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MYB transcription factors, active players in abiotic stress signaling

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ABSTRACT

The MYB family of proteins is a group of large, functionally diverse transcription factors, and widely present in all eukaryotes. The MYB family of proteins in plants is characterized by the presence of a conserved MYB DNA-binding domain that typically contains one to four imperfect repeats. In the past decades, extensive information has been accumulated on the roles of these proteins in regulating important processes in plants, including development, metabolism, and responses to environmental stresses. In this review, we summarize the MYB proteins that play crucial roles in plant responses to diverse abiotic stresses, and highlight the possible mechanisms underlying how MYB proteins are regulated at the transcriptional, posttranscriptional and protein levels, and how they regulate downstream target gene networks in association with abiotic stresses.

1. Introduction

The MYB family of transcription factors (TFs) is named by its conserved MYB domain and is present in all eukaryotes. The first identified MYB gene is the *v-Myb* oncogene of an avian myeloblastosis virus (AMV) (Klempnauer et al., 1982). Thereafter, many MYB genes were recognized in animals, plants, fungi and slime molds. The structures and functions of MYB transcription factors in plants are conserved compared with those in animals and yeasts.

The MYB family is one of the largest TF families in plants, representing about 9% of the total TFs in *Arabidopsis* (Riechmann et al., 2000). In *Arabidopsis*, more than 1600 TFs have been identified, accounting for about 6% of the whole genome (Riechmann et al., 2000; Chen et al., 2006). The MYB TFs in plants are characterized by the presence of a highly conserved MYB DNA-binding domain that typically contains one to four imperfect repeats. According to the structure of the DNA-binding domain, they are grouped into four different subfamilies. The first identified gene encoding a MYB domain protein in plants is *COLORED1* (*C1*), which is involved in anthocyanin synthesis in the aleurone layer of maize (*Zea mays*) kernels (Paz-Ares et al., 1987). The presence of numerous MYB proteins in plants implicates that they may individually play unique roles, which have been demonstrated by a large number of studies. It is now clear that MYB proteins function in diverse biological processes including regulation of primary and secondary metabolism, seed and floral development, cell fate and identity, defense and stress responses in plants (Dubos et al., 2010). Here, we review the structures and functions, and emphasize on the possible mechanisms underlying the roles of MYB proteins in responses to abiotic stresses, as well as the possible regulation of MYB gene expression and protein activities in plants.

2. Structure and diversity of the MYB family in plants

The common feature of MYB proteins is the DNA-binding domain (MYB domain), which is generally composed of one to four imperfect repeats (R) in plants (Fig. 1). Each repeat, with about 52 amino acid residues, forms a helix–turn–helix structure with three regularly spaced tryptophan residues in the hydrophobic core that extend into the DNA major groove and mediate recognition of specific DNA sequences (Ogata et al., 1996; Jia et al., 2004). The MYB family is classified into four subfamilies based on the number and position of repeats, namely 4R-MYB, R1R2R3-MYB, R2R3-MYB and 1R-MYB (Dubos et al., 2010).

The 4R-MYB subfamily is the smallest group of the MYB family in plants, each member of which contains four R1/R2 repeats (Fig. 1). Only one 4R-MYB protein was found in several plant species, for example At3g18100 in *Arabidopsis* (Chen et al., 2006). Very little is known about the functions of the members of this subfamily. The R1R2R3-MYB (3R-MYB) subfamily is an evolutionarily conserved group in plants, whose members contain three repeats (Fig. 1), each similar to the vertebrate MYB repeats (Ito, 2005). In contrast to the predominant roles of 3R-MYB group, relatively few 3R-MYB proteins are present amongst plant MYB proteins. For example, there are five genes encoding 3R-MYB

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proteins in *Arabidopsis* and tobacco, and four or five genes in rice (Ito et al., 2001; Stracke, 2001; Dubos et al., 2010; Katiyar et al., 2012).

The R2R3-MYB (2R-MYB) subfamily is the largest group of the plant MYB family, probably evolved from a 3R-MYB ancestor by loss of R1 or from an R1-MYB by duplication (Fig. 1) (Rosinski and Atchley, 1998; Jiang et al., 2004). The 2R-MYB subfamily in plants is classified into three subgroups by phylogenetic analysis, which is consistent with the classification of DNA-binding specificity: subgroup A includes proteins most similar to c-MYB, subgroup B contains proteins encoded by genes with an intron at a conserved position, and subgroup C is the largest group representing genes with an intron at another position (Romero et al., 1998). The structure of 2R-MYB proteins contains two parts: a DNA-binding domain at N terminus and a C-terminal conserved amino acid sequence motif-containing domain. Based on the domains, the 2R-MYB subfamily is categorized into 22 subgroups (Kranz et al., 1998). There are more than 120 members of the 2R-MYB subfamily in *Arabidopsis* and about 90 members in rice (Katiyar et al., 2012). The expansion of 2R-MYB proteins indicates that they may play essential roles in plant-specific processes, which is consistent with studies in the past decade. 2R-MYB proteins have been demonstrated to be involved in the regulation of metabolism, development, cell fate and identity, hormone pathways and responses to stresses in plants. For example, 2R-MYB proteins such as ZmC1, production of anthocyanin pigment 1–4 (PAP1–4) (namely AtMYB75, AtMYB90, AtMYB113, AtMYB114), TT2 (AtMYB123), VvMYBPA2 and VvMYBA2 regulate anthocyanin and proanthocyanidin pathways (Paz-Ares et al., 1987; Borevitz et al., 2000; Nesi et al., 2001; Gonzalez et al., 2008; Heppel et al., 2013); AtMYB7 functions as a repressor of flavonol biosynthesis, which is down-regulated by AtMYB4 (Fornalé et al., 2014).

The 1R-MYB subfamily, also called MYB-related group, is a heterogeneous group, which contains proteins with an intact or partial repeat (Fig. 1). This subfamily is divided into several subgroups including CCA1-like, CPC-like, TRF-like, TBP-like, I-box-binding like and other MYB-related proteins (Chen et al., 2006). It is the second largest group of the MYB family, and is widely distributed in plants. There are 64 members in *Arabidopsis*, 70 members in rice (Dubos et al., 2010). MybSt1 of potato, acting as a transcriptional activator, is the first identified MYB-related protein in plants (Baranowskij et al., 1994). Phylogenetic and expression analyses revealed the conservation and diversity of MYB-related genes, and functional studies demonstrated that they regulate plant development and stress responses (Du et al., 2013).

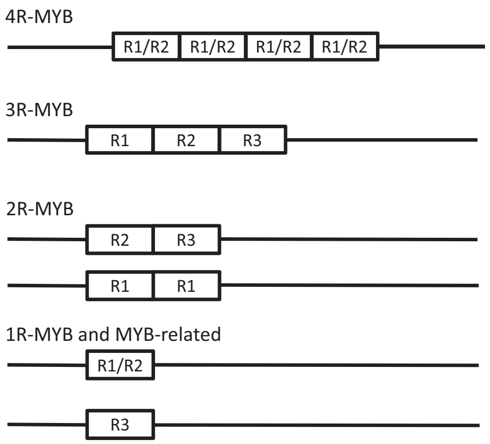

Fig. 1. Illustration of structure and classification of plant MYB transcription factors, showing that their classification depends on the number of adjacent MYB repeats (R).

3. Roles in abiotic stress responses

Plants are challenged by a variety of environmental stresses because they are sessile. Thus, they have evolved numerous strategies to sense and adapt to environmental stresses. Environmental conditions, such as salinity, moisture and temperature, affect plant development, growth and productivity. Therefore, responses and adaptation to abiotic stresses are vital mechanisms for plants to survive. Many genes and proteins are regulated under abiotic stresses, out of which transcription factors are indispensable. As one of the largest TF groups in plants, the MYB family has been shown to be essential for the responses to abiotic stresses (Dubos et al., 2010).

3.1. Drought stress

Drought is a major abiotic stress that negatively affects vegetative and reproductive development of plants, and reduces plant productivity. Expression of many MYB genes has been shown to be responsive to drought stress, and may be involved in drought responses in plants. Genome-wide transcriptomic and microarray analyses have shown that many MYB proteins and MYB-binding element-containing genes are responsive to drought in *Arabidopsis thaliana*, *Zea mays*, *Gossypium herbaceum*, *Macrotyloma uniflorum*, *Malus pumila*, *Populus euphratic*a, *Musa* and *Glycine max* (Jia et al., 2006; Davey et al., 2009; Golldack et al., 2011; Pereira et al., 2011; Ranjan et al., 2012; Yan et al., 2012; Bhardwaj et al., 2013; Cao et al., 2013).

In *Arabidopsis*, the stress-induced accumulation of flavonoids was shown to be a positive response to drought stress (Koops et al., 2011). Overexpression of *PAP1* or *MYB12*, two flavonol synthesis regulators, results in less water loss (Nakabayashi et al., 2014). Many R2R3-MYB proteins in *Arabidopsis* have been identified to participate in drought responses. For example, MYB60, a regulator of stomatal movement, is down-regulated by drought stress, and its overexpression results in hypersensitivity to water deficiency (Oh et al., 2011). MYB96, MYB15 and MYB2, induced by drought, act as positive regulators of drought tolerance by activating the transcription of dehydration responsive genes, such as *RD22* (Urao et al., 1996; Abe et al., 2003; Ding et al., 2009; Seo et al., 2009). The biosynthesis of cuticular wax activated by MYB96 is required for the drought tolerance of plants (Seo et al., 2009, 2011). Flu-like protein (FLP) and MYB88, important for normal stomata production, were shown to positively modulate stress responsive genes and drought responses (Xie et al., 2010). AtMYB41 is induced by drought and may function as a transcription factor in modulating cell expansion and cuticle deposition during drought stress (Cominelli et al., 2008b). *MYB44* overexpression confers drought resistance to *Arabidopsis* plants by repressing protein phosphatase 2C (PP2C) genes (Jung et al., 2008). Botrytis susceptible1 (BOS1) and AtMYB102 were also shown to be positive regulators of drought tolerance (Denekamp and Smeekens 2003; Mengiste et al., 2003).

In addition to MYB proteins in *Arabidopsis*, several MYB proteins have also been found to be involved in drought responses in other species. In apple, *MdoMYB121* is induced by drought stress and its overexpression in tomato and apple confers improved tolerance (Cao et al., 2013). *MdSIMYB1*, induced by drought and other abiotic stresses, positively controls the drought resistance by inducing stress and auxin responsive genes (Wang et al., 2014). In rice, *OsMYB4*, *OsMYB3R-2* and *OsMYB2* are induced by drought, and their ectopic expression facilitates drought resistance (Mattana et al., 2005; Dai et al., 2007; Pasquali et al., 2008; Yang et al., 2012a). The *OsMYB59* promoter contains a *DRE cis*-element, and *OsMYB59* is positively regulated by heterogeneous expression of tomato stress-responsive factor1 (*TSRF1*), indicating that *OsMYB59* plays a