Research progress of MYB transcription factor family in plant stress resistance

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Abstract

The MYB (v-MYB avian myoblast viral oncogene homolog) family of transcription factors is a large class of transcription factors that are widely distributed in eukaryotes and found in nearly all eukaryotes. The MYB protein exhibits the typical structure and function of transcription factors. Its protein molecular structure consists of a highly conserved DNA-binding domain known as the MYB domain, as well as a relatively less conserved transcriptional activation region and negative regulatory region. MYB proteins can regulate plant growth and development, primary and secondary metabolism, and respond to various abiotic stresses such as drought, high temperature, and high salt. In this paper, we summarize the structural characteristics of MYB family transcription factors, as well as their roles in biotic and abiotic stresses. We also elaborate on the progress of relevant research, aiming to provide theoretical insights for better understanding the functions and regulatory mechanisms of all members of the MYB family in plants. Furthermore, we aim to explore the potential utilization of these transcription factor family members in crop improvement.

Keywords: MYB transcription factors; protein structure; plant; stress

Introduction

Plants are vulnerable to long-term adverse environmental disturbances, such as biotic stress caused by diseases, pests, and other organisms; and abiotic stress caused by drought, high salt, heavy metals, extreme temperatures, etc. Among them, drought, salinity, and extreme temperatures are the primary environmental factors that limit agricultural plant productivity and jeopardize crop safety (Chen et al., 2022). The ongoing climate changes further intensify the influence of abiotic stress on plants. In order to withstand both biotic and abiotic stresses, plants have developed diverse defense mechanisms. However, these stresses continue to significantly impact crop quality and yield. Reports indicate that China's major crops, including rice, wheat, and corn, are particularly vulnerable to drought and high salinity soils. It is expected that by 2050, climate change may cause 50% of the land to become severely saline and alkaline (Javed et al., 2020).

Transcription factors (TFs), also known as trans-effectors, regulate the processes of biological life activities and participate in various signal transduction and regulatory processes (Pratyusha and Sarada, 2022). They are key regulatory factors for gene expression in organisms. TFs directly or indirectly bind to cis-acting
elements to regulate the inhibition or enhancement of target gene transcription efficiency, enabling plants to respond to stress (Ma et al., 2022), and play an important role in plant stress resistance (Inukai et al., 2017). Typical plant transcription factors have four functional regions: a DNA binding region (DBD), a nuclear localization signal, an oligomerization site, and a transcriptional regulatory region (Dubos et al., 2010). Usually, transcription factors can be divided into several families based on the characteristics of DNA binding regions. Among these families, four main categories are related to plant stress resistance: bZIP, WRKY, AP2/ERF, and MYB (Li et al., 2019).

The MYB (v-MYB avian myeloblastosis viral oncogene homolog) family is a transcription factor family with diverse functions and a wide distribution (Liu et al., 2008). The first MYB transcription factor cloned from Gramineae plants is the ZmMYBC1 gene (Paz-Ares et al., 1987). This gene primarily regulates the biosynthesis of anthocyanins in corn. The varying number of structural domains in the MYB family gives them different functions. They not only regulate plant growth and development, cell morphology, and physiological metabolism, and other physiological processes (Grotewold et al., 1994), but also participate in the regulation of secondary metabolism, control of cell morphogenesis, and plant nitrogen metabolism (Ambawat et al., 2013).

In this paper, we provide a summary of the fundamental structural characteristics of the MYB transcription factor family and its response to both biotic and abiotic stresses. The aim is to offer theoretical insights for future research on the function and regulatory mechanisms of the MYB transcription factor family, as well as to enhance the utilization of these transcription factors in crop improvement engineering.

**Basic structural characteristics of MYB transcription factor family**

The MYB transcription factor family has a highly conserved DNA binding domain known as the MYB domain. This domain typically contains incomplete repeats of 1-4 tandem MYB repeat sequences (Rs) at the N-terminus. Each repeating sequence typically contains 50-53 amino acids and encodes three α-helices. The second and third helices form a helix-turn-helix (HTH) structure that binds to larger grooves in DNA (Kranz et al., 1998; Dubos et al., 2010; Rosinski and Atchley, 1998). There are three tryptophan residues in the MYB domain, separated by approximately 18 amino acids, which are crucial for maintaining the hydrophobic structure of the HTH (Baldoni et al., 2015). Tryptophan is sometimes replaced by aromatic or hydrophobic amino acids (Ogata et al., 1996). In most MYB transcription factors, there are transcriptional activation domains rich in acidic amino acids located between the C-terminal and DNA binding domains. These domains can regulate protein activity and play an crucial role in maintaining protein functional diversity (Kranz et al., 1998).

MYB can be divided into the following four categories based on the number and position of repetitive sequences in the MYB domain (Figure 1): 1R-MYB (R1/R2, R3-MYB), 2R-MYB (R2R3-MYB), 3R-MYB (R1R2R3-MYB), and 4R-MYB (R1/R2-MYB) (Wang et al., 2021b). 1R-MYB (MYB-related) is an important telomere-binding factor responsible for maintaining the integrity of chromosome structure and regulating gene transcription (Yu et al., 2000; Romero et al., 1998). 2R-MYB, also known as R2R3-MYB, is the most abundant and functional MYB protein in plants. R2R3-MYB participates in cell differentiation, organogenesis, leaf morphogenesis, hormone response, secondary metabolism, and defense against various stressors (Yu et al., 2023; Yan et al., 2021). 3R-MYB primarily regulates the cell cycle, cell differentiation, and plant tolerance to stress (Haga et al., 2007). 4R-MYB is only found in Arabidopsis, grapes, and Populus tomentosa, so its functional research has not been fully developed (Wilkins et al., 2009; Du et al., 2013; Matus et al., 2008). In these classifications, the R2R3-MYB transcription factor has been widely studied for its various roles in plants (Li et al., 2019). Currently, with the advancement of research progress and the emergence of whole genome sequencing, a significant number of MYB transcription factor family members have been identified in plants,
including 217 transcription factors found in potatoes (Li et al., 2021); 187 transcription factors were found in radish (Muleke et al., 2021). The expression levels of these MYBs vary among different plant species. They are widely involved in various response mechanisms and play an important regulatory role in combating biotic and abiotic stresses (Ma and Constabel, 2019; Pratyusha and Sarada, 2022; Shimotohno et al., 2021).

![Figure 1.](image)

**Figure 1.** A Classification of MYB TFs in plants; B Structure of several MYB TFs (The red rectangles in the R3 domain represent the basic-helix-loop-helix binding domain) (Ma and Constabel, 2019)

**The role of MYB transcription factors in biotic stress**

Biotic stress refers to the collective term for various biological factors that are detrimental to the survival and development of plants (Abe et al., 1997). Usually caused by infections and competition between plants, such as diseases, pests, and weed hazards. In plants, for example, when soybeans can be invaded by *Sphromonas fabricius*, tomatoes can be infected by *Botrytis cinerea*, and cucumbers can be infected by powdery mildew (Aoyagi et al., 2014; Liu et al., 2016; Meng et al., 2022), MYB transcription factors are induced in response to pathogen attacks. *AtMYB30* has been confirmed to be induced by reactive oxygen species treatment in *Arabidopsis*. In addition, *AtMYB30* targets lipid transfer protein 1 (LTPG1) and LTPG2, which are anchored by GPI, forming a MYB30-dependent regulatory network that triggers an immune response to bacteria (Mabuchi et al., 2018). Identification of the R2R3-MYB gene *TaRIM1* from transcriptome data and cloning from resistant *Wheat CI12633* for positive regulation of tolerance to *Rhizoctonia solani* (Shan et al., 2016).

The MYB transcription factor combats pests by regulating the accumulation of flavonoids and glucosinolates. In *Arabidopsis*, *AtMYB41* can resist external insect invasion by inducing dehydration after injury (Cominelli, 2008). Experimental evidence has shown that in *Brassicaceae*, MYB29 is highly induced under pest treatment, and most genes regulating indole glucosinolate were found to be upregulated in the experiment. Homologous MYB proteins exhibit a high degree of complexity in transcriptional regulation under stimulation (Augustine, 2015).

In addition, as demonstrated by mutation and overexpression studies on eggplants have demonstrated that the *SmMYB44* gene in *Solanum* plants positively regulates the tolerance of *Ralstonia solanacearum* (Qiu et al., 2019). Several other genes, including *AtMYB15*, *AtMYB30*, *AtMYB73*, *MdMYB30*, and *PacMYBA*, have also been identified as positive regulators of *Pst DC3000* stress in transgenic *Arabidopsis* (Kim et al., 2020; Jia et al., 2011; Shen et al., 2017; Zhang et al., 2019; Vailleau et al., 2002). Similarly, three MYB transcription
factors have been found in cotton: GhMYB4, GhMYB36, and GhODO1. These factors enhance Dahlia’s tolerance to *Verticillium wilt* by regulating several defense mechanisms (Zhu et al., 2022; Liu et al., 2022; Xiao et al., 2021). Unlike many other transcription factors, CaPHL8, a MYB transcription factor in chili peppers, plays a positive regulatory role in the response to *Ralstonia solanacearum* but is not related to high-temperature stress tolerance.

In addition, some MYB transcription factors act as repressors in the interaction between hosts and pathogens. For example, when Arabidopsis is stressed by *PstDC3000*, the signaling of jasmonic acid (JA) and salicylic acid (SA) is upregulated in JA/SA insensitive mutants. This indicates that *AtMYB13* is involved in the plant’s response to *PstDC3000* stress in the JA/SA independent pathway. Further research reports suggest that the loss of *AtMYB13* function can promote sugar deposition and accelerate cell death, indicating a negative role in immune responses against pathogens (Chen et al., 2013). In summary, MYB transcription factors can enhance the tolerance of plants to pathogen infection, activate or inhibit responses to various stresses, and play a positive role in plant resistance to biotic stress.

The role of MYB transcription factors in abiotic stress

The role of MYB transcription factors under drought stress

Drought stress is one of the primary abiotic stresses in plants, which not only impacts plant growth and development but also jeopardizes crop yield and quality (Li et al., 2019). According to reports, MYB transcription factors can directly or indirectly participate in drought signaling pathways through various mechanisms, with the majority belonging to R2R3-MYB and 3RMYB. Stomatal regulation is one of the important mechanisms for controlling plant water loss (Gupta et al., 2020).

*AtMYB60* is the first transcription factor involved in the regulation of stomatal movement (Simeoni et al., 2022). Overexpressed *AtMYB60* plants are sensitive to drought stress (Oh et al., 2011). Under drought stress, most MYB transcription factors are associated with the abscisic acid (ABA) signaling pathway. The regulation of ABA by MYB transcription factors can be divided into three types. The first type is the induced type, which primarily participates in plant responses to abiotic stress by inducing the accumulation of ABA. The expression of the *PtrMYB94* gene, which encodes the R2R3MYB transcription factor in *Populus tomentosa*, is induced by dehydration stress. With the enhancement of ABA, the drought resistance of plants will increase (Fang et al., 2020); The second type is mediated, which enhances plant stress tolerance by regulating the size of stomata through ABA mediation. *TaMYB33* in wheat is regulated by ABA-mediated stress response signals and enhances drought tolerance by accumulating intracellular osmoregulatory substances and enhancing the ability of cells to clear reactive oxygen species (Qin et al., 2012); The third type is ABA-dependent, which can confer abiotic stress tolerance by regulating the expression levels of various stress markers in the ABA-dependent pathway. For example, the overexpression of *GaMYB85* in cotton can enhance the accumulation of free proline and chlorophyll in transgenic plants. It can also increase the expression of stress response genes such as *RD22*, *ADH1*, *RD29A*, *P5CS*, and *ABI5*. As a result, the resistance of transgenic plants to drought stress is enhanced (Butt et al., 2017).

However, the expression of the *BcMYB1* gene significantly increased under drought stress, but was very low under exogenous ABA treatment. This indicates that the *BcMYB1* gene is independently involved in the response to drought stress through the ABA pathway (Chen et al., 2005). In addition, the *IbMYB116* gene in barley activates the reactive oxygen species scavenging system through the JA signaling pathway and participates in drought stress responses (Zhou et al., 2019). MYB transcription factors participate in drought tolerance related to leaf permeability by regulating the synthesis of flavonoids and stratum corneum, which are related to leaf permeability (Wang et al., 2021a).
The role of MYB transcription factors under high salt stress

Due to the combined effects of salt and drought stress, which result in water scarcity, certain MYB transcription factors have been found to play a similar role in salt responses. They respond to drought and salt stress through a series of regulatory mechanisms, such as accumulating osmotic regulatory substances to improve osmotic pressure and antioxidant capacity, altering secondary metabolism, and enhancing membrane stability (Abe et al., 1997). The majority of MYB genes involved in salt stress response are R2R3-MYB. Research has shown that a few MYB-related genes and 3RMYB genes are also involved in salt stress regulation. For example, under high salt stress conditions, the levels of reactive oxygen species and malondialdehyde decrease in transgenic \textit{FtMYB13} plants, while protein content and photosynthetic efficiency increase. This improvement in salt tolerance has been observed (Huang et al., 2018). MYB transcription factors can also improve plant salt tolerance by increasing the expression level of stress-related genes. For example, overexpressing \textit{CmMYB2} plants can delay flowering time, increase sensitivity to ABA, and decrease stomatal opening (Shan et al., 2012). Further analysis showed that the expression levels of some stress-related genes, including \textit{RD22, RD29A, COR47}, and \textit{ABA1}, increased. These results indicate that the overexpression of \textit{CmMYB2} can significantly enhance salt tolerance in plants. Furthermore, \textit{PtrSSRI} gene of \textit{Populus tomentosa} enhances salt tolerance in transgenic plants by regulating lateral root development and ABA signaling (Fang et al., 2017); \textit{AtMYB73} negatively regulates the response of SOS to salt stress in \textit{Arabidopsis} (Kim et al., 2013).

The role of MYB transcription factors under heavy metal stress

Plants have evolved tolerance mechanisms to withstand heavy metal stress over the course of long-term evolution. Research has found that the MYB transcription factor family is involved in the response to metal stress in plants, although most of the research has focused on iron and aluminum stress. Iron is an essential
nutrient element for plant photosynthesis and respiration, and it plays a role in various metabolic processes in plants, including photosynthesis, respiration, and nitrogen fixation. The product encoded by the \textit{MxMYB1} gene in small mallow is a regulatory protein related to plant iron absorption and utilization. It serves as a negative regulator of iron transport and storage (Shen et al., 2008). The \textit{DwMYB2} gene, a R2R3-MYB transcription factor in orchids, can be ectopically expressed in \textit{Arabidopsis}. This expression regulates iron transporter genes and increases \textit{Arabidopsis}' sensitivity to iron deficiency (Chen et al., 2006). Aluminum toxicity is the primary factor that limits plant growth and development in acidic soils. In wild soybeans, the overexpression of \textit{GsMYB7} and \textit{GsMYB10} genes enhances the tolerance of transgenic soybean plants to aluminum acid stress. This finding proves that \textit{GsMYB7} gene is an essential transcription factor for responding to aluminum stress (Zeng et al., 2012). Overexpression of the \textit{RsMYB1} gene, a member of the factor family can enhance the expression of genes related to heavy metal detoxification, such as glutathione gene (\textit{GSH}), phytochelatins (\textit{PCs}), and antioxidant genes (\textit{SOD}, \textit{CAT}, and \textit{POX}). This, in turn, improves the resistance of transgenic plants to heavy metal ions like zinc, copper, and chromium (Ai et al., 2018).

\textit{The role of MYB transcription factors under temperature stress}

Analysis of the plant transcriptome under temperature stress indicates that many MYB transcription factors are involved in the response to temperature stress (Tian et al., 2013). High temperatures can inhibit plant photosynthesis and respiration, disrupt cellular structure, and consequently affect the stability of various components within cells and the normal progression of various physiological and biochemical reactions. Under high temperature conditions, plants overexpressed with \textit{OsMYB55} showed significantly higher growth compared to wild-type plants, suggesting that \textit{OsMYB55} can enhance the heat tolerance of rice varieties (El-Kereamy et al., 2012). Under high temperature conditions in \textit{Arabidopsis}, the activity of \textit{AtMYB68} in \textit{Arabidopsis} roots significantly increases, and the growth activity of the mutant \textit{myb68} is significantly lower than that of the wild-type, indicating that \textit{AtMYB68} is involved in the plant's response to high temperature tolerance (Deng et al., 2020). The \textit{AtMYB30} gene can bind to the \textit{ANN1} and \textit{ANN4} promoters and inhibit their expression (Liao et al., 2017). Research has found that MYB transcription factors regulated by calcium signaling are also involved in the response mechanism of grape leaves to high temperature stress after heat shock (Liu et al., 2012).

Low temperatures can also cause serious damage to plants, including frostbite. At present, plants have two regulatory pathways for low temperature stress, namely the ABA-dependent and ABA-independent regulatory pathways (Figure 2). ABA independent regulatory pathways can be further divided into CBF-dependent pathways and CBF-independent pathways (Park et al., 2015). Currently, the most popular research topic is the CBF-dependent pathway (Ma et al., 2022). As a negative regulatory factor in response to low temperature stress, \textit{AtMYB15} can bind to the trans-acting element in the CBF gene promoter region, inhibit the expression of CBF, and reduce plant cold resistance (Agarwal et al., 2006). \textit{OsMYBS3} is a positive regulatory factor for cold resistance, which can inhibit the DREB/CBF-dependent cold signaling pathway in rice. This indicates that different pathways play a gradual role in adapting to short-term and long-term cold stress (Su et al., 2010). \textit{AtMYB31} can promote the expression of the CBF gene under low temperature, enhancing plant resistance to low temperature and oxidative stress (Su et al., 2010; Li et al., 2019). Research has found that \textit{MYBS3} participates in the response of rice to low temperature stress by inhibiting the DREB/CBF-dependent cold signaling pathway, which appears to have a role in the transcriptional regulation. Unlike the rapid and transient response of the DREB/CBF signaling pathway to stress, \textit{OsMYBS3} responds slowly to low-temperature stress. Therefore, it can be concluded that there may be a new signaling pathway involved in the short-term and long-term responses of plants to low temperature stress, which complements the DREB/CBF signaling pathway. MYB transcription factors can also assist other transcription factors in inducing the
expression of cold stress genes, thereby enhancing the plant’s ability to withstand low temperature stress. *MdMYB308L* can interact with *MdbHLH33*, enhancing the binding ability of *MdCBF2* and *MdDFR* promoters, and improving the cold resistance of apple callus tissue (An et al., 2020).

The MYB transcription factor family is a highly significant and extensive group of transcription factors. Table 1 presents the stress resistance function of various MYB families in different species. This paper not only summarizes the plants’ response to drought, high salt, temperature, and heavy metals, but also examines the regulation and expression of these responses under ultraviolet and low nitrogen stresses. Through years of research on the MYB family, it is not only possible to predict the biological functions of unknown MYBs in different species based on the correlation between the structure and My transcription factors (MYB-TFs), but also to provide a theoretical basis for the breeding and improvement of plant varieties (Yu et al., 2023).

### Table 1. Research on the function of MYB family in resistance to stress

<table>
<thead>
<tr>
<th>MYB genes</th>
<th>Functions in plant defense</th>
<th>Species</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>OsFLP</td>
<td>Drought/Salt tolerance</td>
<td><em>Oryza sativa</em></td>
<td>(Qu et al., 2022; Zhang et al., 2022)</td>
</tr>
<tr>
<td>CgMYB1</td>
<td>Low temperature tolerance</td>
<td><em>Chenopodium</em></td>
<td>(Zhou et al., 2023)</td>
</tr>
<tr>
<td>MYB68</td>
<td>High temperature tolerance</td>
<td><em>Arabidopsis thaliana</em></td>
<td>(Feng et al., 2004)</td>
</tr>
<tr>
<td>GhMYB36</td>
<td>Verticillium dahlia</td>
<td><em>Gossypium hirsutum</em></td>
<td>(Liu et al., 2022; Zha et al., 2022)</td>
</tr>
<tr>
<td>GhODO1</td>
<td>Low temperature tolerance</td>
<td><em>Arabidopsis thaliana</em></td>
<td>(Qian et al., 2020)</td>
</tr>
<tr>
<td>MYB13</td>
<td>Ultraviolet B tolerance</td>
<td><em>Arabidopsis thaliana</em></td>
<td>(Ge et al., 2019)</td>
</tr>
<tr>
<td>SiMYB3</td>
<td>Low nitrogen tolerance</td>
<td><em>Setaria italica</em></td>
<td>(Ai et al., 2018)</td>
</tr>
<tr>
<td>RMYB1</td>
<td>Heavy metal ions tolerance</td>
<td><em>Petunia</em></td>
<td>(Zhou, Windhorst et al., 2023)</td>
</tr>
<tr>
<td>MYB12</td>
<td>Ultraviolet B tolerance</td>
<td><em>Arabidopsis thaliana</em></td>
<td>(Abid et al., 2023)</td>
</tr>
<tr>
<td>GhBM</td>
<td>Ultraviolet B tolerance</td>
<td><em>G. barbadense</em></td>
<td>(An et al., 2023)</td>
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<tr>
<td>Myb-7B</td>
<td>Ultraviolet B tolerance</td>
<td>Wheat</td>
<td>(Liu et al., 2023)</td>
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<tr>
<td>Myb-7D</td>
<td>Ultraviolet B tolerance</td>
<td>Grapes</td>
<td>(Ma et al., 2023)</td>
</tr>
<tr>
<td>CmMYB42</td>
<td>Low nitrogen tolerance</td>
<td><em>Chrysanthemum</em></td>
<td>(Zhang et al., 2023)</td>
</tr>
<tr>
<td>SiMYB30</td>
<td>Low nitrogen tolerance</td>
<td><em>Setaria italica</em></td>
<td>(Wang et al., 2018)</td>
</tr>
<tr>
<td>MYB113</td>
<td>Low nitrogen tolerance</td>
<td><em>Arabidopsis thaliana</em></td>
<td>(Qin et al., 2022)</td>
</tr>
<tr>
<td>MYB114</td>
<td>Low nitrogen tolerance</td>
<td><em>Arabidopsis thaliana</em></td>
<td>(Wang et al., 2018)</td>
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<tr>
<td>CsMYB21</td>
<td>Low nitrogen tolerance</td>
<td>Cucumber</td>
<td>(Wang et al., 2018)</td>
</tr>
</tbody>
</table>

**Conclusions**

At the same time, the MYB transcription factor serves as a molecular link, integrating various resistance genes and defense signaling pathways, making it essential for plant disease resistance. The structure and defense function of MYB have been widely studied, including the interactions between different defense molecules and signals that help organisms cope with biological stress (Zhang et al., 2023). Although MYB plays a crucial role in plant immunity, its specific molecular function remains unclear. Unlocking the potential molecular mechanism of MYB-mediated immune response is an important step in addressing plant biotic stress.

In addition, so far, although the expression of MYB can be induced by various signals, there are still many doubts about the regulation of these MYBs are regulated during the regulatory process. Meanwhile, due to the diverse functions of most MYBs, it is challenging to uncover the functions and regulatory mechanisms of specific members using traditional molecular biology methods. Therefore, it is crucial to conduct more in-depth research on MYB using new experimental techniques and methods.
Authors’ Contributions

Both authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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