dare AP, Sipari N, Espley RV, Martinussen I, Jaakola L.** Red and blue light treatments of ripening bilberry fruits reveal differences in signalling through abscisic acid-regulated anthocyanin biosynthesis. *Plant Cell Environ.* 2021;**44**(10):3227–3245. <https://doi.org/10.1111/pce.14158>
- Seto Y, Yasui R, Kameoka H, Tamiru M, Cao M, Terauchi R, Sakurada A, Hirano R, Kisugi T, Hanada A, et al.** Strigolactone perception and deactivation by a hydrolase receptor DWARF14. *Nat Commun.* 2019;**10**(1):191. <https://doi.org/10.1038/s41467-018-08124-7>
- Shen X, Zhao K, Liu L, Zhang K, Yuan H, Liao X, Wang Q, Guo X, Li F, Li T.** A role for PacMYBA in ABA-regulated anthocyanin biosynthesis in red-colored sweet cherry cv. Hong Deng. *Plant Cell Physiol.* 2014;**55**(5):862–880. <https://doi.org/10.1093/pcp/pcu013>
- Sicilia A, Scialò E, Puglisi I, Lo Piero AR.** Anthocyanin biosynthesis and DNA methylation dynamics in sweet orange fruit under cold stress. *J Agric Food Chem.* 2020;**68**(26):7024–7031. <https://doi.org/10.1021/acs.jafc.0c02360>
- Solfanelli C, Poggi A, Loreti E, Alpi A, Perata P.** Sucrose-specific induction of the anthocyanin biosynthetic pathway in *Arabidopsis*. *Plant Physiol.* 2006;**140**(2):637–646. <https://doi.org/10.1104/pp.105.072579>
- Song S, Liu B, Song J, Pang S, Song T, Gao S, Zhang Y, Huang H, Qi T.** A molecular framework for signaling crosstalk between jasmonate and ethylene in anthocyanin biosynthesis, trichome development, and defenses against insect herbivores in *Arabidopsis*. *J Integr Plant Biol.* 2022;**64**(9):1770–1788. <https://doi.org/10.1111/jipb.13319>
- Sun C, Deng L, Du M, Zhao J, Chen Q, Huang T, Jiang H, Li CB, Li C.** A transcriptional network promotes anthocyanin biosynthesis in tomato flesh. *Mol Plant.* 2020;**13**(1):42–58. <https://doi.org/10.1016/j.molp.2019.10.010>
- Tang J, Chu C.** Strigolactone signaling: repressor proteins are transcription factors. *Trends Plant Sci.* 2020;**25**(10):960–963. <https://doi.org/10.1016/j.tplants.2020.07.002>
- Tang Y, Qu Z, Lei J, He R, Adelson DL, Zhu Y, Yang Z, Wang D.** The long noncoding RNA FRILAIR regulates strawberry fruit ripening by functioning as a noncanonical target mimic. *PLoS Genet.* 2021;**17**(3):e1009461. <https://doi.org/10.1371/journal.pgen.1009461>
- Tao R, Bai S, Ni J, Yang Q, Zhao Y, Teng Y.** The blue light signal transduction pathway is involved in anthocyanin accumulation in 'Red Zaosu' pear. *Planta.* 2018;**248**(1):37–48. <https://doi.org/10.1007/s00425-018-2877-y>
- Tao R, Yu W, Gao Y, Ni J, Yin L, Zhang X, Li H, Wang D, Bai S, Teng Y.** Light-induced basic/helix-loop-helix64 enhances anthocyanin biosynthesis and undergoes CONSTITUTIVELY PHOTOMORPHOGENIC1-mediated degradation in pear. *Plant Physiol.* 2020;**184**(4):1684–1701. <https://doi.org/10.1104/pp.20.01188>
- Telias A, Lin-Wang K, Stevenson DE, Cooney JM, Hellens RP, Allan AC, Hoover EE, Bradeen JM.** Apple skin patterning is associated with differential expression of MYB10. *BMC Plant Biol.* 2011;**11**(1):93. <https://doi.org/10.1186/1471-2229-11-93>
- Thines B, Katsir L, Melotto M, Niu Y, Mandaokar A, Liu G, Nomura K, He SY, Howe GA, Browse J.** JAZ Repressor proteins are targets of the SCF(COI1) complex during jasmonate signalling. *Nature.* 2007;**448**(7154):661–665. <https://doi.org/10.1038/nature05960>
- Tirumalai V, Swetha C, Nair A, Pandit A, Shivaprasad PV.** Mir828 and miR858 regulate VvMYB114 to promote anthocyanin and flavonol accumulation in grapes. *J Exp Bot.* 2019;**70**(18):4775–4792. <https://doi.org/10.1093/jxb/erz264>
- Vergara A, Torrealba M, Alcalde JA, Pérez-Donoso AG.** Commercial brassinosteroid increases the concentration of anthocyanin in red table grape cultivars (*Vitis vinifera* L.). *Aust J Grape Wine Res.* 2020;**26**(4):427–433. <https://doi.org/10.1111/ajgw.12457>
- Wang X, Chen X, Luo S, Ma W, Li N, Zhang W, Tikunov Y, Xuan S, Zhao J, Wang Y, et al.** Discovery of a DFR gene that controls anthocyanin accumulation in the spiny *Solanum* group: roles of a natural promoter variant and alternative splicing. *Plant J.* 2022a;**111**(4):1096–1109. <https://doi.org/10.1111/tpj.15877>
- Wang P, Ge M, Yu A, Song W, Fang J, Leng X.** Effects of ethylene on berry ripening and anthocyanin accumulation of 'fujiminori' grape in protected cultivation. *J Sci Food Agric.* 2022d;**102**(3):1124–1136. <https://doi.org/10.1002/jsfa.11449>
- Wang F, Han T, Song Q, Ye W, Song X, Chu J, Li J, Chen ZJ.** The rice circadian clock regulates tiller growth and panicle development through strigolactone signaling and sugar sensing. *Plant Cell.* 2020d;**32**(10):3124–3138. <https://doi.org/10.1105/tpc.20.00289>
- Wang S, Li LX, Fang Y, Li D, Mao Z, Zhu Z, Chen XS, Feng SQ.** MdERF1B-MdMYC2 module integrates ethylene and jasmonic acid to regulate the biosynthesis of anthocyanin in apple. *Hortic Res.* 2022f;**9**:uhac142. <https://doi.org/10.1093/hr/uhac142>
- Wang S, Li LX, Zhang Z, Fang Y, Li D, Chen XS, Feng SQ.** Ethylene precisely regulates anthocyanin synthesis in apple via a module comprising MdEIL1, MdMYB1, and MdMYB17. *Hortic Res.* 2022e;**9**:uhac034. <https://doi.org/10.1093/hr/uhac034>
- Wang Y, Liu W, Jiang H, Mao Z, Wang N, Jiang S, Xu H, Yang G, Zhang Z, Chen X.** The R2R3-MYB transcription factor MdMYB24-like is involved in methyl jasmonate-induced anthocyanin biosynthesis in apple. *Plant Physiol Biochem.* 2019;**139**:273–282. <https://doi.org/10.1016/j.plaphy.2019.03.031>
- Wang Y, Mao Z, Jiang H, Zhang Z, Wang N, Chen X.** Brassinolide inhibits flavonoid biosynthesis and red-flesh coloration via the MdBEH2.2-MdMYB60 complex in apple. *J Exp Bot.* 2021c;**72**(18):6382–6399. <https://doi.org/10.1093/jxb/erab284>
- Wang Z, Meng D, Wang A, Li T, Jiang S, Cong P, Li T.** The methylation of the PcMYB10 promoter is associated with green-skinned sport in max red Bartlett pear. *Plant Physiol.* 2013;**162**(2):885–896. <https://doi.org/10.1104/pp.113.214700>
- Wang WQ, Moss SMA, Zeng L, Espley RV, Wang T, Lin-Wang K, Fu BL, Schwinn KE, Allan AC, Yin XR.** The red flesh of kiwifruit is differentially controlled by specific activation–repression systems. *New Phytol.* 2022c;**235**(2):630–645. <https://doi.org/10.1111/nph.18122>

- Wang SY, Shi XC, Liu FQ, Laborda P. Effects of exogenous methyl jasmonate on quality and preservation of postharvest fruits: a review. *Food Chem.* 2021b;353:129482. <https://doi.org/10.1016/j.foodchem.2021.129482>
- Wang S, Shi M, Zhang Y, Pan Z, Xie X, Zhang L, Sun P, Feng H, Xue H, Fang C, et al. The R2R3-MYB transcription factor FaMYB63 participates in regulation of eugenol production in strawberry. *Plant Physiol.* 2022b;188(4):2146–2165. <https://doi.org/10.1093/plphys/kiac014>
- Wang W, Wang P, Li X, Wang Y, Tian S, Qin G. The transcription factor SlHY5 regulates the ripening of tomato fruit at both the transcriptional and translational levels. *Hortic Res.* 2021a;8(1):83. <https://doi.org/10.1038/s41438-021-00523-0>
- Wang S, Wang T, Li Q, Xu C, Tian J, Wang Y, Zhang X, Xu X, Han Z, Wu T. Phosphorylation of MdERF17 by MdMPK4 promotes apple fruit peel degreening during light/dark transitions. *Plant Cell.* 2022g;34(5):1980–2000. <https://doi.org/10.1093/plcell/koac049>
- Wang Y, Wang Y, Song Z, Zhang H. Repression of MYBL2 by both microRNA858a and HYS leads to the activation of anthocyanin biosynthetic pathway in *Arabidopsis*. *Mol Plant.* 2016;9(10):1395–1405. <https://doi.org/10.1016/j.molp.2016.07.003>
- Wang YC, Wang N, Xu HF, Jiang SH, Fang HC, Su MY, Zhang ZY, Zhang TL, Chen XS. Auxin regulates anthocyanin biosynthesis through the aux/IAA-ARF signaling pathway in apple. *Hortic Res.* 2018;5(1):59. <https://doi.org/10.1038/s41438-018-0068-4>
- Wang L, Wang B, Yu H, Guo H, Lin T, Kou L, Wang A, Shao N, Ma H, Xiong G, et al. Transcriptional regulation of strigolactone signalling in *Arabidopsis*. *Nature.* 2020c;583(7815):277–281. <https://doi.org/10.1038/s41586-020-2382-x>
- Wang Y, Zhu Y, Jiang H, Mao Z, Zhang J, Fang H, Liu W, Zhang Z, Chen X, Wang N. The regulatory module MdBZR1-MdCOL6 mediates brassinosteroid- and light-regulated anthocyanin synthesis in apple. *New Phytol.* 2023:online. <https://doi.org/10.1111/nph.18779>
- Wu LB, Eom JS, Isoda R, Li C, Char SN, Luo D, Schepler-Luu V, Nakamura M, Yang B, Frommer WB. OsSWEET11b, a potential sixth leaf blight susceptibility gene involved in sugar transport-dependent male fertility. *New Phytol.* 2022;234(3):975–989. <https://doi.org/10.1111/nph.18054>
- Xie XB, Li S, Zhang RF, Zhao J, Chen YC, Zhao Q, Yao YX, You CX, Zhang XS, Hao YJ. The bHLH transcription factor MdbHLH3 promotes anthocyanin accumulation and fruit colouration in response to low temperature in apples. *Plant Cell Environ.* 2012;35(11):1884–1897. <https://doi.org/10.1111/j.1365-3040.2012.02523.x>
- Xie Y, Tan H, Ma Z, Huang J. ELLA proteins promote anthocyanin biosynthesis via sequestering MYBL2 and JAZ suppressors of the MYB/bHLH/WD40 complex in *Arabidopsis thaliana*. *Mol Plant* 2016;9(5):711–721 <https://doi.org/10.1016/j.molp.2016.01.014>
- Xu W, Dubos C, Lepiniec L. Transcriptional control of flavonoid biosynthesis by MYB-bHLH-WDR complexes. *Trends Plant Sci.* 2015;20(3):176–185. <https://doi.org/10.1016/j.tplants.2014.12.001>
- Xu H, Zou Q, Yang G, Jiang S, Fang H, Wang Y, Zhang J, Zhang Z, Wang N, Chen X. MdMYB6 regulates anthocyanin formation in apple both through direct inhibition of the biosynthesis pathway and through substrate removal. *Hortic Res.* 2020;7(1):72. <https://doi.org/10.1038/s41438-020-0294-4>
- Yan S, Chen N, Huang Z, Li D, Zhi J, Yu B, Liu X, Cao B, Qiu Z. Anthocyanin fruit encodes an R2R3-MYB transcription factor, SlAN2-like, activating the transcription of SlMYBATV to fine-tune anthocyanin content in tomato fruit. *New Phytol.* 2020;225(5):2048–2063. <https://doi.org/10.1111/nph.16272>
- Yang T, Ma H, Li Y, Zhang Y, Zhang J, Wu T, Song T, Yao Y, Tian J. Apple MPK4 mediates phosphorylation of MYB1 to enhance light-induced anthocyanin accumulation. *Plant J.* 2021a;106(6):1728–1745. <https://doi.org/10.1111/tpj.15267>
- Yang N, Zhou Y, Wang Z, Zhang Z, Xi Z, Wang X. Emerging roles of brassinosteroids and light in anthocyanin biosynthesis and ripeness of climacteric and non-climacteric fruits. *Crit Rev Food Sci Nutr.* 2021b;18:1–13. <https://doi.org/10.1080/10408398.2021.2004579>
- Yao G, Ming M, Allan AC, Gu C, Li L, Wu X, Wang R, Chang Y, Qi K, Zhang S, et al. Map-based cloning of the pear gene MYB114 identifies an interaction with other transcription factors to coordinately regulate fruit anthocyanin biosynthesis. *Plant J.* 2017;92(3):437–451. <https://doi.org/10.1111/tpj.13666>
- Yu Q, Hua X, Yao H, Zhang Q, He J, Peng L, Li D, Yang Y, Li X. Abscisic acid receptors are involved in the jasmonate signaling in *Arabidopsis*. *Plant Signal Behav.* 2021;16(10):1948243. <https://doi.org/10.1080/15592324.2021.1948243>
- Yu J, Qiu K, Sun W, Yang T, Wu T, Song T, Zhang J, Yao Y, Tian J. A long noncoding RNA functions in high-light-induced anthocyanin accumulation in apple by activating ethylene synthesis. *Plant Physiol.* 2022;189(1):66–83. <https://doi.org/10.1093/plphys/kiac049>
- Zahedipour-Sheshglani P, Asghari M. Impact of foliar spray with 24-epibrassinolide on yield, quality, ripening physiology and productivity of the strawberry. *Sci Hortic.* 2020;268:109376. <https://doi.org/10.1016/j.scienta.2020.109376>
- Zhang L, Hu J, Han X, Li J, Gao Y, Richards CM, Zhang C, Tian Y, Liu G, Gul H, et al. A high-quality apple genome assembly reveals the association of a retrotransposon and red fruit colour. *Nat Commun.* 2019;10(1):1494. <https://doi.org/10.1038/s41467-019-09518-x>
- Zhang Z, Shi Y, Ma Y, Yang X, Yin X, Zhang Y, Xiao Y, Liu W, Li Y, Li S, et al. The strawberry transcription factor FaRAV1 positively regulates anthocyanin accumulation by activation of FaMYB10 and anthocyanin pathway genes. *Plant Biotechnol J.* 2020;18(11):2267–2279. <https://doi.org/10.1111/pbi.13382>
- Zhang B, Yang HJ, Qu D, Zhu ZZ, Yang YZ, Zhao ZY. The MdBBX22-miR858-MdMYB9/11/12 module regulates proanthocyanidin biosynthesis in apple peel. *Plant Biotechnol J.* 2022;20(9):1683–1700. <https://doi.org/10.1111/pbi.13839>
- Zhao J. Flavonoid transport mechanisms: how to go, and with whom. *Trends Plant Sci.* 2015;20(9):576–585. <https://doi.org/10.1016/j.tplants.2015.06.007>
- Zhao Y, Dong W, Zhu Y, Allan AC, Lin-Wang K, Xu CJ. PpGST1, an anthocyanin-related glutathione S-transferase gene, is essential for fruit coloration in peach. *Plant Biotechnol J.* 2020;18(5):1284–1295. <https://doi.org/10.1111/pbi.13291>
- Zhao L, Sun J, Cai Y, Yang Q, Zhang Y, Ogutu CO, Liu J, Zhao Y, Wang F, He H, et al. PpHYH is responsible for light-induced anthocyanin accumulation in fruit peel of *Prunus persica*. *Tree Physiol.* 2022;42(8):1662–1677. <https://doi.org/10.1093/treephys/tpac025>
- Zhou H, Lin-Wang K, Wang F, Espley RV, Ren F, Zhao J, Ogutu C, He H, Jiang Q, Allan AC, et al. Activator-type R2R3-MYB genes induce a repressor-type R2R3-MYB gene to balance anthocyanin and proanthocyanidin accumulation. *New Phytol.* 2019;221(4):1919–1934. <https://doi.org/10.1111/nph.15486>
- Zhou H, Lin-Wang K, Wang H, Gu C, Dare AP, Espley RV, He H, Allan AC, Han Y. Molecular genetics of blood-fleshed peach reveals activation of anthocyanin biosynthesis by NAC transcription factors. *Plant J.* 2015;82(1):105–121. <https://doi.org/10.1111/tpj.12792>
- Zhou Y, Yuan C, Ruan S, Zhang Z, Meng J, Xi Z. Exogenous 24-epibrassinolide interacts with light to regulate anthocyanin and proanthocyanidin biosynthesis in cabernet sauvignon (*Vitis vinifera* L.). *Molecules.* 2018;23(1):93. <https://doi.org/10.3390/molecules23010093>
- Zhou M, Zhang K, Sun Z, Yan M, Chen C, Zhang X, Tang Y, Wu Y. LNK1 and LNK2 corepressors interact with the MYB3 transcription factor in phenylpropanoid biosynthesis. *Plant Physiol.* 2017;174(3):1348–1358. <https://doi.org/10.1104/pp.17.00160>
- Zhu YC, Zhang B, Allan AC, Lin-Wang K, Zhao Y, Wang K, Chen KS, Xu CJ. DNA Demethylation is involved in the regulation of temperature-dependent anthocyanin accumulation in peach. *Plant J.* 2020;102(5):965–976. <https://doi.org/10.1111/tpj.14680>
- Zipor G, Duarte P, Carquejeiro I, Shahar L, Ovadia R, Teper-Bamnlker P, Eshel D, Levin Y, Doron-Faigenboim A, Sottomayor M, et al. In planta anthocyanin degradation by a vacuolar class III peroxidase in *Brunfelsia calycina* flowers. *New Phytol.* 2015;205(2):653–665. <https://doi.org/10.1111/nph.13038>