MYB transcription factors (TFs) belong to one of the largest and important gene families, which regulate development under changing environmental conditions, primary and secondary metabolism, and plant response to stresses (biotic and abiotic stresses). MYB repressors have a conserved N-terminal domain like other MYB TFs, but the C-terminal domain makes them structurally and functionally different from the rest. MYB repressors usually possess some repressive motifs, such as EAR (ethylene-responsive element binding factor-associated amphiphilic repression motif), SID (Sensitive to ABA and Drought 2 protein interact motif), and TLLLFR motifs, which contribute to their repression function through a variety of complex regulatory mechanisms. In this review, we summarize recent developments in research of MYB repressors and suggest directions to future research.

KEYWORDS
EAR motif; gene regulation; MBW complex; MYB transcription factor; secondary metabolism

I. Introduction

MYB transcription factors (TFs) are identified in many eukarya (Jia et al., 2004), and are well-researched in plants. The first plant MYB transcription factor (TF) was isolated from maize (Zea mays) in the 1980s and showed 40% sequence homology to the animal MYB proto-oncogene (Paz-Ares et al., 1987). Subsequently, the structure and function of various MYB proteins have been extensively studied in many plant species. MYB proteins usually have the following two discrete regions: N-terminal and C-terminal. The N-terminal region has a conserved MYB domain that is crucial for DNA binding, whereas the C-terminal region is variable defines the functional multiplicity of this class of TFs. Generally, the MYB domain contains one to four imperfect repeats (R), and each repeat comprised of 50-53 amino acid residues has three \(\alpha\)-helicies. The second and third helices form a 3D helix-turn-helix (HTH) structure with a hydrophobic moiety, which contributes to the recognition of the specific target gene (Ogata et al., 1996). The third helix is responsible for direct contact with the major DNA groove (Jia et al., 2004). Depending on the location and number of these repeats, MYB proteins can be divided into the following four main classes: 1R (R1/2, R3-MYB), 2R (R2R3-MYB), 3R (R1R2R3-MYB), and 4R (R1/R2-like repeats) (Figure 1) (Dubos et al., 2010).

MYB proteins are essential for regulating pathways involved in primary and secondary metabolism, growth and development, and biotic and abiotic stress responses (Dubos et al., 2010; Liu et al., 2015; Ma and Constabel, 2019). The MYB proteins function by directly or indirectly binding the cis-acting element of DNA to activate or inhibit the downstream genes. In this review, we summarized the structure and function of MYB repressors and the regulatory mechanisms of these TFs in plant secondary metabolism.

II. Structure of MYB repressor proteins

A. Signature features of MYB repressors

The DNA-binding domain of MYB repressors is in the N-terminal region, highly conserved, and consists of different numbers of repeats. The repressive function of these proteins usually depends upon the
distinct motifs in the C-terminal region (Figure 1). In the study of Arabidopsis thaliana MYB family, the majority of MYB repressors belonged to the subgroup 4 of R2R3-MYB proteins, whose C-terminal has a conserved motif, C1 or C2. C1 LlsrGIDPxT/sHRxI/L is referred to as the GIDP domain and C2 pdLNLD/ELxiG/S is referred to as an EAR motif (ethylene-responsive element binding factor-associated amphiphilic repression motif). Additionally, some members have Zinc-finger domain CX1_2CX7_12CX2C (Kranz et al., 1998). These conserved domains are considered responsible for the repression activity of these proteins. EAR motif was first identified in AtERF4 as pdLNL D/ELxiG/S (Ohta et al., 2001). Members of other TF families, such as ERF (ethylene-responsive element binding factor), ZCT (zinc finger Catharanthus protein), and AUX/IAA (auxin/indole-3-acetic acid proteins), also contain EAR domains and act as repressors in the regulation of signaling pathways (Kazan, 2006). The EAR-containing TF AtMYB4 is a negative regulator of the sinapate ester biosynthesis induced by UV-B in Arabidopsis (Jin et al., 2000). In rice, the negative regulator of disease resistance NRR (Chern et al., 2005) and its homologs in Arabidopsis NIMIN2 (Weigel et al., 2001) and tobacco G8-1 (Horvath et al., 1998) have an LDLNxXP in the C-terminal, which resembles the EAR motif. Tobacco ZFT1 lost its repressive activity when the EAR domain was deleted (Uehara et al., 2005). The repressing activity of ZCT1, ZCT2, and ZCT3 in Catharanthus roseus is also dependent on the LxLxL type EAR motif (Pauw et al., 2004). Although the EAR motif is a ubiquitous core suppression domain among a large number of plant TFs, the TLLLFR and R/KLFGV motifs exhibit repressive functions (Matsui et al., 2008; Ikeda and Ohme-Takagi, 2009). The TLLLFR was first identified in Arabidopsis AtMYBL2 (R3-MYB) repressor (Matsui et al., 2008), and subsequently in VvMYBC2L-1, VvMYBC2L-2, VvMYBC2L-3, PtMYB165, and PtMYB194 (Cavallini et al., 2015; Yoshida et al., 2015). R/KLFGV was identified as a repressive domain in various TFs, including MYB, HSF, and AP2 by transient expression analysis, however, the regulatory mechanism remains unclear and requires further investigation (Ikeda and Ohme-Takagi, 2009).

B. Classification of MYB repressors

The characteristics of MYB repressors were summarized by using the online tool MEME (http://meme-suite.org/) to search specific motifs of 37 MYB repressors (Table 1). The majority contained an EAR motif with the conserved sequence LxLxL (Figure 2A). Moreover, 14 of those 37 proteins contained conserved GY/FDFLGL sequences, also known as SAD2 interacting motif (SID motif) (Figure 2B). The protein sequence alignment of those 14 SID-containing MYB

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**Figure 1.** Four types of MYB transcription factors. The N-terminal of MYBs are divided into four groups, R1, R2, and R3 are three types of R repeat with similarity to R1, R2 or R3 of c-Myb. The 1R group contains 1R only, the 2R group contains 2R and 3R repeat, which are also known as R2R3-MYB subfamily. The 3R group contains three R repeats: R1, R2, and R3. The 4R group contains four R repeats, one R1 and R1/2, and two R2 subgroups. The C-terminal of MYB repressors often contain one or two distinct motifs like EAR motif (ERF-associated amphiphilic repression), SID motif (Sensitive to ABA and Drought 2 protein interact motif), and TLLLFR motif.
| Name       | Species                          | Motif                  | Function                             | Accession       | Reference          |
|------------|----------------------------------|------------------------|--------------------------------------|-----------------|--------------------|
| AtMYB4     | Arabidopsis thaliana             | EAR, SID               | flavonoid                            | AT4G38620       | Jin et al., 2000   |
| AtMYB7     | A. thaliana                      | EAR, SID               | flavonol                             | AT2G16720       | Fornale et al., 2014|
| AtMYB23    | A. thaliana                      | EAR                    | anthocyanin                          | AT5G40330       | Hiratsu et al., 2003|
| AtMYB60    | A. thaliana                      | EAR                    | anthocyanin                          | AT1G08810       | Park et al., 2008   |
| AtMYB1D    | A. thaliana                      | TLLLFR                 | flavonoid, anthocyanin               | AT1G71030       | Matsui et al., 2008|
| EJMYB2     | Eriobotrya japonica              | EAR, SID               | anthocyanin                          | KF767454        | Xu et al., 2014     |
| EgMYB1     | E. gnunni                        | EAR, SID               | lignin                               | AJ576024        | Legay et al., 2010  |
| FaMYB1     | Fragaria × ananassa              | EAR                    | anthocyanin, flavonol                | AF401220        | Aharoni et al., 2001|
| FcMYB1     | F. chloensis                     | EAR                    | anthocyanin                          | GQ067222        | Salvatiera et al., 2013|
| FtMYB11    | F. tataricum                     | F. tataricum           | EAR, SID                             | FT1279658       | Zhou et al., 2017   |
| FtMYB13    | F. tataricum                     | F. tataricum           | SID                                  | KY290579        | Zhang et al., 2018  |
| FtMYB14    | F. tataricum                     | F. tataricum           | SID                                  | KY290580        | Zhang et al., 2018  |
| FtMYB15    | F. tataricum                     | F. tataricum           | rutin                                | KY290580        | Zhang et al., 2018  |
| GmMYB100   | Glycine max                      | EAR                    | isoflavonoid, flavonol               | Glyma07g33960.1 | Yan et al., 2015    |
| LIMYB1     | Leucaena leucocephala            | EAR, SID               | lignin, phenylpropanoid              | G091209         | Omer et al., 2013   |
| LIMYB2     | Medicago truncatula              | EAR                    | anthocyanin                          | XM_003616340    | Jun et al., 2015    |
| MasaMYB31  | Musa cultivar Rastali            | EAR                    | anthocyanin, polyphenols             | KU07534         | Anwar et al., 2018  |
| NMYB2      | Narcissus. tazetta               | EAR                    | anthocyanin                          | KY60527         | Albert et al., 2014 |
| PHM4       | Petunia × hybrida                | EAR                    | anthocyanin                          | KF96523         | Spelt et al., 2000  |
| PHMYB7     | Petunia × hybrida                | EAR                    | anthocyanin                          | KF96522         | Albert et al., 2014 |
| PHMYBx     | Petunia × hybrida                | EAR                    | anthocyanin                          | KF159234        | Zhou et al., 2017   |
| PpMYB18    | Prunus persica                   | EAR                    | PAS, anthocyanin                     | Potri011G114000 | Ma et al., 2018     |
| PtMYB165   | Populus trichocarpa              | EAR, TLLLFR            | flavonoid, anthocyanin               | Potri010G114000 | Ma et al., 2018     |
| PtMYB57    | P. trichocarpa                   | EAR                    | PAS, anthocyanin                     | Potri010G114000 | Ma et al., 2018     |
| PtrMYB194  | P. trichocarpa                   | EAR, TLLLFR            | flavonoid, anthocyanin               | Potri010G128500 | Ma et al., 2018     |
| PtrMYB221  | P. trichocarpa                   | EAR, TLLLFR            | flavonoid, anthocyanin               | Potri010G128500 | Ma et al., 2018     |
| PtrRML1    | P. trichocarpa                   | EAR, TLLLFR            | secondary wall biosynthesis          | KK273518        | Hu et al., 2016     |
| TaMyb1D    | Triticum. aestivum               | EAR                    | anthocyanin                          | KLY79302        | Wei et al., 2017    |
| SITHM27    | Solanum lycopersicum             | EAR, SID               | anthocyanin                          | NM_001247046    | Lin et al., 1996    |
| Taeos_7AS_2EEC72628.11 | Triticum aestivum             | EAR, SID               | anthocyanin                          | EF113078        | Cavallini et al., 2015|
| VvMYB4a    | Vitis vinifera                   | EAR, SID               | anthocyanin                          | EF113078        | Cavallini et al., 2015|
| VvMYB4b    | V. vinifera                      | EAR, SID               | anthocyanin, phenolic                | FX520800        | Cavallini et al., 2015|
| VvMYB4-like| V. vinifera                      | EAR, SID               | anthocyanin                          | XP_00273328.1   | Pérez-Diaz et al., 2016|
| VvMYBC2-L1 | V. vinifera                      | EAR, TLLLFR            | proanthocyanidins (PAs)              | JX050227        | Huang et al., 2014   |
| VvMYBC2-L3 | V. vinifera                      | EAR, TLLLFR            | anthocyanin                          | KMO46932        | Cavallini et al., 2015|
| ZmMYB11    | Zea mays                         | EAR, SID-like          | lignin                               | GRMZM2G000818   | Vélez-Bermúdez et al., 2015|
| ZmMYB31    | Z. mays                          | EAR, SID-like          | lignin, phenylpropanoid              | NP_001103949    | Fornale et al., 2014 |
| ZmMYB42    | Z. mays                          | EAR, SID-like          | phenylpropanoid                      | HQ858894        | Yilmaz et al., 2009  |
repressors and three homologs of AtMYB4 (SITTHM27, LOC_Os08g43550.1, and Traes_7AS_2EE7C2628.11) (Table 1) showed that SID motifs are relatively conservative in dicot and monocotyledon. Compared to the conserved ERF motif in most plants, SID motifs exhibit differences between dicot and monocotyledon (Figure 2C), and indicated that the SID motif is probably related to the relationship between plants and their evolutionary differences.

Three hundred MYB protein sequences (downloaded from: http://planttfdb.cbi.pku.edu.cn) were identified containing an EAR motif or R/KLFGV and TLLLFR motif among nine species, including seven crop plants (Brassica napus, Oryza sativa subsp. indica, O. sativa subsp. japonica, Solanum lycopersicum, Triticum aestivum, Z. mays and Fagopyrum tataricum), one well-researched model plant (A. thaliana), and Aquilegia coerulea, the intermediate plant between dicots and monocots. A neighbor end-joining phylogenetic tree was constructed, which classified these proteins into 27 subgroups based on the bootstrap values greater than 70 (Figure 3). Subgroup 4, comprised of R2R3 MYB proteins having an EAR motif, are widespread in plants. Members of subgroup 22 also have an EAR motif in the N-terminal, such as AtMYB77 (AT3G50060.1) that can enhance auxin signaling under IAA and ABA treatment (Zhao et al., 2014). These types of MYB proteins might play a complex role in regulating plant signaling. There are many proteins that have an EAR motif in the subgroup 20, but their function is not known. Among these 300 sequences, only AtMYBL2 has a TLLLFR motif, At5g61620 has an R/KLFGV motif, and At3g16350, At5g47390, At5g56840 have both an EAR motif and R/KLFGV. At5g61620, At3g16350, At5g47390, At5g56840 are homologs of AtMYBD (a MYB-like protein), and their idiographic function has not been identified.

### III. MYB repressors function

After the first MYB was identified in maize (Paz-Ares et al., 1987), many MYB TFs in plants have been characterized (Jin et al., 2000; Legay et al., 2010; Xu et al., 2014; Jun et al., 2015; Zhou et al., 2017). Through functional characterization of MYB repressors, a large proportion of these repressors are involved in the biosynthesis of phenylalanine and...
phenylpropanoid-derived compounds (Table 1). These secondary metabolites were required for plant growth and development, the resistance against biotic and abiotic stresses, and the nutritional value. For instance, *MYB308* and *MYB330* were selected from six highly expressed genes in the flowers of the *Antirrhinum* spp. (Jackson *et al.*, 1991), and the heterologous expression of these, in tobacco, resulted in the regulation of monolignol, phenolic acid, and lignin (Tamagnone *et al.*, 1998).

The genome sequence of *A. thaliana* released in the year 2000 greatly promoted the research on the functions of various genes, including MYB repressors (Arabidopsis Genome Initiative, 2000). The EAR-containing AtMYB4 protein negatively regulated the sinapate ester accumulation (Jin *et al.*, 2000). AtMYB7, a homolog of AtMYB4, repressed the expression of *DFR* and UDP sugar glycosyltransferase (*UGT*) genes that encode key enzymes in the flavonoid pathway (Fornale *et al.*, 2014). Ectopic expression of the UV-B irradiation responsive gene AtMYB60 in lettuce (*Lactuca sativa*) inhibited the anthocyanin biosynthesis by suppressing the expression of *DFR* (Park *et al.*, 2008). A leaf specific one-repeat MYB, MYBL2

![Figure 3. Neighbor-joining phylogenetic tree of 300 MYB transcription factors. Neighbor-joining phylogenetic tree constructed using 300 amino acid sequences including the MYB proteins, which contain an EAR motif from *A. thaliana*, *B. napus*, *O. sativa* subsp. *indica*, *O. sativa* subsp. *japonica*, *S. lycopersicum*, *T. aestivum*, *Z. mays*, *F. tataricum*, *A. coerulea*.](163)
(Kirik and Baumlein, 1996), was identified as a negative regulator of the flavonoid biosynthesis in A. thaliana (Matsui et al., 2008; Dubos et al., 2010). Subsequently, overexpression of MYBL2 reduced the anthocyanin biosynthesis in Arabidopsis (Matsui et al., 2008). AtMYB23 repressed the expression of Glabra2 (GL2), which affected the development of epidermal cells of leaf, stem, and roots (Matsui et al., 2005).

MYB repressors were also identified and characterized in other dicots. Ectopic expression of eucalypt (Eucalyptus gunnii) gene EgMYB1 in poplar (Populus trichocarpa) and Arabidopsis results in the reduction of lignin biosynthesis, thus, repressing secondary wall formation (Legay et al., 2010). EjMYB2 identified from loquat (Eriobotrya japonica) down-regulated the lignin biosynthesis genes by countering the inductive effects of the activator EjMYB1 (Xu et al., 2014). The transcription repressor PtrMYB165 of poplar suppressed the flavonoid biosynthesis by repressing the flavonoid promoters, like PtrHHL131 (Ma et al., 2018). FtMYB11, FtMYB13, FtMYB14, FtMYB15, and FtMYB16 are repressors of rutin biosynthesis in F. tataricum, through spatially repressing the key enzyme genes (Zhou et al., 2017; Zhang et al., 2018). Moreover, FtMYB16 interfered with the transport of rutin precursors by directly repressing the expression of multidrug and toxic compound extrusion (MATE) transporter gene FtMATE1 (Li et al., 2019).

MYB repressors are involved in the regulation of proanthocyanidin (PA) and anthocyanin biosynthesis in various plants. In grape, VvMYBC2-L3, VvMYB4b, VvMYB4a, and VvMYB4-like reduced PA and anthocyanin accumulation and down-regulated structural and regulatory genes of the flavonoid biosynthesis pathway (Cavallini et al., 2015; Pérez-Díaz et al., 2016). Overexpression of NtMYB2 from Chinese narcissus (Narcissus tazetta) in tobacco repressed anthocyanin biosynthesis genes, particularly the UFGT gene (Anwar et al., 2018). Expression of FaMYB1 from strawberry in tobacco resulted in decreased flavonoids accumulation (Aharoni et al., 2001). RNAi-based gene silencing of FcMYB1, the homolog of FaMYB1, in Fragaria chiloensis resulted in the overexpression of anthocyanidin synthase (ANS) and down-regulation of anthocyanidin reductase and leucoanthocyanidin reductase (Salvatierra et al., 2013). MtMYB2 functions as part of a multidimensional regulatory network to regulate anthocyanin and PA accumulation during various developmental stages (Jun et al., 2015). Although the first plant MYB was found in maize (Z. mays), MYB repressors are not well studied in monocotyledonous plants. In maize, three MYB repressors, MYB11, MYB31, MYB42 were identified in the down-regulation of a set of lignin genes by the interaction with a TIFY family protein ZML2 in the wound-induced lignification pathway (Vélez-Bermúdez et al., 2015). The wheat (T. aestivum) MYB repressor TaMYB1D, which belongs to the subgroup 4 of the R2R3-MYB subfamily, has a dual function. Overexpression of TaMYB1D in tobacco (Nicotiana tabacum) resulted in the accumulation of lignin in stems and the enhanced expression of ROS- and stress-related genes in response to drought stress, however, the flavonoid content in leaves decreased (Wei et al., 2017). Ectopic expression of banana (Musa acuminate) MYB repressor MaMYB3 in tomato decreased degradation of starch and delayed fruit ripening by inhibiting starch metabolism genes and a positive regulator of starch degradation MabHLH6 (Fan et al., 2018).

IV. Regulation models of MYB repressors

A. The JAZ-MYB complex and the JAZ-MYB-SAD complex

In the 1990s, the consensus sequence (C/T)G(A/G)(A/C)GTT(A/G) was found to be an MYB-recognition element (MRE), by studying the c-MYB protein in mice (Howe and Watson, 1991). Later, MRE and ACE (ACGT-containing element) were identified as MYB-recognition elements in A. thaliana (Hartmann et al., 2005). In loquat, EjMYB1 interfered with the function of EjMYB2 through competitive interaction with ACE in the promoter region of lignin biosynthesis genes, such as Ej4CL1 (Ikeda and Ohme-Takagi, 2009; Xu et al., 2014). These consensus sequences are widely distributed throughout plant genomes, and their function as cis-element needs to be studied by specific experiments. With the advancement in the field and improvement in our understanding, TFs do not always function independently but require interaction with other TFs for proper action. MYB repressors were involved in different plant life processes through complex regulatory mechanisms (Deng and Lu, 2017; Allan and Espley, 2018; Ma and Constabel, 2019).

In Arabidopsis, JAZ (jasmonate ZIM-domain) proteins interacted with the R2R3-MYBs through ZIM-domain and N-terminal (approximately pre-130 aa) of JAZ proteins and R2R3 MYB, respectively (Song et al., 2011). In buckwheat, JAZ bound the SID-like motif of MYB TFs, and the Asp126 of MYB contributed a key role in the interaction (Zhou et al., 2017). However, the specific motif responsible for the interaction between JAZ and MYB in the MYB protein
sequence remains to be studied. Two 1R MYB proteins, TRY (the small MYB proteins TRIPETYCHON) and At4g01060, and five R2R3 MYB proteins including the MYB repressor AtMYB4 were tested for interaction with R/B-like bHLH factors AtbHLH012 and TT8 in a yeast two-hybrid assay, and showed the amino acid motif [DE]Lx2[HK]x3Lx6Lx3R in MYBs was the core sequence for protein interaction (Zimmermann et al., 2004; Kui et al., 2010). SAD2 (Sensitive to ABA and Drought 2 protein), an important β-domain protein in Arabidopsis, was involved in ABA signal transduction, salt stress and UV-B protection (Verslues et al., 2006; Zhao et al., 2007; Gao et al., 2008). SAD2 interacted with AtMYB4, which is required for the nuclear localization of AtMYB4 (Zhao et al., 2007). Soon afterward, a putative zinc-finger domain and a SID motif were found in the C-terminal of sub-group 4 R2R3-type MYB TFs MYB4, MYB7, and MYB32. Unlike the EAR motif that is widely distributed in the MYB protein family, the SID motif is relatively rare. Through multiple sequence alignment, the SID motif was determined to be relatively conserved in higher dicotyledons and diverse in Aquilegia, the earliest diverging branch of the eudicots and monocots (Figure 2), which may concern with different evolution history and physiological structure and monocots (Uncu et al., 2017), which may concern with different evolution history and physiological structure (Zhao et al., 2007; Zhou et al., 2015, 2017; Zhang et al., 2018).

B. The MBW complex

The MBW complex is a widespread regulatory model of the phenylpropanoid biosynthesis pathway and epidermal cell fate. The MBW complex is comprised of three kinds of TFs: MYB, bHLH, and WDR (Figure 5) (Albert et al., 2011, 2014). Through the study of relative expression of TFs and structural genes of anthocyanin biosynthesis pathway in petunia (Petunia hybridra), the AN1 (bHLH) was regulated by AN11 (WDR) and AN2 (MYB), and these three TFs function in a complex regulatory hierarchy (Spelt et al., 2000). In A. thaliana, the interactions among TTG1 (WDR), TT2 (MYB), and TT8 (bHLH) were identified through the yeast two-hybrid system and yeast three-hybrid system. Mutant studies showed that this interaction was required for the expression of downstream genes, confirmed through histochemical studies and A. thaliana protoplasts transactivation assay (Baudry et al., 2004). WD40 repeat protein (WDR) made up of 40 residues contains a β-propeller protein group, and the core region has a glycine–histidine (GH) dipeptide and a tryptophan–aspartate (WD) dipeptide (Smith et al., 1999). WDR proteins do not execute an enzymatic function and can only interact with other protein or promote protein-protein interactions (Ramsay and Glover, 2005). bHLH proteins recognize and bind to specific DNA sequence through the bHLH domain (Voronova and Baltimore, 1990). MBW complex can facilitate or inhibit the expression of genes. Activation or inhibition of downstream genes was often related to MYB protein (Xu et al., 2015). For instance, in petunia, two light stress induced MYB repressors PhMYBx and PhMYB27 negatively regulated anthocyanin pathway gene expression by competing with another MYB activator (AN1) to form an inhibitory MYB complex (Albert et al., 2011, 2014). The regulation mechanism of strawberry MYB repressor FaMYB1 resembled the mechanism of petunia MBW (PHZ, AN1, and AN11) complex (Dubos et al., 2010; Paolocci et al., 2011). In the forage legume, Trifolium repens, Tr-MYB133, and Tr-MYB134, the biosynthesis of anthocyanin and PA by suppressing the activator MBW complex (Albert, 2015). PtrMYB37 formed an
inhibitor MBW complex with bHLH131 and PtrTTG1 (WDR), decreased the biosynthesis of anthocyanins and PAs (Wan et al., 2017). However, PtrRML1 (R3 MYB-LIKE1) reduced the anthocyanin accumulation by repressing MBW component genes (Hu et al., 2016). Some MYB repressors interacted with other TFs to repress the activator MBW complex. MtMYB2 in *Medicago truncatula* bound with MtTT9 to inhibit

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**Figure 4.** The JAZ-MYB-SAD complex. The importin such as sensitive to ABA and Drought 2 (SAD2) protein and Frimportin-s1 recognizes the nuclear pore complex. MYB repressors function as transcription repressors by regulating the expression of other genes through binding their cis-acting element like MRE or ACE. When MYBs interact with them, the nuclear pore complex can transport the complex into the nucleus. In the nucleus, JAZ protein interacts with MYB repressors (MYB rep in the figure) and SAD acts as a co-repressor strongly repressing (bold line) the expression of the downstream genes like phenylalanine ammonia lyase (PAl) by binding to MYB binding sites like MRE or ACE. Some MYB repressors from a JAZ-MYB complex repress (plain line) the downstream genes. MYB repressors also can directly bind MYB binding sites like MRE or ACE and repress (thin line) downstream genes. However, in the presence of jasmonic acids (JAs), the inhibitory effect becomes weaker by the ubiquitin 26S proteasome degrading JAZ through JAZ proteins, binding JAs and from SCFCOI1 complex. Simultaneously, some MYB repressors are degraded through the ubiquitin 26S proteasome when JAs are present. Moreover, MYB activators (MYB act in the figure) compete with MYB repressors and bind to MRE or ACE activating the expression of downstream genes.

**Figure 5.** The MBW complex. The MBW complex consists of three kinds of transcription factors, MYB, bHLH, and WDR. The downstream genes are inhibited when the MYB repressors bind with bHLH and WDR to form the MBW complex and get activated when the activator binds the complex. Otherwise, some MYB repressors interact with other TFs to repress activator MBW complex. MYB repressor (MtMYB2) binds with bHLH (MtTT9) to inhibit the activity of MBW complex (MtMYB4/MtMYB5-MtTT8-MtTTG1), thus, reducing the anthocyanin and PAs accumulation. MYB repressor (AtMYBL2) and JAZ interact with bHLH and MYB/bHLH, respectively, to suppress the MBW complex and reduce the anthocyanin accumulation. During stress, DELLA proteins sequester with MYB repressor (AtMYBL2) and JAZ to activate the MBW complex and subsequently increase the anthocyanin accumulation.
the activity of MYB activators (MtMYB4 and MtMYB5) in MtTT8-MtTTG1 MBW complex, and thus reduced the anthocyanin and PAs accumulation (Jun et al., 2015). AtMYBL2 and JAZ interacted with bHLH and MYB/bHLH respectively to suppress the MBW complex and reduce anthocyanin accumulation. During stress, DELLA protein (RGA) interacted with AtMYBL2 and JAZ to activate the MBW complex and subsequently increase anthocyanin accumulation (Xie et al., 2016). Additionally, DELLA and JAZ proteins modulated gibberellin (GA) and jasmonate (JA) signaling synergy by interacting with the bHLH TFs GL3/EGL3 and the MYB TF GL1. GA and JA induced degradation of DELLA and JAZ and resulted in the activation of the MBW complex (Qi et al., 2014).

V. Conclusion and prospects

Plants have developed intricate regulatory mechanisms to respond to various environmental changes. TFs mediate genes expression via direct interaction with promoter sequences and/or with other TFs. The studies on MYB TFs indicate that a large proportion of MYB repressors belong to R2R3 MYB family and R3 MYB family, and their repression activity mainly depends on the repression motifs, such as EAR and SID in the C-terminus of protein. These motifs are important for binding with bHLH proteins or recruiting repressor and corepressors. However, the precise function and repression mechanism of TLLLFR motif needs to be studied. MYB TFs can regulate the gene expression by competitive binding with the cis-acting element in the promoter region. The whole genome ChIP-seq data will contribute to a better understanding of the MYB regulated genes and the identification of other variants of MYB binding sites in the promoters region of MYB regulated genes. A better understanding of the regulation mechanisms of MYB repressors requires some questions to be answered: how MYB repressors perceive environmental signals, what is the role of micro RNA in the regulation of MYB repressors, does post-translational modifications play any role in the regulation?

Disclosure statement

No conflict of interest was declared.

Author contributions

M.Z. and X.Z designed the paper. C.C., K.Z, and M.K. analyzed the data. C.C., K.Z, M.K., M.H., M.I.G., X.Z and M.Z wrote the paper.

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