

Review

Advancements in the Regulation of Flavonoid Compounds in Monocotyledons and Dicotyledons by Plant MYB Transcription Factors

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Abstract

Flavonoids are essential secondary metabolites in plants, predominantly found in flowers, leaves, and fruits. They mainly include anthocyanins, proanthocyanidins, and flavonols. Transcription factors are a crucial family of proteins in plants, playing a significant role in regulating the biosynthesis of secondary metabolites. This review introduces flavonoids and explores the characteristics and biological functions of MYB transcription factors. It establishes a phylogenetic tree using *Arabidopsis thaliana* MYB transcription factors as an example, which includes 17 subgroups (S1–S17). The subgroups related to flavonoids are primarily concentrated in S17, further classified into A, C, D, E, and F. The review also discusses the different regulatory roles of MYB transcription factors in flavonoid synthesis in monocotyledonous and dicotyledonous plants. This knowledge provides a theoretical foundation for further studies on the diverse regulatory functions of MYB transcription factors in flavonoid biosynthesis across the plant kingdom.

Keywords: flavonoids; MYB transcription factors; phylogenetic tree; monocotyledonous plants; dicotyledonous plants



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1. Introduction

During the long process of natural selection and evolution, plants have developed unique gene expression profiles and regulatory mechanisms to adapt to constantly changing environments [1]. Gene expression and silencing are tightly controlled to regulate diverse physiological processes throughout development, operating at multiple interdependent levels—including DNA modification, transcription, and translation [2]. Among these, transcriptional regulation is the most complex. It involves both cis-acting elements and trans-acting factors, which bind to specific nucleotide sequences and interact to precisely modulate the expression of structural genes, thereby executing regulatory functions [3]. MYB transcription factors represent one of the largest and most widespread families of regulatory proteins in plants and play key roles in the biosynthesis of numerous secondary metabolites. Recent genomic studies in safflower have shown that overexpression of R2R3-MYB genes significantly upregulates structural genes involved in flavonoid biosynthesis and enhances flavonol accumulation [4]; similarly, whole-genome identification in the

medicinal orchid *Dendrobium officinale* revealed that certain R2R3-MYB members negatively regulate flavonoid synthesis by repressing key enzyme genes [5]. However, the field of MYB-mediated flavonoid regulation still faces considerable challenges. For instance, within a given species, multiple MYB homologs may regulate distinct branches of flavonoid metabolism or respond to different signals via functional differentiation. Moreover, understanding how epigenetic modifications of MYB genes and their target genes influence flavonoid synthesis and accumulation remains a major unresolved question. Flavonoids, an important class of plant secondary metabolites, are abundantly present in flowers, leaves, and fruits [6]. In *Arabidopsis thaliana*, early biosynthetic genes (EBGs) are activated by functionally redundant R2R3-MYB regulators (*MYB11*, *MYB12*, and *MYB111*), whereas late biosynthetic genes (LBGs) require the assembly of a ternary MYB–bHLH–WD40 (MBW) complex. In contrast, in monocot species such as maize (*Zea mays*), the MBW complex activates both EBGs and LBGs uniformly. Similar regulatory distinctions have been observed between other dicot and monocot species, suggesting fundamental differences in the flavonoid (particularly anthocyanin) regulatory networks between these two groups of plants [7]. By examining the characteristics and biological functions of MYB transcription factors, constructing a phylogeny of MYBs involved in flavonoid biosynthesis, and comparing their regulatory roles in monocots (e.g., rice and maize) and dicots (e.g., *Arabidopsis thaliana*), this study aims to provide a theoretical foundation for understanding the functional diversity and evolutionary divergence of MYB-mediated flavonoid regulation across the plant kingdom.

2. Flavonoid Biosynthetic Pathways

Flavonoids, which represent one of the primary classes of secondary metabolites in plants, mainly comprise anthocyanins, proanthocyanidins, and flavonols [8]. Among these, flavonols are the earliest evolved flavonoids, with their biosynthetic origins traceable to bryophytes, such as *Physcomitrium patens* and *Marchantia polymorpha* [9]. Proanthocyanidins have been identified in ferns, whereas anthocyanins are believed to have originated prior to the divergence of gymnosperms and angiosperms [10].

Anthocyanins are one of the principal pigments found in flowers, leaves, stems, fruits, and other tissues and organs of plants. Their primary function is to impart diverse colors, contributing to the vibrant pigmentation observed in various plant species. Stable anthocyanins are typically localized within vesicles of epidermal cells [11]. The coloration of anthocyanins is determined by the number of hydroxyl groups on the B-ring; an increased number of hydroxyl groups results in a bluer hue. Proanthocyanidins are widely distributed in various plant tissues, including tree bark, flowers, seeds, and fruit peels. Maynard et al. (1967) first isolated four polyphenolic compounds from grape skin and grape seed extracts that yielded red anthocyanidins upon acid hydrolysis under heating; these were subsequently designated collectively as proanthocyanidins [12]. The regulation of proanthocyanidin biosynthesis in plants is more complex than that of anthocyanins. Nevertheless, their synthesis is primarily controlled by MYB transcription factors. In most species, proanthocyanidin accumulation is regulated by multiple MYB transcription factors that exhibit functional divergence or act in concert through specific regulatory sequences [13]. Flavonols represent the most abundant and ubiquitous subclass of flavonoid compounds. Common examples include quercetin, kaempferol, isorhamnetin, and myricetin, which are present in various plant organs such as roots, stems, leaves, flowers, and fruits [14]. They often co-localize with anthocyanins and contribute to color development in plant tissues while also acting as a defense mechanism against environmental stressors such as insect herbivory, UV radiation, and bacterial infection [15].

In current horticultural crop studies focusing on secondary metabolism, the metabolic pathways underlying flavonoid biosynthesis have been characterized in greater detail (Figure 1). As a conserved and pivotal component of the phenylpropanoid pathway across plant taxa, flavonoid biosynthesis is governed by two primary gene categories: structural genes, further classified into early and late subsets [16]. In the anthocyanin branch, enzymes such as CHS, CHI, F3H, F3'H, and F3'5'H constitute the EBGs, while DFR, ANS/LDOX, and UFGT are designated as LBGs [17]; regulatory genes exemplified by transcription factors (Table 1). Key enzymes in the anthocyanin pathway are coordinately regulated by the MBW transcriptional activation complex, comprising members from the MYB, bHLH, and WD40 repeat protein families, as well as additional TFs such as WRKY and NAC [16]. The synthesis of flavonoids begins with phenylalanine within the phenylalanine pathway, where phenylalanine aminolyase serves as the initial enzyme. Phenylalanine Ammonia-Lyase (PAL) catalyzes the conversion of phenylalanine into cinnamic acid, subsequently processed by cinnamic acid-4-hydroxylase and 4CL4-coumarate coenzyme A ligase to yield 4-coumaroyl coenzyme A. Chalcone synthase then acts on malonyl coenzyme A and 4-coumaroyl coenzyme A, producing chalcone. While chalcone isomerase (CHI) is not mandatory for this reaction in plants, its absence slows down the process significantly, showcasing tissue-specific expression. Dihydroflavonols are generated from 4,5,7-trihydroxyflavanones catalyzed by flavanone 3-hydroxylase, a common substrate for flavonoid 3'-hydroxylase and flavonoid 3',5'-hydroxylase. F3H plays a regulatory role in the synthesis of flavonols and anthocyanin products and is a key enzyme in the metabolic pathway of flavonoid substances with a central position in the whole flavonoid metabolism process. Dihydroxyflavonol reductase, reliant on NADPH, catalyzes the formation of colorless anthocyanins from flavonols. Its expression varies across species and tissues. These colorless anthocyanins are later oxidized by anthocyanin synthase into colored anthocyanins. Anthocyanins, inherently unstable, undergo modification by uridine diphosphate glucosyltransferase, leading to glycosylation, hydroxylation, and methylation, ultimately producing stable, colored anthocyanins. Alternatively, anthocyanin reductase and colorless anthocyanin reductase facilitate the conversion of unmodified colorless anthocyanins or anthocyanins into proanthocyanidins [18] (Figure 1).

Abbreviations are as follows: EBGs, early biosynthetic genes; LBGs, late biosynthetic genes; PAL, phenylalanine ammonium lyase; C4H, cinnamate-4-hydroxylase; 4CL, 4-coumaroyl-CoA synthase; CHS, chalcone synthase; CHI, chalcone isomerase; F3H, flavanone 3-hydroxylase; F3'H, flavonoid 3'-hydroxylase; F3'5'H, flavonoid 3'5'-hydroxylase; FLS, flavonol synthase; DFR, dihydroflavonol reductase; ANS, anthocyanidin synthase; LDOX, leucoanthocyanidin dioxygenase; LAR, leucoanthocyanidin reductase; ANR, anthocyanidin reductase; UFGT, UDP-Glc:flavonoid 3-O-glucosyltransferase; OMT, O-methyl transferase.

Biosynthetic pathways exhibit considerable taxonomic variation across plant lineages, reflecting divergent evolutionary trajectories and ecological adaptations. Although core enzymatic mechanisms are often conserved, key differences emerge through gene family expansion, alterations in enzyme substrate specificity, and lineage-specific transcriptional regulation—particularly involving MYB transcription factors [19]. These variations give rise to distinct profiles of specialized metabolites, such as differences in flavonoid composition between monocots and dicots [20].

Although monocots and dicots share the core biochemical pathway for flavonoid biosynthesis, significant divergences exist between them in terms of metabolic profile, regulatory mechanisms, and compound specificity. With regard to product accumulation, dicots produce a wide diversity of anthocyanins, such as pelargonidin, cyanidin, and delphinidin, resulting in a broad spectrum of flower colors [21]. In contrast, monocots—

particularly those in the Poaceae family—exhibit more conservative floral pigmentation, predominantly accumulating cyanidin-3-glucoside, which confines their coloration to red and purple hues [22]. At the molecular regulatory level, although both groups rely on the MYB-bHLH-WD40 (MBW) transcriptional complex to control gene expression in this pathway, key MYB transcription factors in monocots show low homology to those in dicots, indicating distinct evolutionary trajectories [23]. Furthermore, monocots are notably specialized in the accumulation of characteristic metabolites such as C-glycosyl flavonoids (e.g., orientin and isoorientin), which are less common in dicots and contribute to enhanced antioxidant capacity and stress adaptation [23]. These differences collectively reflect the metabolic diversity that has emerged through adaptation to distinct ecological and developmental constraints during the evolution of these two major plant groups.

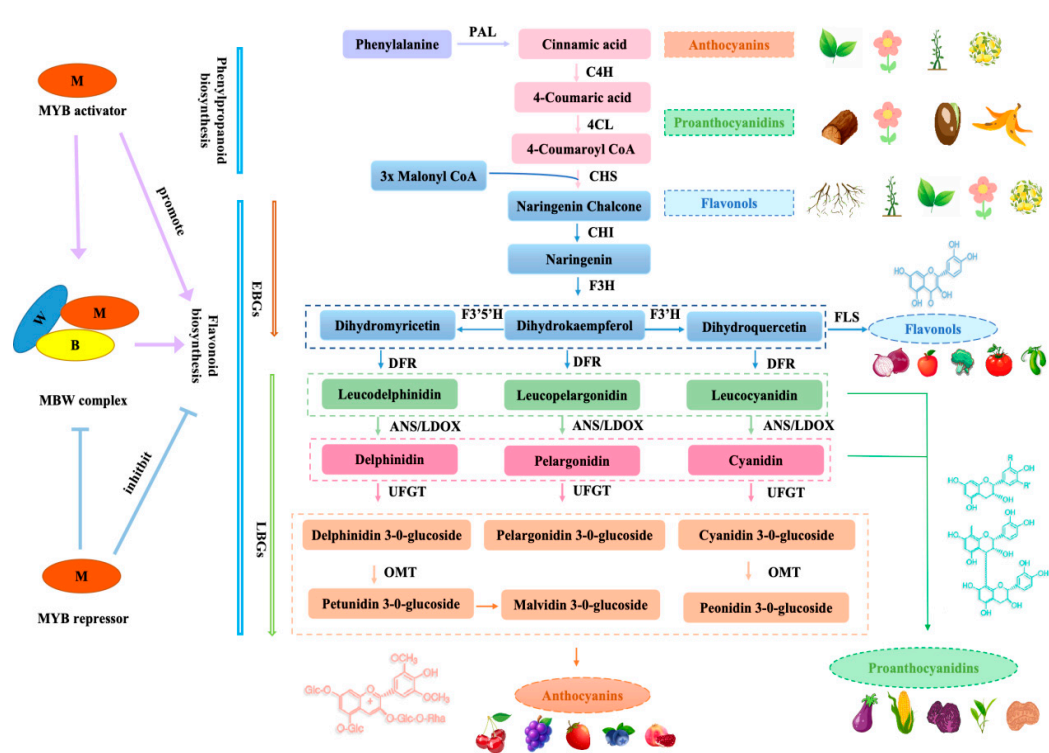


Figure 1. Simplified model for the flavonoid biosynthetic pathway and the function of MYB transcription factors.

Table 1. Classification and functions of EBGs and LBGs.

Collective Term	Classification	Function	Category	Roles in Biosynthesis	Reference
Structural Genes	EBG	Catalyze the initial reaction in secondary metabolism	PAL	Catalyzes the deamination of phenylalanine to form trans-cinnamic acid	[13]
			C4H	Catalyzes the hydroxylation of trans-cinnamic acid to form <i>p</i> -coumaric acid	[13]
			4CL	Catalyzes the conjugation of <i>p</i> -coumaric acid with CoA to form 4-coumaroyl-CoA	[14]
			CHI	Catalyzes the intramolecular isomerization of chalcone	[16]
			CHS	Catalyzes the synthesis of proanthocyanidins, generates chalcone, and regulates the production efficiency of chalcone	[16]

Table 1. Cont.

Collective Term	Classification	Function	Category	Roles in Biosynthesis	Reference
Structural Genes	EBG	Catalyze the initial reaction in secondary metabolism	F3'H	Catalyzes the hydroxylation of flavanone to generate dihydrokaempferol	[16]
			F3'5'H	Catalyzes the conversion of flavanone to trihydroxyflavanone and the conversion of dihydrokaempferol to dihydromyricetin	[16]
			F3H	Catalyzes the conversion of flavanone and dihydrokaempferol to dihydroquercetin	[17]
	LBG	Directs metabolic flux toward the proanthocyanidin biosynthetic branch	FLS	Catalyzes the oxidative cyclization of dihydroflavonols to generate flavonols	[17]
			DFR	Catalyzes the conversion of dihydroflavonols to leucoanthocyanidins	[18]
			UFGT	Catalyzes the glycosylation of anthocyanidins to form stable anthocyanins	[18]
			ANS	Catalyzes the oxidative cyclization of leucoanthocyanidins to generate anthocyanidins	[17]

3. Structural Characteristics and Origin of MYB Transcription Factors

The functional diversification of transcription factors is primarily driven by gene duplication and subsequent functional divergence [24]. Duplicated paralogs may undergo subfunctionalization—where ancestral functions are partitioned among copies—or neofunctionalization, in which one copy acquires a novel function, thereby expanding functional diversity. Additionally, mutations in cis-regulatory elements, alterations in protein interaction interfaces, and structural domain rearrangements further promote functional innovation in DNA-binding specificity, regulatory activity, and signal responsiveness [25]. These evolutionary mechanisms ultimately enable transcription factors to regulate a broader array of biological processes and enhance organismal adaptability to environmental challenges [26]. Dedicated databases have been developed to catalog transcription factors across species—examples include the Plant Transcription Factor Database (PlantTFDB) and the Grass Transcription Factor Database (Grassius)—with well-characterized families such as MYB, WRKY, NAC, and AP2/ERF being widely recognized as key regulators of these metabolic pathways [27].

3.1. Structural Characteristics and Classification of MYB Transcription Factors

MYB transcription factors are named after their highly conserved DNA-binding domain, the MYB domain, which typically comprises 1–4 tandem and partially repeated R units (R1, R2, R3, and in rare cases R4). Each R unit consists of approximately 50–53 amino acids that form a helix-turn-helix (HTH) motif capable of binding DNA. Key tryptophan residues—spaced at roughly 18-amino acid intervals—form a hydrophobic core essential for stabilizing the HTH conformation. Substitutions of these tryptophans, particularly the first tryptophan in the R3 repeat, with other aromatic or hydrophobic residues such as phenylalanine or leucine, are often observed and may influence DNA-binding specificity [28].

Based on the number and arrangement of R repeats, MYB proteins are classified into four major categories: (1) 1R-MYB (MYB-related) proteins contain a single R repeat and are subdivided into R3-type, R1/R2-type, and other variants. R3-type members—such as CAPRICE (CPC), TRIPTYCHON (TRY), and MYBL2—participate in cell fate determination and secondary metabolism. R1/R2-type proteins, including LHY and CCA1, play key roles in circadian rhythm regulation [29].

(2) R2R3-MYB proteins contain two adjacent R repeats and represent the largest MYB subfamily in plants. They feature a conserved N-terminal DNA-binding domain and a

divergent C-terminal region that often contains transcriptional activation or repression domains, enabling diverse regulatory functions [30].

(3) R1R2R3-MYB (3R-MYB) proteins comprise three R repeats and form an evolutionarily ancient group with limited membership. For instance, only five 3R-MYB genes are found in *Arabidopsis* and tobacco, and four to five in rice [31].

(4) 4R-MYB proteins, containing four R repeats, are the rarest class. These proteins consist of four tandem R1/R2-like repeats and are encoded by very few genes across plant species. Their functional roles remain poorly characterized [31].

Among these, R2R3-MYB and R3-MYB family members are notably involved in the regulation of anthocyanin biosynthesis, with many R3-MYBs acting as transcriptional repressors in this pathway [32].

3.2. Origin and Differentiation of MYB Transcription Factors

Two principal models have been proposed to explain the evolution of MYB genes in plants. The first model posits that the MYB DNA-binding domain originated over a billion years ago. According to this view, MYB proteins containing two or three repeats emerged through sequence duplication and amplification events. Differential expansion of these genes across lineages accounts for the striking abundance of MYB transcription factors in plants—for example, the hundreds of R2R3-MYB genes found in *Arabidopsis*—compared to the more limited repertoires in animals and bacteria. This model further suggests that R2R3-MYB genes arose through the evolutionary loss of the R1 repeat from ancestral R1R2R3-MYB genes [33]. An alternative model proposes that R1R2R3-MYB transcription factors evolved through the acquisition of an additional R1 repeat, forming three-repeat proteins from simpler precursors [34]. Despite their differences, both models agree that MYB genes originated from single-repeat ancestral genes prior to the evolutionary divergence of plants and animals.

We generated a phylogenetic tree utilizing *Arabidopsis* MYB transcription factors as a model. The *Arabidopsis* MYB transcription factor family members were sourced from TAIR (<https://www.Arabidopsis.org/>, accessed on 5 February 2024), while those specifically associated with flavonoid biosynthesis were retrieved from the NCBI website (<https://www.ncbi.nlm.nih.gov/>, accessed on 8 February 2024). A total of 126 *Arabidopsis* R2R3-MYBs and 93 R2R3-MYBs linked to flavonoid biosynthesis were aligned using MAFFT, and subsequently, an ML tree was constructed employing IQ-TREE 2. This analysis delineated a significant *Arabidopsis* MYB family comprising 17 subgroups that regulate diverse metabolic pathways. In this study, the MYB transcription factors of primary interest, which are involved in the regulation of flavonoid biosynthesis, were positioned on Section S17 in Figure 2 to facilitate more detailed and focused analysis. R2R3 MYBs, which control flavonoids, have been discovered in an increasing variety of plants, and these gene homologs are frequently believed to control the same pathway [35]. In order to analyze the MYB gene related to flavonoids more clearly, we have subdivided it according to its different functions [36]. Flavonoid-related MYBs are divided into five clades, containing flavonol-related, proanthocyanin-related, anthocyanin-related, and repressor (Figure 2). While some R2R3 MYBs specifically control the expression of a single gene, others influence multiple genes and aspects of the flavonoid pathway.

To enable a more precise investigation of the S17 subgroup, we performed correlation analyses of key parameters, yielding the following technical data. Multiple sequence alignment was performed with MAFFT v7.525 (129 sequences (S17), 1131 sites), comprising 277 conserved sites (24.5%), 298 singleton sites (26.4%), and 556 parsimony-informative sites (49.1%). AliStat v1.16 analysis indicated an average *p*-distance of 0.543, corresponding to ~45.7% mean identity. Phylogenetic inference was conducted in IQ-TREE v3.0.1 under

the best-fit substitution model JTT+R7 selected by ModelFinder (BIC). Branch support was assessed with 1000 ultrafast bootstrap replicates, and values are shown on the consensus ML tree.

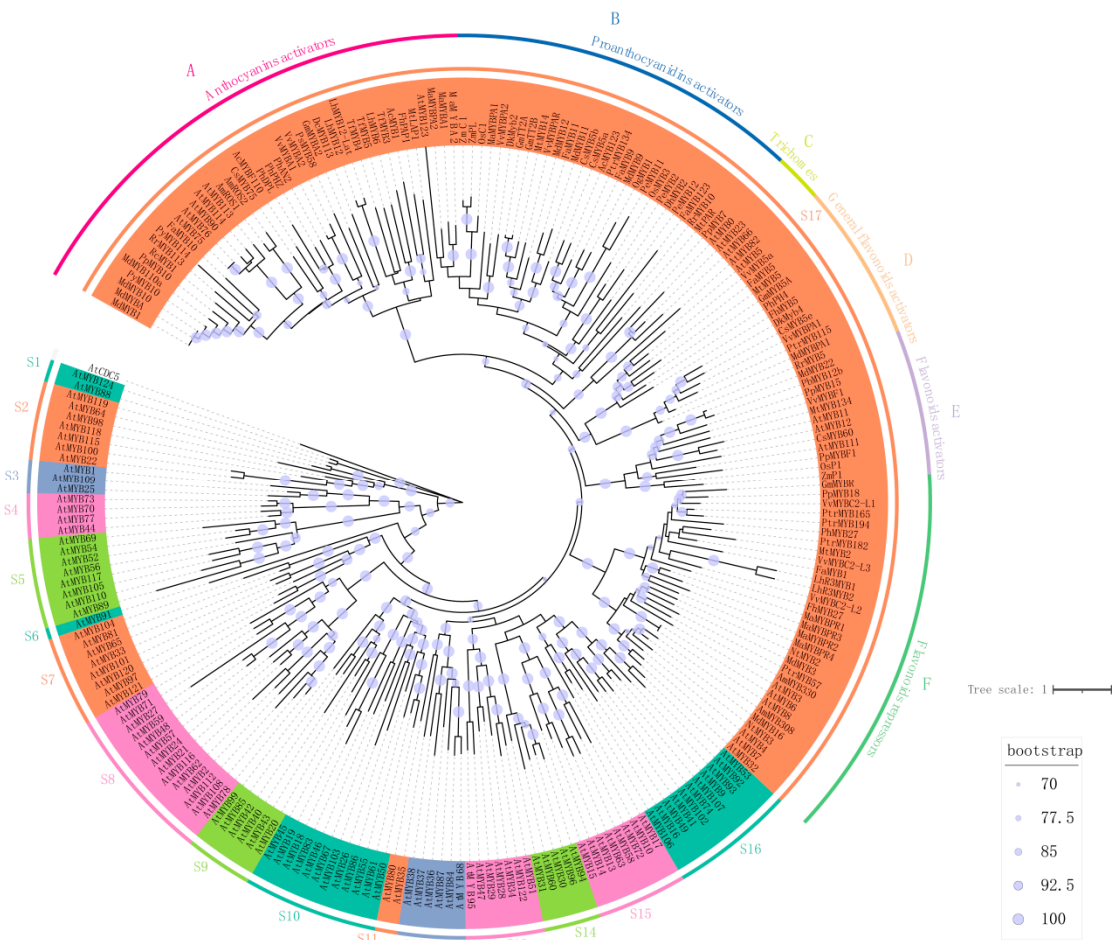


Figure 2. Phylogenetic tree of the R2R3-MYB genes in *Arabidopsis thaliana* [37] and functionally characterized genes related to flavonoid biosynthesis in plants. The tree was constructed by the maximum likelihood (ML) method using IQ-TREE 2, and ModelFinder was used to choose the best model. The tree was rooted using AtCDC5 as the outgroup. Bootstrap values $\geq 50\%$ are shown as dark blue dots in the phylogenetic tree. The candidate R2R3-MYB proteins are clustered into 17 subfamilies (designated as S1 to S17). And the S17 subfamily is further divided into six groups, namely A (anthocyanin activators), B (proanthocyanidin activators), C (trichomes), D (general flavonoid activators), E (flavonol activators), and F (flavonoid repressors).

MYB transcription factors exhibit both evolutionary convergence and divergence in their functions. Evolutionary convergence refers to the process whereby MYB genes from distinct evolutionary lineages and independent origins gradually develop similar molecular functions through long-term natural selection and adaptation to shared physiological demands, such as responses to environmental stress or regulation of specific branches of flavonoid metabolism. For example, OsMYB12 in monocot rice and AtMYB12 in dicot *Arabidopsis thaliana*, despite belonging to divergent plant clades without direct evolutionary connections, both activate key promoters of flavonoid biosynthesis genes to regulate the accumulation of flavonols, demonstrating functional convergence [38,39]. In contrast, evolutionary divergence occurs when MYB genes derived from a common ancestor acquire functional specificity over time in different species or lineages due to accumulated genetic variations, ecological niche differentiation, and distinct selective pressures. For instance, an ancestral MYB gene initially involved in basal flavonoid regulation may have diverged

in gymnosperms to control defensive flavonoid compounds in conifer needles, while in angiosperms, it further specialized into subtypes regulating distinct metabolites such as anthocyanins or proanthocyanidins [30]. Some MYBs even evolved from transcriptional activators into repressors, fine-tuning the balance of flavonoid metabolic networks. This dynamic interplay of convergence and divergence not only shapes the functional diversity of the MYB family but also underpins plants' adaptation to varied ecological environments and enables precise regulation of metabolic pathways [40]. It is central to understanding the widespread yet functionally specialized distribution of key secondary metabolic pathways, such as flavonoid biosynthesis, across the plant kingdom.

4. The Regulation of Flavonoid Synthesis by MYB Transcription Factors

The evolutionary divergence between monocots and dicots is characterized by several distinct genomic and phenotypic patterns, driven by mechanisms such as lineage-specific whole-genome duplications, differential expansion of gene families, and functional diversification of key regulatory components [41]. For example, subfunctionalization of MADS-box genes has led to profound differences in floral architecture, while divergent expansion and expression of transcription factor families—including MYB and NAC—underpin variations in stress adaptation and secondary metabolism [42]. Structural innovations, such as the scattered vascular bundles characteristic of monocots and the robust secondary growth typical of many dicots, further illustrate how developmental and ecological constraints have shaped independent evolutionary trajectories. Together, these patterns highlight the deep phylogenetic and adaptive changes that have generated the morphological, physiological, and molecular distinctions defining these two major angiosperm groups.

MYB transcription factors in plants stand out from their animal and yeast counterparts due to their remarkable structural and functional conservation. They serve as pivotal players in a diverse array of biological processes, exerting a unique influence on plant growth. Engaging in multiple facets of plant development, MYB transcription factors govern cell fate, morphogenesis, and various developmental stages. They also oversee primary and specialized metabolic pathways, as well as orchestrate responses to both biotic and abiotic stresses. Notably, MYB transcription factors are actively involved in plant flavonoid metabolic pathways, regulating flower, fruit, and seed color, among others, in monocotyledonous plants such as rice and maize, and in dicotyledonous plants such as *Arabidopsis thaliana*. EBGs in *Arabidopsis* are activated by functionally redundant R2R3MYB regulatory genes (*MYB11*, *MYB12*, and *MYB111*), and the initiation of LBGs requires the MYB regulatory factor and bHLH factor, as well as the WD40 protein to make up the ternary MBW complex. In contrast, in monocotyledonous maize and rice, the MBW complex can activate both EBGs and LBGs as a single unit; therefore, we suggest that the regulatory mechanism of flavonoid synthesis in dicotyledons is different from that in monocotyledons (Figure 3). In *Arabidopsis*, the early synthetic genes EBGs associated with flavonoid synthesis are regulated by *AtMYB12/PFG1* [43], and the late synthetic genes, LBGs, are mainly regulated by *AtMYB75/PAP1*, *AtMYB90/PAP2*, *AtMYB5*, *AtMYB123/AtTT2*, *AtMYB113*, *AtMYB114* [44–47], *AtMYB3*, *AtMYB4*, *AtMYB7*, and *MYB32* overexpression inhibited both early synthesis genes EBGs and late synthesis genes, LBGs [48–50], *AtMYBL2* and *AtCPC* also inhibited the control of flavonoid production [51,52]. In monocotyledonous plants, of all the MYB genes present in the model plant rice, *OsP1* (*PERICARP COLOUR1*) and *OsMYB3/Kala3* are overexpressed to increase the transcriptional level of EBGs, and *OsC1* (*COLOURESS1*) is overexpressed to increase the transcriptional level of LBGs, promoting the production of anthocyanins [53–55]. In another model plant, maize, *ZmP1* is overexpressed to increase the transcriptional level of EBG [56], and *ZMC1* and *ZMPL* are

overexpressed to increase the transcriptional level of EBGs and LBGs, which promote the production of flavonoids [57,58].

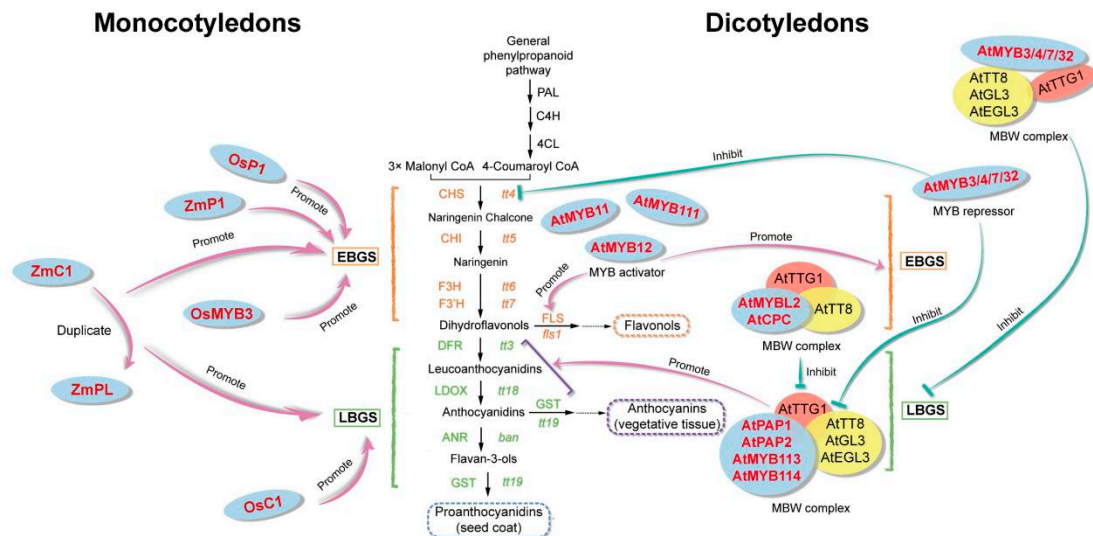


Figure 3. MYB regulation of the flavonoid biosynthetic pathway in monocotyledons and dicotyledons.

Activation-type and repression-type MYB transcription factors can exhibit both functional paralogy and convergent evolution, enhancing the complexity and adaptability of regulatory networks in plants. Functional paralogy often arises from gene duplication events, where paralogous genes diverge to assume opposing roles—one activating and one repressing the same pathway—as observed in anthocyanin biosynthesis regulators such as *AtMYB75* and *AtMYB27* in *Arabidopsis* [59]. Meanwhile, convergent evolution is reflected in the independent emergence of repressive motifs in non-homologous MYB repressors across distantly related species, enabling analogous suppression of flavonoid biosynthesis in both monocots and eudicots [60]. These evolutionary mechanisms collectively fine-tune metabolic responses and contribute to phenotypic diversity under environmental constraints.

4.1. Involvement of MYB Transcription Factors in Monocotyledonous Plants in Flavonoid Metabolism, Regulating the Color of Flowers, Fruits, etc.

In monocotyledonous plants, MYB transcription factors regulate flavonoid biosynthesis, which is more typical of rice and maize. Among all MYB genes present in rice, an R2R3 type (*C1*) regulates anthocyanin biosynthesis, *OsC1*(*COLOURLESS1*), *OsP1*(*PERICARP COLOUR1*), and *OsMYB3/Kala3* overexpressed in rice plants trigger anthocyanin production through augmentation of the transcript level of late ABP genes [53–55] (Table 2). The maize *ZmMYBC1* gene, which is the first MYB-like gene to be discovered in plants, is ectopically expressed in tissue cells and interacts with the bHLH protein to jointly elicit the manifestation of the structural enzyme genes *DFR* and *3GT* in the anthocyanin synthesis pathway, leading to massive synthesis and accumulation of anthocyanin in pigment-free maize tissue cells [56]. *ZMP1* and *ZMPL* bind to and activate transcription of the *A1* gene required for 3-deoxy flavonoid to promote the production of flavonoid compounds [57,58] (Table 2).

In other monocotyledons, MYB transcription factors promote or inhibit flavonoid production (Table 3). In lily, *LhMYB6* and *LhMYB12* interact with *bHLH* transcription factors to activate the expression of *DFR* and the formation of spots on tepals [61], *LhMYB12-Lat* promotes anthocyanin synthesis [62], overexpression of *LhR3MYB1* and *LhR3MYB2* actually inhibits anthocyanin biosynthesis [63]; In orchids, the *OgMYB1* was associated with anthocyanin synthesis in the flowers of Mandarin orchids [64]; In Tulip, *TfMYB3*,

TfMYB4 and *TfMYB5* interact with *TfbHLH1*, *TfMYB5* activates the promoter of *TfCHS1*, while *TfMYB3* and *TfMYB4* promote the promoter activity of *TfANS1* were participated in the regulating of anthocyanin biosynthesis [65]; In *Phalaenopsis*, *PeMYB2*, *PeMYB11* and *PeMYB12* regulate the anthocyanin synthesizing Enzymes *F3'5'H*, *DFR1*, and *ANS3* to accumulate anthocyanin synthesis [66]; In Bananas, *MaMYBPA1* and *MaMYBPA2* interact with *MaANS* to promote flavonoid synthesis [67,68], *MaMYBA1* and *MaMYBA2* function as components of transcription factor complexes with bHLH and WD40 proteins to activate anthocyanin biosynthesis [67], while *MaMYBPR1/MaMYB4*, *MaMYBPR2*, *MaMYBPR3* and *MaMYBPR4* inhibit the synthesis of anthocyanins [68,69]; In Onions, *AcMYB1* binds to the promoters of anthocyanidin synthase (*AcANS*) and flavonoid 3-hydroxylase 1 (*AcF3H1*) and activates their expression [70]; In *Dendrobium officinale*, *DhMYB2* and *DhbHLH1* interact and are expressed together with *DhDFR* and *DhANS*, promote anthocyanin accumulation [71]. In *Freesia hybrida*, the R2R3-MYB factor *FhMYB5* regulates the biosynthesis of anthocyanins and proanthocyanidins, *FhMYB27* and *FhMYBx* inhibit anthocyanin synthesis by activating MBW; in contrast, *FhPAP1* promotes anthocyanin synthesis [72]. In Daffodils, the *NtMYB2* and *NtMYB3* from *Narcissus* R2R3-MYB inhibit the biosynthesis of anthocyanin and flavonoids [73].

Table 2. MYB transcription factors involved in the regulation of flavonoid compounds in model plants.

Species (Family)	Gene	Type	Metabolism	Function	Accession	Reference
<i>Arabidopsis thaliana</i> (Brassicaceae)	<i>AtMYB5</i>	R2R3-MYB	Flavonoids, Proanthocyanidins	Activation	AT3G13540.1	[54]
	<i>AtMYB11/PFG2</i>	R2R3-MYB	Flavonols	Activation	AT3G62610.1	[74]
	<i>AtMYB12/PFG1</i>	R2R3-MYB	Flavonols	Activation	AT2G47460.1	[43]
	<i>AtMYB75/PAP1</i>	R2R3-MYB	Anthocyanins	Activation	AT1G56650.1	[45]
	<i>AtMYB90/PAP2</i>	R2R3-MYB	Anthocyanins	Activation	AT1G66390.1	[45]
	<i>AtMYB111/PFG3</i>	R2R3-MYB	Flavonols	Activation	AT5G49330.1	[74]
	<i>AtMYB113</i>	R2R3-MYB	Anthocyanins	Activation	AT1G66370.1	[44]
	<i>AtMYB114</i>	R2R3-MYB	Anthocyanins	Activation	AT1G66380.1	[44]
	<i>AtMYB123/AtTT2</i>	R2R3-MYB	Proanthocyanidins	Activation	AT5G35550.1	[46]
	<i>AtMYB3</i>	R2R3-MYB	Flavonoids	Inhibition	AT1G22640.1	[75]
	<i>AtMYB4</i>	R2R3-MYB	Flavonoids	Inhibition	AT4G38620.1	[48]
	<i>AtMYB7</i>	R2R3-MYB	Flavonols	Inhibition	AT2G16720.1	[76]
	<i>AtMYB32</i>	R2R3-MYB	Flavonoids	Inhibition	AT4G34990.1	[50]
	<i>AtMYBL2</i>	R3-MYB	Anthocyanins	Inhibition	AT1G71030.1	[52]
	<i>AtCPC</i>	R3-MYB	Anthocyanins	Inhibition	AT2G46410.1	[75]
<i>Oryza sativa</i> (Poaceae)	<i>OsC1(COLOURLESS1)</i>	R2R3-MYB	Anthocyanins	Activation	LOC_Os06g10350.1	[54]
	<i>OsP1(PERICARP COLOUR1)</i>	R2R3-MYB	Flavonols	Activation	LOC_Os03g19120.1	[55]
	<i>OsMYB3/Kala3</i>	R2R3-MYB	Anthocyanins	Activation	LOC_Os03g29614.1	[53]
<i>Zea mays</i> (Poaceae)	<i>ZmC1(COLOURLESS1)</i>	R2R3-MYB	Anthocyanins	Activation	Zm00001d044975_P001	[56]
	<i>ZmPL(PURPLE LEAF)</i>	R2R3-MYB	Anthocyanins	Activation	Zm00001d037118_P001	[58]
	<i>ZmP1(PERICARP COLOUR)</i>	R2R3-MYB	Flavonols	Activation	Zm00001d028850_P001	[57]

Table 3. MYB transcription factors involved in the regulation of flavonoid compounds in monocotyledon plants.

Species (Family)	Gene	Type	Metabolism	Function	Accession	Reference
<i>Lilium</i> spp. (Liliaceae)	<i>LhMYB6</i>	R2R3-MYB	Anthocyanins	Activation	BAJ05399.1	[61]
	<i>LhMYB12</i>	R2R3-MYB	Anthocyanins	Activation	BAJ05398.1	[61]
	<i>LhMYB12-Lat</i>	R2R3-MYB	Anthocyanins	Activation	BAO04194.1	[62]
	<i>LhR3MYB1</i>	R3-MYB	Anthocyanins	Inhibition	BBG71951.1	[63]
	<i>LhR3MYB2</i>	R3-MYB	Anthocyanins	Inhibition	BBG71952.1	[63]
<i>Oncidium</i> spp. (Orchidaceae)	<i>OgMYB1</i>	R2R3-MYB	Anthocyanins	Activation	ABS58501.1	[64]
<i>Tulipa fosteriana</i> (Liliaceae)	<i>TfMYB3</i>	R2R3-MYB	Anthocyanins	Activation	AHY20034.1	[65]
	<i>TfMYB4</i>	R2R3-MYB	Anthocyanins	Activation	AHY20035.1	[65]
	<i>TfMYB5</i>	R2R3-MYB	Anthocyanins	Activation	AHY20036.1	[65]
<i>Phalaenopsis aphrodite</i> (Orchidaceae)	<i>PeMYB2</i>	R2R3-MYB	Anthocyanins	Activation	AIS35919.1	[66]
	<i>PeMYB11</i>	R2R3-MYB	Anthocyanins	Activation	AIS35928.1	[66]
	<i>PeMYB12</i>	R2R3-MYB	Anthocyanins	Activation	AIS35929.1	[66]
<i>Musa acuminata</i> (Musaceae)	<i>MaMYBPA1</i>	R2R3-MYB	Proanthocyanidins	Activation	Ma03_g07840.1	[68]
	<i>MaMYBPA2</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	Ma10_g17650.1	[67,68]
	<i>MaMYBA1</i>	R2R3-MYB	Anthocyanins	Activation	Ma06_g05960.1	[67]
	<i>MaMYBA2</i>	R2R3-MYB	Anthocyanins	Activation	Ma09_g27990.1	[67]
	<i>MaMYBPR1/MaMYB4</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	Ma03_g21920.1	[68]
	<i>MaMYBPR2</i>	R2R3-MYB	Anthocyanins	Inhibition	Ma06_g11140.1	[68]
	<i>MaMYBPR3</i>	R2R3-MYB	Anthocyanins	Inhibition	Ma08_g16760.1	[68]
	<i>MaMYBPR4</i>	R2R3-MYB	Anthocyanins	Inhibition	Ma10_g19970.1	[68]
<i>Allium cepa</i> (Amaryllidaceae)	<i>AcMYB1</i>	R2R3-MYB	Anthocyanins	Activation	AQP25672.1	[70]
<i>Dendrobium</i> spp. (Orchidaceae)	<i>DhMYB2</i>	R2R3-MYB	Anthocyanins	Activation	AQS79852.1	[71]
<i>Freesia hybrida</i> (Iridaceae)	<i>FhMYB5</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	QAX87835.1	[72]
	<i>FhPAP1</i>	R2R3-MYB	Anthocyanins	Activation	QJW70307.1	[72]
	<i>FhMYB27</i>	R2R3-MYB	Anthocyanins	Inhibition	QJW70308.1	[72]
	<i>FhMYBx</i>	R3-MYB	Anthocyanins	Inhibition	QJW70309.1	[72]
<i>Narcissus tazetta</i> (Amaryllidaceae)	<i>NtMYB2</i>	R2R3-MYB	Anthocyanins	Inhibition	ATO58377.1	[73]
	<i>NtMYB3</i>	R2R3-MYB	Flavonoids	Inhibition	AGO33166.1	[73]

4.2. Involvement of MYB Transcription Factors in Dicotyledonous Plants in Flavonoid Metabolism, Regulating the Color of Flowers, Fruits, etc.

In dicotyledonous plants, many R2R3 MYBs have been shown to play an important role in flavonoid biosynthesis, among which *Arabidopsis* is a very representative class and a focus of research (Table 2). In *Arabidopsis*, the early synthesis genes (EBGs) related to flavonoid synthesis are promoted and regulated by *AtMYB12/PFG1*, *AtMYB11/PFG2*, and *AtMYB111/PFG3* [43], and the LBGs related to flavonoid synthesis are promoted and regulated by *AtMYB75/PAP1*, *AtMYB90/PAP2*, *AtMYB5*, and *AtMYB123/AtTT2* [44,45]. In the study of the synthesis pathways of flavonoids such as *Arabidopsis* anthocyanins, proanthocyanidins, and flavonols, some MYB transcription factors, *AtMYB123/AtTT2* and *AtMYB5* bind to the promoters of different key enzyme genes to promote flavonols

synthesis [77,78], *AtMYB11/PFG2* and *AtMYB111/PFG3*, three members of subfamily 7 of the MYB family in *Arabidopsis*, can activate structural enzyme genes related to flavonol synthesis in different plant parts of *Arabidopsis* to regulate flavonol synthesis and control the accumulation of flavonol analogs in various tissues or organs of the plant [74], while *AtMYB3* inhibits the synthesis of flavonoids in *Arabidopsis thaliana* [79], *AtMYB4* and *AtMYB32* interact with the bHLH transcription factors TT8, GL3 and EGL3 and thereby interfere with the transcriptional activity of the MBW complexes to inhibit the synthesis of anthocyanins [48–50], *AtMYB7* inhibits the flavonol biosynthesis by controlling *DFR* and *UGT* [76], ectopic expression of *AtMYBL2* or of a chimeric repressor that is a dominant negative form of *AtMYBL2* suppressed the expression of the biosynthesis of anthocyanin [51,52], anthocyanin synthesis genes are down-regulated in *AtCPC* overexpressing plants [75].

In addition to its role in *Arabidopsis*, there is a large amount of new evidence indicating the role of R2R3 MYBs in transcriptional regulation of flavonoid metabolism in other aspects (Table 4). In grapes, the *VvMYBF1* can directly activate the structural enzyme genes related to flavonol [80], the *VvMYBA1* and *VvMYBA2* promote anthocyanin synthesis by activating *UFGT*, *CHS3* and *LDOX* [81], *VvMYBPA1* and *VvMYBPA2* activate the promoters of *LAR* and *ANR* to promote the synthesis of anthocyanins [82,83], *VvMYB5a* and *VvMYB5b* activate the grapevine promoters of several structural genes of the flavonoid pathway to regulate of the flavonoid [84], *VvMYBPAR* induces proanthocyanidin synthase to promote proanthocyanidin accumulation [85], *VvMYBC2-L1*, *VvMYBC2-L2* and *VvMYBC2-L3* inhibit anthocyanin synthesis by affecting *PAL*, *C4H*, *CHS*, *DFR*, and *UFGT* [86,87]. In poplar, *PtrMYB134* and *PtrMYB115* regulate proanthocyanidin biosynthesis by activating key flavonoid genes through a transcription factor complex composed of *bHLH* and *WD-40* proteins [88], whereas *PtrMYB165* and *PtrMYB194* inhibit the activation of flavonoid promoters and reduce anthocyanin and proanthocyanidin synthesis by interacting with *bHLH131* [89], overexpression of *PtrMYB57* and *PtrMYB182* led to a decrease in anthocyanin and PA accumulation in poplar, demonstrating that *PtrMYB57* and *PtrMYB182* play a negative role in the regulation of anthocyanin and PA biosynthesis in poplar [90,91], *PtrRML1* controls inhibition of anthocyanins and synthesis such as *DFR* and *UFGT* [92]. In *Medicago truncatula*, *MtPAR* and *MtTT8* regulate genes encoding enzymes of the flavonoid–PA pathway via a activation of *WD40-1* to regulate proanthocyanidin biosynthesis [93,94], *MtMYB5* and *MtMYB14* interact and activate the promoters of anthocyanidin reductase and leucoanthocyanidin reductase [95], *MtMYB134* activate *AtCHS* and *AtFLS1* to promote flavonol biosynthesis [96], ectopic expression of *MtLAP1* transcription factor activates the anthocyanin [97], overexpression of *MtMYB2* abolishes anthocyanin and PA accumulation in *Arabidopsis thaliana* seeds [98]; In soybean, *GmTT2A*, *GmTT2B* and *GmMYB5A* induce the accumulation of proanthocyanidins and anthocyanins [99], Ectopic expression of *GmMYBA2* conferred the enhanced accumulation of delphinidin and cyanidin types of anthocyanins in W1t and w1T backgrounds, *GmMYBR* is an inhibitor of anthocyanins [100]. In strawberry, *FaMYB123* interacts with *FabHLH3* to regulate anthocyanin [101], *FaMYB5* is an R2R3-MYB activator involved in the composition of MBW to regulate the biosynthesis of anthocyanin and proanthocyanidin [102], *FaMYB9* and *FaMYB11* activate the proanthocyanidin reductase gene promoter and promote proanthocyanidin accumulation [103], *FaMYB10* regulates the expression of most of the EBGs and the LBGs to involve in anthocyanin production [104], the *FaMYB1* of strawberry significantly inhibited the synthesis of anthocyanins and flavonols [105]. In rose, *RcMYB1* activates its own gene promoter and those of other EBGs and LBGs; overexpression of *RcMYB1* promotes anthocyanin accumulation [106]. In tea trees, *CsMYB5a*, *CsMYB5b*, and *CsMYB5e* promote the gene expression of *CsLAR* and *CsANR*, *CsMYB5f* and *CsMYB5g* only upregulate the gene expression of *CsLAR* but not *CsANR* to regulate proanthocyanidin

biosynthesis [107], *CsMYB75* promotes the expression of *CsGSTF1* to improve anthocyanin synthesis [108]. In apple, the *MdMYB1* gene from apple and validated it in *Arabidopsis* and isolated grapevine somatic cells and found that *MdMYB1* is capable of ectopic expression for the synthesis of anthocyanin and has abundant polymorphisms in its promoter region, overexpression of *MdMYB3* has resulted in transcriptional activation of several anthocyanins and flavonol pathway genes, including *CHS*, *CHI*, *UFGT* and *FLS* [109], *MdMYB9*, *MdMYB10* and *MdMYB11* interact with *MdbHLH3*, bind to the promoters of *ANS*, *ANR*, and *LAR*, and promote anthocyanin synthesis [110,111], *MdMYB12* interacts with *bHLH3* and *bHLH33* and played an essential role in proanthocyanidin synthesis [112], *MdMYB22* activate flavonol pathways by combining directly with the flavonol synthase promoter. *MdMYB24L* positively regulates the transcription of *MdDFR* and *MdUFGT* and promotes anthocyanin accumulation [113], *MdWRKY11* binds to W-box cis-elements in the *MdMYB10* and *MdUFGT* promoters and promotes anthocyanin synthesis in apple [114], *MdMYB110a* binds to the promoter of *CHS* and promotes anthocyanin synthesis [115], *MdMYBA* bound to an anthocyanidin synthase (*MdANS*) promoter region to control the increase in anthocyanins [116], the interaction between *MdMYBPA1* and *MdbHLH33* forms a complex, promote the production of proanthocyanidin [117], *MdbHLH33* in callus overexpressing *MdMYB16* and found that it weakened the inhibitory effect of *MdMYB16* on anthocyanin synthesis [118]. In kiwifruit, *AcMYBF110* and *AcbHLH1*, *AcbHLH4*, *AcbHLH5* and *AcWDR1* together activate the kiwifruit anthocyanin synthesis promoter and regulate anthocyanin accumulation [119], *AcMYB123* activates promoters of *AcANS* and *AcF3GT1* that encode the dedicated enzymes for anthocyanin biosynthesis to affect the accumulation of anthocyanins [120]. In tomato, the *SlMYB75/AN2* regulates chlorophyll, carotenoids, and flavonoids [121], and *SlMYBATV* plays a repressive role in anthocyanin biosynthesis in tomato [122]. In cucumber, *CsMYB60* activates *CsFLS* and *CsLAR* to promote biosynthesis of flavonols and proanthocyanidins in cucumber [123]. In peony flowers, *PsMYB58* interacted with *PsbHLH1* and *PsbHLH3* to enhance anthocyanin accumulation in various organs [124]. In carrot, *DcMYB113* induces *DcbHLH3*, which controls anthocyanin biosynthesis gene expression and promotes anthocyanin biosynthesis [125,126].

Table 4. MYB transcription factors involved in the regulation of flavonoid compounds in dicotyledonous plants.

Species (Family)	Gene	Type	Metabolism	Function	Accession	Reference
<i>Vitis vinifera</i> (Vitaceae)	<i>VvMYBF1</i>	R2R3-MYB	Flavonols	Activation	ACV81697.1	[80]
	<i>VvMYBA1</i>	R2R3-MYB	Anthocyanins	Activation	BAD18977.1	[81]
	<i>VvMYBA2</i>	R2R3-MYB	Anthocyanins	Activation	BAD18978.1	[81]
	<i>VvMYBPA1</i>	R2R3-MYB	Proanthocyanidins	Activation	CAJ90831.1	[82]
	<i>VvMYBPA2</i>	R2R3-MYB	Proanthocyanidins	Activation	ACK56131.1	[83]
	<i>VvMYB5a</i>	R2R3-MYB	Flavonoids	Activation	AAS68190.1	[84]
	<i>VvMYB5b</i>	R2R3-MYB	Flavonoids	Activation	AAX51291.1	[84]
	<i>VvMYBPAR</i>	R2R3-MYB	Proanthocyanidins	Activation	BAP39802.1	[85]
	<i>VvMYBC2-L1</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	AFX64995.1	[86]
<i>Populus trichocarpa</i> (Salicaceae)	<i>VvMYBC2-L2</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	ACX50288.2	[87]
	<i>VvMYBC2-L3</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	AIP98385.1	[86]
	<i>PtrMYB115</i>	R2R3-MYB	Proanthocyanidins	Activation	Potri.002G173900.1	[88]
	<i>PtrMYB134</i>	R2R3-MYB	Proanthocyanidins	Activation	Potri.006G221800.1	[88]

Table 4. Cont.

Species (Family)	Gene	Type	Metabolism	Function	Accession	Reference
<i>Medicago sativa</i> (Fabaceae)	<i>PtrMYB165</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	Potri.010G114000.1	[89]
	<i>PtrMYB182</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	Potri.004G088100.1	[91]
	<i>PtrMYB194</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	Potri.008G128500.1	[89]
	<i>PtrMYB57</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	Potri.T011400.1	[90]
	<i>PtrRML1</i>	R3-MYB	Anthocyanins	Inhibition	Potri.012G031200.1	[92]
	<i>MtPAR</i>	R2R3-MYB	Proanthocyanidins	Activation	ADU78729.1	[93]
	<i>MtMYB5</i>	R2R3-MYB	Proanthocyanidins	Activation	XP_003601609.1	[95]
	<i>MtMYB14</i>	R2R3-MYB	Proanthocyanidins	Activation	AFJ53058.1	[95]
	<i>MtMYB134</i>	R2R3-MYB	Flavonols	Activation	QUD39823.1	[96]
	<i>MtLAP1</i>	R2R3-MYB	Anthocyanins	Activation	ACN79541.1	[97]
<i>Glycine max</i> (Fabaceae)	<i>MtMYB2</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	XP_003616388.1	[98]
	<i>GmTT2A</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	XP_003541301.1	[99]
	<i>GmTT2B</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	NP_001342587.1	[99]
	<i>GmMYB5A</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	NP_001241492.1	[99]
	<i>GmMYBA2</i>	R2R3-MYB	Anthocyanins	Activation	Glyma.09G235100.1	[100]
<i>Fragaria × ananassa</i> (Rosaceae)	<i>GmMYBR</i>	R2R3-MYB	Anthocyanins	Inhibition	Glyma.20G013000.1	[100]
	<i>FaMYB123</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	FvH4_5g32460.t2	[101]
	<i>FaMYB5</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	USN17642.1	[102]
	<i>FaMYB9</i>	R2R3-MYB	Proanthocyanidins	Activation	AFL02460.1	[103]
	<i>FaMYB10</i>	R2R3-MYB	Anthocyanins	Activation	ABX79947.1	[104]
	<i>FaMYB11</i>	R2R3-MYB	Proanthocyanidins	Activation	AFL02461.1	[103]
	<i>FaMYB1</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	AAK84064.1	[105]
<i>Rosa chinensis</i> (Rosaceae)	<i>RcMYB1</i>	R2R3-MYB	Anthocyanins	Activation	XP_024189921.1	[106]
<i>Camellia sinensis</i> (Theaceae)	<i>CsMYB5a</i>	R2R3-MYB	Proanthocyanidins	Activation	KAF5936438.1	[107]
	<i>CsMYB5b</i>	R2R3-MYB	Proanthocyanidins	Activation	XP_028089226.1	[107]
	<i>CsMYB5e</i>	R2R3-MYB	Proanthocyanidins	Activation	XP_028116920.1	[107]
	<i>CsMYB75</i>	R2R3-MYB	Anthocyanins	Activation	UYR25389.1	[108]
<i>Malus domestica</i> (Rosaceae)	<i>MdMYB1</i>	R2R3-MYB	Anthocyanin	Activation	ADQ27443.1	[109]
	<i>MdMYB3</i>	R2R3-MYB	Anthocyanins, Flavonols	Activation	AEX08668.1	[109]
	<i>MdMYB9</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	ABB84757.1	[110]
	<i>MdMYB10</i>	R2R3-MYB	Anthocyanins	Activation	ACQ45201.1	[111,114]
	<i>MdMYB11</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Activation	AAZ20431.1	[110]
	<i>MdMYB12</i>	R2R3-MYB	Proanthocyanidins	Activation	XP_008337875.1	[112]
	<i>MdMYB22</i>	R2R3-MYB	Flavonols	Activation	AAZ20438.1	[113]
	<i>MdMYB110a</i>	R2R3-MYB	Anthocyanins	Activation	AFC88038.1	[115]
	<i>MdMYBA</i>	R2R3-MYB	Anthocyanins	Activation	BAF80582.1	[116]

Table 4. Cont.

Species (Family)	Gene	Type	Metabolism	Function	Accession	Reference
<i>Actinidia chinensis</i> (Actinidiaceae)	<i>MdMYBPA1</i>	R2R3-MYB	Proanthocyanidins	Activation	AIF70441.1	[117]
	<i>MdMYB16</i>	R2R3-MYB	Anthocyanins	Inhibition	ADL36756.1	[118]
	<i>AcMYBF110</i>	R2R3-MYB	Anthocyanins	Activation	AYJ72555.1	[119]
<i>Solanum lycopersicum</i> (Solanaceae)	<i>AcMYB123</i>	R2R3-MYB	Anthocyanins	Activation	QAT77713.1	[120]
	<i>SlMYB75/AN2</i>	R2R3-MYB	Anthocyanins	Activation	Solyc10g086250.2.1	[121]
	<i>SlMYBATV</i>	R3-MYB	Anthocyanins	Inhibition	Solyc07g052490.3.1	[122]
<i>Cucumis sativus</i> (Cucurbitaceae)	<i>CsMYB60</i>	R2R3-MYB	Flavonols, Proanthocyanidins	Activation	CsaV3_4G001130.1	[123]
<i>Paeonia suffruticosa</i> (Paeoniaceae)	<i>PsMYB58</i>	R2R3-MYB	Anthocyanins	Activation	AMW36067.1	[124]
<i>Daucus carota</i> (Apiaceae)	<i>DcMYB113</i>	R2R3-MYB	Anthocyanins	Activation	DCAR_008994	[125,126]
<i>Diospyros kaki</i> (Ebenaceae)	<i>DkMyb2</i>	R2R3-MYB	Proanthocyanidins	Activation	BAI49719.1	[127]
	<i>DkMyb4</i>	R2R3-MYB	Proanthocyanidins	Activation	BAI49721.1	[128]
	<i>PpMYB7</i>	R2R3-MYB	Proanthocyanidins	Activation	ALO81018.1	[129]
<i>Prunus persica</i> (Rosaceae)	<i>PpMYB15</i>	R2R3-MYB	Flavonols	Activation	Prupe.8G270000	[130]
	<i>PpMYBF1</i>	R2R3-MYB	Flavonols	Activation	Prupe.1G125300	[130]
	<i>PpMYB10</i>	R2R3-MYB	Anthocyanin	Activation	ABX79945.1	[131]
	<i>PpMYB18</i>	R2R3-MYB	Anthocyanins, Proanthocyanidins	Inhibition	ALO81021.1	[131]
<i>Antirrhinum majus</i> (Plantaginaceae)	<i>AmROS1</i>	R2R3-MYB	Anthocyanins	Activation	ABB83826.1	[132]
	<i>AmROS2</i>	R2R3-MYB	Anthocyanins	Activation	ABB83827.1	[132]
	<i>AmVENOSA</i>	R2R3-MYB	Anthocyanins	Activation	ABB83828.1	[132]
	<i>AmMYB340</i>	R2R3-MYB	Flavonols	Activation	-	[133]
	<i>AmMYB305</i>	R2R3-MYB	Flavonols	Activation	-	[133]
	<i>AmMYB308</i>	R2R3-MYB	Flavonoids	Inhibition	P81393	[134]
	<i>AmMYB330</i>	R2R3-MYB	Flavonoids	Inhibition	P81395	[134]
<i>Petunia hybrida</i> (Solanaceae)	<i>PhAN2</i>	R2R3-MYB	Anthocyanins	Activation	AAF66727.1	[135]
	<i>PhPH4</i>	R2R3-MYB	Anthocyanins	Activation	AAY51377.1	[136]
	<i>PhDPL</i>	R2R3-MYB	Anthocyanins	Activation	ADW94950.1	[137]
	<i>PhPHZ</i>	R2R3-MYB	Anthocyanins	Activation	ADW94951.1	[137]
	<i>PhMYB27</i>	R2R3-MYB	Anthocyanins	Inhibition	AHX24372.1	[138]
	<i>PhMYBx</i>	R3-MYB	Anthocyanins	Inhibition	AHX24371.1	[138]
<i>Rosa rugosa</i> (Rosaceae)	<i>RrMYB5</i>	R2R3-MYB	Proanthocyanidins	Activation	AYP10274.1	[139]
	<i>RrMYB10</i>	R2R3-MYB	Proanthocyanidins	Activation	CCA29099.1	[139]
	<i>RrMYB113</i>	R2R3-MYB	Anthocyanins	Activation	AXQ12351.1	[140]
<i>Pyrus</i> spp. (Rosaceae)	<i>PbMYB12b</i>	R2R3-MYB	Flavonols	Activation	XP_009339792.2	[141]
	<i>PyMYB10</i>	R2R3-MYB	Anthocyanins	Activation	ADN26574.1	[142]
	<i>PyMYB114</i>	R2R3-MYB	Anthocyanins	Activation	ASY06612.1	[143]

5. Prospects

MYB transcription factors are central regulators of the flavonoid biosynthesis pathway in both monocot and dicot species. Comparative analyses between model monocots and the dicot *Arabidopsis thaliana* have revealed fundamental divergences in regulatory circuitry. In *Arabidopsis*, EBGs are primarily activated by functionally redundant R2R3-MYB proteins, while LBGs require the assembly of MBW complexes for transcriptional activation. In

contrast, monocots exhibit a more integrated regulatory model in which the MBW complex directly coordinates both EBGs and LBGs. This functional plasticity suggests that the MBW module has undergone lineage-specific evolution, leading to distinct architectural logics in flavonoid pathway regulation. Despite progress in characterizing the MBW complex, major knowledge gaps persist regarding the evolutionary mechanisms and molecular determinants underlying these regulatory divergences. Key unanswered questions include how the MBW complex acquired extended target gene specificity in monocots, the role of cis-regulatory element evolution and chromatin accessibility in shaping regulatory divergence, and the contribution of non-MYB factors and post-translational modifications to pathway fine-tuning in a lineage-specific manner. Addressing these questions is critical not only for understanding the evolutionary rewiring of metabolic networks but also for harnessing MYB regulators in biotechnology. Targeted manipulation of MYBs—through overexpression, silencing, or genome editing—holds substantial promise for tailoring flavonoid profiles to enhance crop resilience, nutritional content, and visual traits. Examples include increasing antioxidant levels in food crops, modifying flower and fruit pigmentation, and reducing antinutrient accumulation. Thus, elucidating the mechanistic basis of MYB regulatory divergence offers a foundation for predictive metabolic engineering across economically important plant species.

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