

The Flavonoid Biosynthesis Network in Plants

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Flavonoids have long been a major focus of research into secondary metabolism. We present a systematic summary of what is known of the flavonoid biosynthetic pathway in plants, presenting a model of flavonoid biosynthesis that includes eight branches (stilbene, aurone, flavone, isoflavone, flavonol, phlobaphene, proanthocyanidin, and anthocyanin biosynthesis) and four important intermediate metabolites (chalcone, flavanone, dihydroflavonol, and leucoanthocyanidin).

flavonoids

biosynthesis

molecular structure

biosynthetic enzyme

gene regulation

1. Introduction

Flavonoids comprise a group of phenylpropanoids that as water-soluble pigments stored in the vacuoles of plant cells [1]. Except for the stilbenes (a class of flavonoids), which has a C6-C2-C6 structure (Figure 1), the basic structure of flavonoids consists of a C6-C3-C6 carbon skeleton (Figure 1) comprising two 6-carbon benzene rings (rings A and B) linked by a 3-carbon heterocyclic ring (ring C) [2]. Flavonoids can be classified into 12 subgroups—chalcones, stilbenes, aurones, flavanones, flavones, isoflavones, phlobaphenes, dihydroflavonols, flavonols, leucoanthocyanidins, proanthocyanidins, and anthocyanins (**Figure 1**) [3][4]—based on the degree of oxidation of the heterocyclic ring and the number of hydroxyl or methyl groups on the benzene ring. At the same time, various modifications (glycosylation, acylation, and others) and molecular polymerization lead to the formation of a large number of flavonoid compounds [5][6]. To date, more than 9,000 plant flavonoids have been isolated and identified [7].

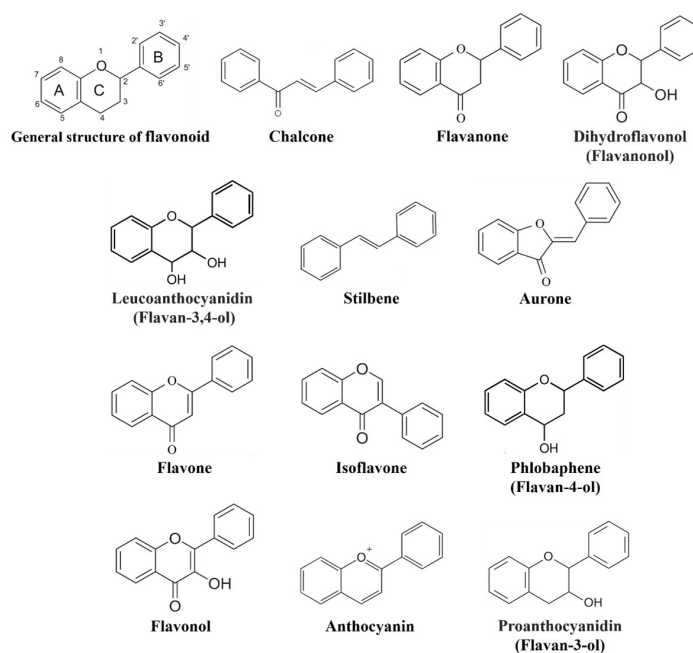


Figure 1. General structure of flavonoids

Some flavonoids play an important role in plant development and defense. Flavonoids constitute one of the main pigments in plants, such as the anthocyanins (red, orange, blue, and purple pigments); chalcones and aurones (yellow pigments); and flavonols and flavones (white and pale-yellow pigments), that impart on plants a wide variety of colors [8]. Flavonoids, as phytoalexins or antioxidants, have reactive oxygen species (ROS) scavenging ability [9] and protect plants against damage from biotic and abiotic stresses, including UV irradiation, cold stress, pathogen infection, and insect feeding [10][11][12]. In plants, flavonoids can also act as signaling molecules, attracting insects for pollination and participating in auxin metabolism [13]. Plant flavonoids also have widespread use in daily life, such as for food and medicinal purposes. For instance, anthocyanins and proanthocyanidins are important edible pigments and taste-regulating components in food and wine [4], while plant flavonoids, administered as active ingredients, can help delay the aging of the nervous system, immune organs, reproductive system, liver, and skin, and also contribute to the prevention of osteoporosis, cardiovascular disease, Alzheimer's disease, and breast cancer [14][15][16].

2. Flavonoid biosynthesis in plants

Flavonoids have long been a major focus of research into secondary metabolism. On PubMed, performing a search using 'flavonoid' as a search term retrieves more than 10,000 articles in both 2019 and 2020. Recent decades have witnessed a considerable renewed interest in flavonoid biosynthesis in plants. In this review, we present a systematic summary of what is known of the flavonoid biosynthetic pathway in plants, presenting a model of flavonoid biosynthesis that includes eight branches and four intermediate metabolites (**Figure 2**), thereby providing a theoretical basis for the genetic improvement of flavonoid metabolism as well as improving our understanding of their functions and potential uses.

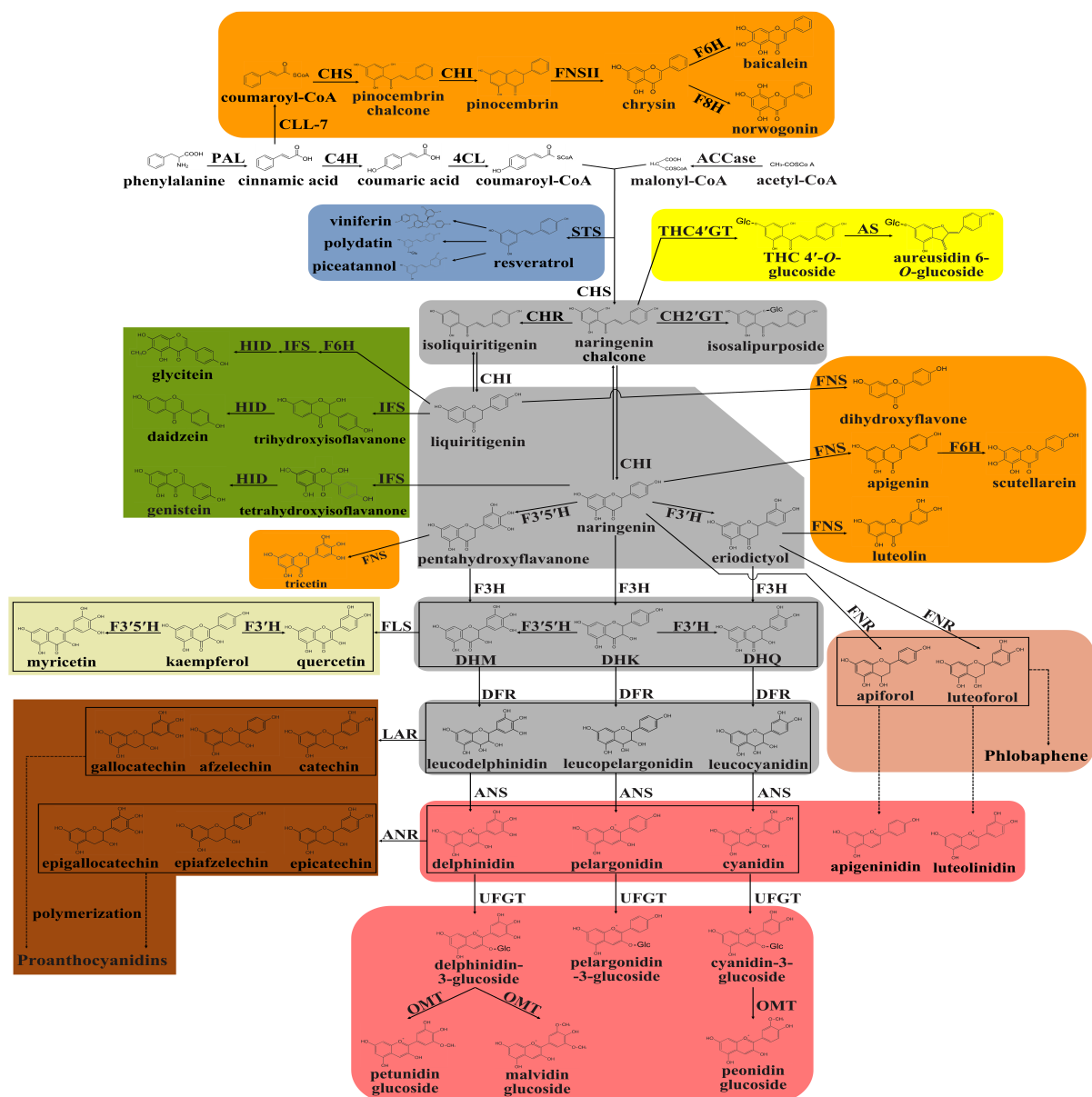


Figure 2. The flavonoid biosynthetic pathway in plants contains eight branches (represented by the eight colored boxes) and four important intermediate metabolites (gray boxes). The enzyme names and flavonoid compounds are abbreviated as follows: PAL, phenylalanine ammonia lyase; C4H, cinnamic acid 4-hydroxylase; 4CL, 4-coumarate: CoA ligase; ACCase, acetyl-CoA carboxylase; STS, stilbene synthase; CHS, chalcone synthase; CHR, chalcone reductase; CH2'GT, chalcone 2'-glucosyltransferase; CH4'GT, chalcone 4'-O-glucosyltransferase; AS, aureusidin synthase; CHI, chalcone isomerase; FNS, flavone synthase; CLL-7, cinnamate-CoA ligase; F6H, flavonoid 6-hydroxylase; F8H, flavonoid 8-hydroxylase; IFS, isoflavone synthase; HID, 2-hydroxyisoflavanone dehydratase; FNR, flavanone 4-reductase; F3H, flavanone 3-hydroxylase; F3'5'H, flavanone 3',5'-hydroxylase; DHK, dihydrokaempferol; DHQ, dihydroquercetin; DHM, dihydromyricetin; FLS, flavonol synthase; DFR, dihydroflavonol 4-reductase; ANS, anthocyanidin synthase; UFGT, UDP-glucose flavonoid 3-O-glucosyltransferase; OMT, O-methyl transferases; LAR, leucoanthocyanidin reductase; ANR, anthocyanidin reductase.

3. Transcriptional regulation of flavonoid biosynthesis in plants

Transcriptional control plays a central role in the modulation of flavonoid biosynthesis (**Figure 3**). The MBW complex, composed of MYB, bHLH, and WD40, is the main transcriptional regulator in flavonoid biosynthesis [17]. MYB transcription factors have a conserved MYB domain in the N-terminus that is required for DNA binding and interaction with other proteins [18]. Members of the R2R3-MYB group are mainly involved in regulating flavonoid metabolism [19]. The overexpression of *AN4* (a R2R3-MYB-encoding gene) can enhance anthocyanin biosynthesis by promoting the expression of anthocyanin biosynthesis genes, such as *CHS*, *CHI*, *F3H*, and *DFR* [20]. In *Cucumis sativus*, the R2R3-MYB transcription factor CsMYB60 induced the expression of CsFLS and CsLAR by binding to their promoters, thereby promoting flavonol and proanthocyanidin biosynthesis [21]. MYB transcription factors also act as repressors in the regulation of flavonoid biosynthesis. For instance, in the apple (*Malus domestica*), MdMYB15L was reported to interact with MdbHLH33 and inhibit the promotion of the MdbHLH33-MYB-WD40 (MBW) complex, thereby also suppressing anthocyanin biosynthesis [22].

bHLH transcription factors have been shown to participate in the regulation of flavonoid biosynthesis. The transient expression of *DhbHLH1* induces anthocyanin synthesis in the white petals of *Dendrobium* hybrids [23]. In *Dianthus caryophyllus*, meanwhile, the “red speckles and stripes on white petals” phenotype results from the local expression of *bHLH*, which promotes the expression of *DFR* and that of downstream enzymes in the anthocyanin biosynthetic pathway [24].

WD40, widely present in eukaryotic cells, contains multiple tandem repeats of a WD motif and interacts with other proteins through its WD domain [1]. Generally, WD40 does not directly bind to target gene promoters, forming instead a complex with MYB and bHLH in the regulation of flavonoid biosynthesis. The WD40 protein TTG1 regulated anthocyanin metabolism through MYB/bHLH/TTG1 complex [25]. Moreover, in tomato, the WD40 protein SIAN11 was shown to induce anthocyanin and proanthocyanidin biosynthesis and limit flavonol accumulation by repressing *FLS* expression [26].

Also in tomato, besides the MBW complex, the transcription factors NF-YA, NF-YB, and NF-YC can reportedly form a NF-Y protein complex that binds to the promoter of the *CHS1* gene, thereby regulating flavonoid synthesis and affecting tomato peel color [27]. Additionally, the ethylene response factors Pp4ERF24 and Pp12ERF96, through interacting with PpMYB114, potentiated the PpMYB114-mediated accumulation of anthocyanin in pear [28]. In the tea plant, UV-B irradiation-mediated bZIP1 upregulation leads to the promotion of flavonol biosynthesis by binding to the promoters of *MYB12*, *FLS*, and *UGT* and activating their expression; under shading, meanwhile, PIF3 inhibited flavonol accumulation by activating the expression of *MYB7*, which encodes a transcriptional repressor [29]. In peach, NAC1 was shown to regulate anthocyanin pigmentation through activating the transcription of *MYB10.1*, while NAC1 was repressed by SPL1 [30]. In the pear, PyWRKY26 interacts with PybHLH3 and activates the expression of PyMYB114, resulting in anthocyanin biosynthesis [31]. The BTB/TAZ protein MdbT2 represses anthocyanin biosynthesis, and MdGRF11 interacts with, and negatively regulates, MdbT2, leading to an increase in the expression of anthocyanin biosynthesis-related genes *via* the enhancement of the abundance of MdMYB1

protein [32]. SIBBX20 can bind the *SIDFR* promoter and directly activate its expression, which augments anthocyanin biosynthesis, while SICSN5, a subunit of the COP9 signalosome, induces the degradation of SIBBX20 by enhancing its ubiquitination [33]. MdARF19 modulates anthocyanin biosynthesis by binding to the promoter of *MdLOB52* and further activating its expression [34]. BES1, a positive regulator in brassinosteroid signaling, inhibits the transcription of the MYB proteins MYB11, MYB12, and MYB111, thereby decreasing flavonol biosynthesis [35].

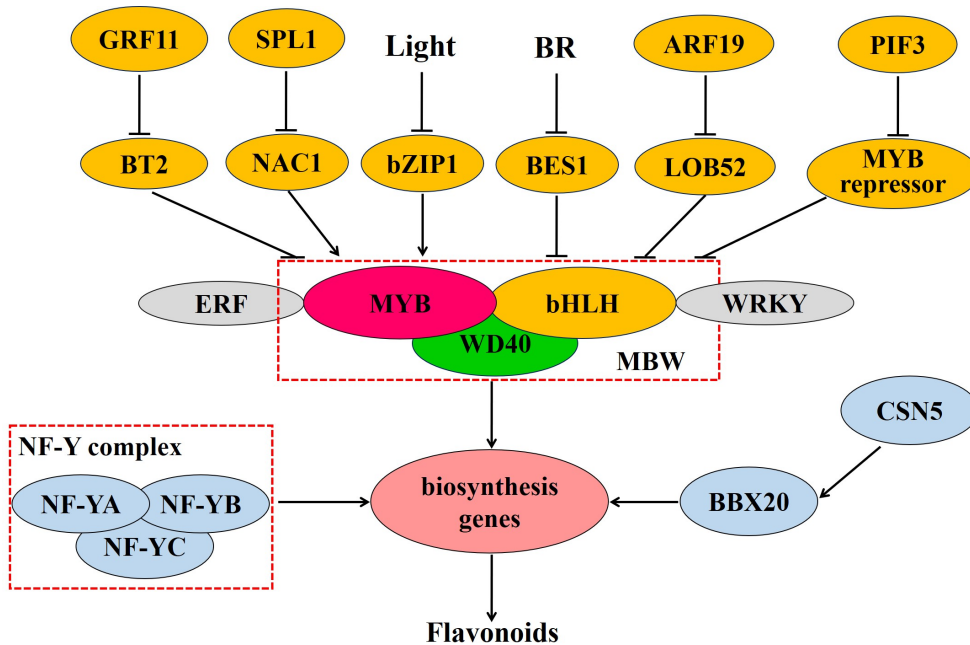


Figure 3. Transcriptional regulation

of flavonoid biosynthesis in plants. Abbreviations are as follows: MYB, *v-myb* avian myeloblastosis viral oncogene homolog; bHLH, basic helix-loop-helix; NF-Y, nuclear factor Y; ERF, ethylene response factor; NAC, (NAM, ATAF, CUC); SPL, squamosa promoter binding protein-like; GRF, growth regulating factor; BT, BTB/TAZ; BBX, b-box protein; ARF, auxin response factor; LOB, lateral organ boundaries; BES1, BRI1-EMS-SUPPRESSOR 1; BR, brassinosteroid. The red dashed box represents the protein complex: MBW complex is constituted of three class of transcription factors (TFs), MYB, bHLH and WD40, while NF-Y complex is composed of TFs NF-YA, NF-YB, and NF-YC. TFs next to each other represent interaction of proteins.

4. Perspectives

Flavonoids are abundantly present in land plants where they have diverse functions; as dietary components, they also exert a variety of beneficial effects in humans [2][16][36][37]. Elucidating the pathways involved in the biosynthesis of flavonoids will aid in better understanding their functions and potential uses. For example, the heterologous transformation of *F3'5'H* from *Campanula medium* (Canterbury bells) and *A3'5'GT* (anthocyanin 3',5'-*O*-glucosyltransferase gene) from *Clitoria ternatea* (butterfly pea) driven by the native (*Chrysanthemum morifolium*) *F3H* promoter induced the synthesis of delphinidin and generated true blue Chrysanthemums [3][6][38]. Flavonoids have also been produced for food and medicine in engineered bacteria. The functional expression of plant-derived *F3H*, *FLS*, and *OMT* in *Corynebacterium glutamicum* yielded pterostilbene, kaempferol, and quercetin at high concentrations and purity [39]. In *Escherichia coli*, cyanidin 3-*O*-glucoside was generated through the induction of

ANS and 3GT using a bicistronic expression cassette [40]. These observations highlight the important application and economic value of deciphering the pathways involved in flavonoid biosynthesis.

Over the past few decades, flavonoid biosynthesis has been among the most intensively investigated secondary metabolic pathways in plant biology, and a considerable number of studies have contributed to revealing the exquisite mechanisms underlying the biosynthesis of flavonoids in plants [1]. However, several questions remain outstanding. For example, no comprehensive model exists as yet regarding which enzymes catalyze the formation of 3-deoxyanthocyanidin; additionally, the biosynthesis of phlobaphenes needs to be further improved.

Plants are rich in diversity and often produce specific secondary metabolites. Recent studies have identified a unique flavone synthesis pathway in the root of the medicinal plant *S. baicalensis*, which generated root-specific flavones such as baicalein and norwogonin [41][42]. Accordingly, whether specific flavonoid biosynthesis pathways and metabolites also exist in other plants warrants further investigation, so as to continuously improve our knowledge of the flavonoid biosynthesis network.

In addition, combined multi-omics (genomics, transcriptomics, proteomics, and metabolomics) analysis provides a direction for the study of plant synthetic biology. In rice, a *flavonoid 7-O-glycosyltransferase* (*OsUGT706C2*) gene with a role in modulating flavonol (kaempferol) and flavone (luteolin and chrysoeriol) metabolism was identified by metabolite-based genome-wide association analysis [43]. Proteomics and transcriptomics, complemented with gas chromatography-mass spectrometry (GC-MS) analysis, aided in elucidating the flavonoid metabolic pathway during seed ripening in *Camellia oleifera* [44]. The constantly evolving multi-omics technology combined with big data analysis will likely lead to the identification of novel flavonoids and increased knowledge of the flavonoid biosynthesis network.

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