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THE ROLE OF R2R3MYB TRANSCRIPTION FACTORS IN PLANT STRESS TOLERANCE

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ABSTRACT

The plant-specific R2R3MYB proteins constitute a largest subfamily in MYB transcription factors and are widely involved in growth and developmental processes. In spite of their highly conserved DNA-binding domains, the biologic functions are strikingly varied across plant species. Recently, their roles in making plant more survivable under adverse environmental conditions including cold, drought, pathogen, salinity have received considerable attention. Nowadays, the R2R3MYBs in response to stresses, here termed as stress-responsive R2R3MYBs (SR-R2R3MYBs), were continuously identified from different plant species. This review mainly focused on the recent progresses in SR-R2R3MYBs gene structure, biological functions and their expression pattern under varied stresses. Additionally, we have also discussed the genetic relationship of SR-R2R3MYB proteins, and their role in integrating a diversity of pathways including metabolic, SOS, signal transduction pathways etc, with an aim to use them for crop improvement via transgenic technologies.

Key words: R2R3MYB, transcription factor, stress signaling, biologic function, target gene.

INTRODUCTION

MYB proteins constitute a super-family of transcription factors (TFs) in plant, and they are characterized by the presence of a functional DNA binding domain (MYB domain) composed of one to three imperfect repeats (R1, R2, and R3), each repeat contains about 52 amino acid residues (Du *et al.,* 2009). According to the number of adjacent repeats in MYB domain, these MYBs can be classified into three subfamilies: R1R2R3MYB, R2R3MYB, and R1MYB (Du *et al.,* 2009). Among them, R2R3MYB subfamily is the largest and specific to higher plants (Du *et al.,* 2012a,b). Through genome-wide analysis, we identified 112 *MYB* genes in *Citrus*, of which 97 belong to *R2R3MYB* genes and their biological bio-functions are in progress to be analyzed. Taking a cue from the above-mentioned findings, we feel that numerous new plant R2R3MYB members remain to be discovered.

In recent years, functional analyses revealed that numerous R2R3MYBs could enhance plant tolerance to stresses (He *et al.,* 2012; Yang *et al.,* 2012). Due to their important role in stress adaptation, the isolation and characterization of SR-R2R3MYBs from plants, especially from fruit tree crops such as citrus, pear, Chinese bayberry etc. become a very active area of research.

SR-R2R3MYBs as TFs can up- or/and down-regulate the expression of many stress-related genes (Xie *et al.,* 2010), and subsequently alter multiple signal transduction pathways and metabolic processes, eventually leading to enhanced plant tolerance; in turn, they are also directly regulated by hormones, stresses and TFs (Mao *et al.,* 2011). The above-mentioned findings indicated that the plant SR-R2R3MYBs perform as nodes to weave a complicated stress-responsive network that enable plant to avoid stress injuries. While, dramatic variations in biologic functions were observed among different SR-R2R3MYBs. In recent years, several reviews on MYBs have been published, briefly introducing their molecular structure, evolution, function and interaction with their target DNA binding sites (Jin *et al.,* 1999; Rtracke *et al.,* 2001; Dubos *et al.,* 2010; Prouse *et al.,* 2012; Ambawat *et al.,* 2013). While, to date, a comprehensive review on plant SR-R2R3MYBs how to regulate plant adaptation to adverse conditions has not been dealt with. Therefore, this review focused on the roles of SR-R2R3MYBs in stress response, mainly including sensing and transducing stress signals as well as activating targeted genes. Our aims are to provide useful information for future research and to develop effective strategies for improving stress adaptability of plants.

Genetic Relationships of SR-R2R3MYBS: Based on the amino acid sequence of all *Arabidopsis* R2R3MYBs and the SR-R2R3MYBs from other plant species, a phylogenetic tress was constructed using MEGA 5.0 (NJ, bootstrap=1000) (Figure 1), which may facilitate the identification of new SR-R2R3MYBs and potential functions in stress response because members of the same subgroups are generally suggested to have similar function. According to Figure 1, it was showed that the

SR-R2R3MYBs were unequally distributed in different subgroups (S1-S15), of which some subgroups contained several SR-R2R3MYBs in response to abiotic or biotic stresses or both (subgroup S1, S2, S3, S11, S14) and some just encompassed one, for example subgroup S15, showing a complicated relationship between sequence architecture and biologic functions. Maybe, this can interpret why sometimes we are hard to precisely speculate the biologic functions of an R2R3MYBs according to its sequence architecture. At the same time, this result suggested that a great number of potential SR-R2R3MYBs remain to be discovered. For example, AtMYB10, AtMYB13, AtMYB58 and AtMYB63 were grouped with several wounding-, pathogen-, cold-, drought-, salt- and UV-B-inducible SR-R2R3MYBs, suggesting these four R2R3MYBs may be involved in stress responses, despite the fact that AtMYB58 and AtMYB63 were involved in the lignin biosynthetic pathway (Zhou *et al.,* 2009). However, little information is available on them. Therefore, whether they have biologic functions in stress response awaits more detailed functional analysis.

Structural Feature of R2R3MYBS: The N-terminus of R2R3MYBs is a highly conserved region containing a DNA-binding MYB domain. The MYB domain has two consecutive repeats i.e. R2 and R3. Generally, the MYB repeat is about 50 to 53 amino acids in length and encodes three a helices, with the second and third helices forming a helix–turn–helix structure (Figure 2). Using heteronuclear multidimensional NMR, Ogata *et al.* (1994) demonstrated that R2 and R3 each contain three helices, and the third helix in each is a recognition helix. These two repeats are closely packed in the major groove of DNA, leading to contact each other directly to cooperatively bind the specific sequence (Ogata *et al.*, 1994), while which not contributes to the functional activity and specificity according to the quadruple 9-mer-Based protein binding microarray analysis of AtMYB44 (Jung *et al.,* 2012). By GFP fusion protein analysis, two basic amino acid regions i.e. KRGK and RKKAQEKKR in R3 repeat were found to be concurrently required for localizing to the nucleus, likely serving as bipartite nuclear localization signals, and these two regions were highly conserved in almost all the *Arabidopsis* R2R3MYB proteins (Li *et al.,* 2006). Besides KRGK and RKKAQEKKR, we believed that the functions of other amino acid regions were also worthy to be characterized.

Outside of the DNA-binding domain (N-terminus), the proteins are highly divergent with the exception of some short conserved amino acid sequence motifs. Based on these motifs, Kranz *et al.*(1998) have divided *Arabidopsis* R2R3MYBs into 22 subgroups; for instance, the members in subgroup 22, one of subgroups involved in stress response, including AtMYB73, AtMYB44, AtMYB77, AtMYB70 share a common conserved motif i.e. GEFMxVVQEMIxxEVRSYM. Because the C-terminus is the transcriptional activation domain responsible for functional activity or/and specificity (Chen *et al.,* 2013), these conserved motifs could facilitate the functional identification of R2R3MYBs, and explain the molecular basis of functional difference among R2R3MYB members. Through aligning the amino acid sequences of SR-R2R3MYBs from different plant species, we found that no conserved motifs existed in C-terminal domain. These SR-R2R3MYBs used to be aligned here generally responded to salts or drought or both, including TaMYB30-B, AtMYB2, TaMYB73, TaMYB33, TaMYB32, CmMYB2, JAMYB, AtMYB2, and AtMYB20. From them, two members with the same functions reported recently i.e. TaMYB33 and CmMYB2 were used to further analyze in order to discover whether a conserved motif exists in their C-terminal domain, but we failed. Therefore, the conserved motifs do not necessarily associated with the biological functions in response to stresses. As an example, AtMYB44 and AtMYB73 act as positive and negative TFs, respectively, showing an obvious difference in biologic functions, but both of them actually contain a common conserved motif (Seo *et al.,* 2012; Kim *et al.,* 2013). In addition, the promoter of target-genes may also affect SR-R2R3MYBs functional activity and specificity of R2R3MYB proteins, which need to be explored in future.

Expression of SR-R2R3MYB Genes: The differences in expression profiles were observed among different *SR-R2R3MYB* genes treated by the same stresses or hormones as well as within the same *SR-R2R3MYB* genes under different stresses or hormones. By gene expression profiles, their biologic functions can be predicted. Based on the data obtained in previous studies, a large number of stresses, such as draught, cold, salt, pathogen and so on, can positively or/and negatively regulated the expression of *SR-R2R3MYB*s (Oh *et al.,* 2011; Shin *et al.,* 2011). For example, *AtMYB14* is down-regulated under cold stress (Chen *et al.,* 2013); whereas *MYB15* is up-regulated by cold treatment (Agarwal *et al.,* 2006). Feng *et al.* (2004) revealed that the *AtMYB68* could especially respond to heat stress; the same case was detected to AtMYB62, which was especially response to Pi deprivation (Devaiah *et al.,* 2009). In addition, some of *SR-R2R3MYBs* are expressed in specific organ under tress condition, such as *AtMYB60*, whose transcripts just is induced in guard cells by drought (Oh *et al.,* 2011).

Besides stresses, hormones can also affect the expression profiles of *SR-R2R3MYBs*. For instance, *AtMYB96* expression was up-regulated in different organs by IAA and ABA, respectively (Seo *et al.,* 2009). According to the data reported previously, the *R2R3MYBs* in response to ABA, were generally related with abiotic tolerance, especially drought (Oh *et al.,*

2011). However, some, for example OsMYB4, not in response to ABA still exhibit tolerance to abiotic stresses (Cheng *et al.*, 2007). Likewise, the *R2R3MYBs* related to biotic stresses generally can be regulated by SA. Thus, according to hormone-responsive expression profiles, we could roughly predict the biologic role of one *SR-R2R3MYB*.

Regulation of SR-R2R3MYBS: The transcript abundance of a gene can be firstly up- or down-regulated by binding of specific TFs to its *cis*-element in the promoter. Although numerous putative stress-responsive *cis*-elements are present in *SR-R2R3MYBs* promoter, far less is know how they are regulated by other transcription factors. These *cis*-elements mainly include GCC-box, MYC, AG-motif-like, Box-P, ABRE, CE1, RY-motif and so on (Denekamp *et al.*, 2003; Maeda *et al.*, 2006; Jung *et al.*, 2008; He *et al.*, 2012). The GCC-box and MYC binding sequence in *DcMYB1* promoter might be necessary for UV-B irradiation, and the AG-motif-like and/or Box-P for elicitor treatment (Maeda *et al.*, 2006). Further analysis found that some *cis*-elements neighboring the TATA-box such as MYB binding sequence and W-box, might take part to influence promoter activity (Maeda *et al.*, 2006). Miyahara *et al.* (2010) reported that binding DcEIL (ethylene insensitive3-like protein) to an inconclusive regulatory region in promoter repressed *DcMYB1* expression, suggesting ethylene was involved in stress response. The stress-responsive expression of NtMYB2 was induced by binding AGP1 (GATA-type zinc finger protein) to AG-motif i.e. AGATCCAA (Sugimoto *et al.*, 2003), while that of AtMYB44 and TaMYB2 might be partly due to the presence of RY motif and MBS (Jung *et al.*, 2008; Mao *et al.*, 2011). Over-expressing NST3 (a secondary cell wall-associated NAC thickening factor) up-regulated AtMYB20 and AtMYB85, indicating these two MYB genes were directly or indirectly regulated by NST3 (Zhong *et al.*, 2008). The ABRE sequence is extensively present in the promoter of *SR-R2R3MYBs*, which is necessary for ABA-responsiveness (Qin *et al.*, 2012); however, there are several exceptions. For example, some ABREs in the BcMYB1 promoter, but exogenous ABA just slightly induced the expression of BcMYB1 (Chen *et al.*, 2005). Based on abovementioned findings, the regulatory role of these *cis*-elements in *SR-R2R3MYBs* transcription remains to be further investigated in detail. At the same time, lots of novel TFs that regulate stress-responsive *SR-R2R3MYBs* also need to be discovered.

Recently, several studies have shown that the MYB genes are post-transcriptionally regulated by microRNA (miRNA) through cleaving target gene. It is well known that miR159 target to anther or pollen development-related *R2R3MYB* genes such as AtMYB33, AtMYB35, AtMYB65 and AtMYB101 (Allen *et al.*, 2007; Addo-Quaye *et al.*, 2008). However, none microRNA, to date, has been reported to control *SR-R2R3MYBs*. Most recently, the primary transcript of a *SR-R2R3MYB* gene, *AtMYB60*, was found to be alternativel spliced, forming two splice variants, one of which lacks the first two exons encoding the first MYB DNA binding domain; these two splice variants locate to the nucleus and enable plant to adapt to draught (Oh *et al.*, 2011). Thus, besides microRNA, the alternative splicing how to affect *SR-R2R3MYB* genes could also be worthy to study.

To the best our knowledge, no other information about regulation of *SR-R2R3-MYB* is available, specifically, post-translational regulation. Therefore, intensive works, in future, need to elucidate the molecular mechanism underlining the regulation of *SR-R2R3MYB*s.

***SR-R2R3MYB* Genes for plant stress tolerance:** Stresses, such as drought, salt, cold and pathogen, adversely affect crop productivity and quality, which have received considerable attention of plant scientists. Recently, the major aim of agronomic researches is to enhance or stabilize agriculture yields under various environmental conditions. A significant approach is to use stress-associated genes to improve crop tolerance to different stresses. Increasing plant *SR-R2R3MYB* genes have been found to have an important role in stress tolerance (Table 1), showing a promise for improving plant adaptation to stresses.

Abiotic stress tolerance: Overexpressing *SR-R2R3MYB* genes in *Arabidopsis* generally produces tolerant plant to most abiotic stresses (Cominelli *et al.*, 2005; Jung *et al.*, 2008), while, some serve as negative regulator, showing opposite function (Agarwal *et al.*, 2006). The functions between *SR-R2R3MYBs* exist obvious discrepancies, of course not exclude redundancy. AtMYB60, AtMYB61 and AtMYB15 enhance plant tolerance to drought by regulating stomatal aperture in dependent- or independent-ABA means, of which AtMYB60 acts as a negative regulator (Cominelli *et al.*, 2005; Liang *et al.*, 2005 Jung *et al.*, 2008). Overexpressing AtMYB15 leads to an increase in salinity tolerance, and a decrease in cold response (Agarwal *et al.*, 2006; Ding *et al.*, 2009), showing functional redundancy. There are a large body of *SR-R2R3MYBs* from different plant species that can modify plant tolerance to abiotic stresses, such as *AtMyb41* (Lippold *et al.*, 2009), *OsMYB2* (Yang *et al.*, 2012), *TaMYB 30* (Zhang *et al.*, 2012a). Many R2R3-MYBs overexpressed in plants remarkably improved stress tolerance without any distinctively adverse effects; while some could produce detrimental consequences in the transgenics, showing dwarfing, small seeds, later flowering etc. (Table 1). These undesirable phenotypes probably can be overcome by using a proper promoter, for example a tissue- or a stress- specific promoter.

Pathogen resistance: During **r**ecent years, RNA knockout/interference and overexpression studies have also revealed the function of SR-R2R3MYBs in various plant-pathogen interactions. For instance, AtMYB30 has been found to regulate plant defense response by activating the hypersensitive cell death program at the infection site (Vailleau *et al.*, 2002). NaMYB8 regulated the accumulation of phenylpropanoid-polyamine conjugates, resulting in local and systemic defense against insect herbivores (Kaur *et al.*, 2010), and could also increase the tolerance to abiotic stresses (Katiyar *et al.*, 2012). AtMYB46 can modulate *Botrytis cinerea* susceptibility likely through integration of cell wall remodeling and activation of pathogen-associated genes (Ramírez *et al.*, 2011). Thus, we could use these *SR-R2R3MYBs* to obtain genetically modified crops with higher resistance to pests and diseases.

Multifunctional SR-R2R3MYBs: Data from recent studies indicated that some SR-R2R3MYBs were implicated in crosstalk between biotic and abiotic stress. Functional analysis revealed that AtMYB96 as a key regulator is involved in biotic and abiotic stresses by mediating ABA signaling and SA biosynthesis (Seo *et al.*, 2009, 2010). Overexpressing AtMYB44 significantly enhances *Pseudomonas syringae* resistance as well as tolerance to salt and drought stresses (Zou *et al.*, 2012; Seo *et al.*, 2012). This regulator also affects the resistance to green peach aphid (Lü *et al.*, 2011). Besides the abovementioned multifunctional *SR-R2R3MYBs*, AtMYB108, JAmyb and TaPIMP1 are also involved in the defense to both biotic and abiotic stress by different regulatory manners (Zhang *et al.*, 2012d; Yokotani *et al.*, 2013). These multifunctional SR-R2R3MYBs are significantly important for making plants survival under extreme stress conditions, since plants often undergo multiple stresses concurrently.

***Cis*-acting elements and target genes of SR-R2R3MYBs:** R2R3MYBs regulate the transcript of their target genes by binding to MYB recognition sequence (MBS). Several years ago, a few studies identified ACC(A/T)(A/T)CC as MBS in the promoter of *PAL* or *CHS*, both of which are involved in phenylalanine metabolism in response to UV-B, nitrogen deficiency, wounding (Miyake *et al.*, 2003, 2004; Maeda *et al.*, 2005; Gális *et al.*, 2006). This MBS highly coincides with the type IIG (H-box-like) which was characterized by YACCWACC as a recognition sequence of a number of MYB transcription factors (Miyake *et al.*, 2003). Agarwal *et al.* (2006) also identified (T/C)(T/G)TTA as MBS motif in the promoter of *AtCBF* genes (Agarwal *et al.*, 2006). Many other MBSs such as MRE4 (TCTCACCTACC), mMREI (CCGGAAAAAAGGAT) and AC element (ACCTAAC or ACCTAC) etc in numerous stress-related gene promoters were gradually identified in recent years (Liao *et al.*, 2008; Michael *et al.*, 2013), indicating SR-R2R3MYBs were widely involved in stress-related processes. Interestingly, the MRE4 sequence contains an AC element i.e. ACCTAC, suggesting that these two MBSs probably were the same and there maybe had several additional nucleotides in MRE4, which need to further assay.

Some reports showed that different type MBSs can be bind with the same one SR-R2R3MYB, and vice versa. For example, TaMYB73 can bind to types I, II, and IIG MYB binding motifs, and then improve corresponding gene expression (He *et al.*, 2012). More interesting, AtMYB15 binds to (T/C)(T/G)TTA in *AtCBFs* promoter, resulting in a decrease in its expression (Agarwal *et al.*, 2006), while to MBSII element (TAACTAAC), enhancing expression (Maeda *et al.*, 2005), the functional difference of which may be due to the difference of MBSs, or the interaction with other partner factors or both. By quadruple 9-mer- based protein binding microarray analysis, Jung *et al.* (2012) revealed that AtMYB44 and AtMYB77 with quite different biological roles could bind the same MBSs in the promoter of many genes, indicating that the binding of one SR-R2R3MYB to MBS in a gene promoter, not mean that this gene is the target of the corresponding SR-R2R3MYB, and this SR-R2R3MYB may function either by interaction with other transcription factors or through stimulus-induced structural modification.

As mentioned above, some SR-R2R3MYBs do require the coexistence of other partner factors (figure 4), such as GmCaM4, ICE1 and EIL3, however the others don't, just like as DcMYB1 (Yoo *et al.*, 2005; Agarwal *et al.*, 2006; Ent *et al.*, 2008). According to the findings reported previously, we can speculate the functions of partner factors are as follows: (1) increase the DNA binding activity of SR-R2R3MYBs; (2) confer binding specificity to SR-R2R3MYBs; (3) alter the biologic roles of SR-R2R3MYBs, all functions of which finally result in a change in the level of gene expression.

Identification of the downstream target genes is helpful to elucidate the molecular mechanisms how SR-R2R3MYBs regulate the plant adaptation to various stress conditions. Recently, these target genes are generally revealed by large-scale transcriptome analysis via over-expressing *SR-R2R3MYB* genes. SR-R2R3MYBs can directly or indirectly regulate a wide range of functional and regulatory genes (table 1) encoding proteins involved in the free radical and superoxide anion scavenging, osmolyte production, material transport, detoxification, signal transduction and regulation of gene expression etc. In general, these stress-related genes contain MBSs in their promoter, while there may exist some genes either without MBS or with a novel MBS, which can also be regulated by stress-responsive R2R3-MYBs, indicating a new mechanism remains to be investigated.

Functional conservation of sr-r2r3mybs in plants: In general, the biological roles of a R2R3-MYB in different plant species are highly conserved. For example, The *AtMYB44*-overexpressing soybeans exhibited significantly enhanced drought and salt stress tolerance, as observed in *Arabidopsis*, indicating the tolerance mechanism activated by AtMYB44 is conserved in these two plant species (Seo *et al.*, 2012). Based on this attribute, we can use one plant *SR-R2R3MYB* gene to modify another plant species tolerance. However, some SR-R2R3MYBs are exceptions. Overexpressing *OsMYB4* gene can enhance tolerance to cold and drought in apple, cold in *Osteospermum ecklonis*, drought but not cold in tomato, salt, cold and drought in rice, and different stresses such as cold, frost, drought, salt, UV and pathogen etc in *Arabidopsis* (Vannini *et al.*, 2007; Mattana *et al.*, 2005; Pasquali *et al.*, 2008; Laura *et al.*, 2010; Yang *et al.*, 2012). Therefore, it's better to detailedly dissect the function of a *SR-R2R3MYBs* before using it for crop improvement. To date, the reason why the same *SR-R2R3MYB* gene exhibits different biological roles in different plant species remains to be explored, maybe which can be explained by the genetic discrepancies formed under adverse environmental conditions via a long period of evolution.

Integration of various metabolic and signaling pathways by SR-R2R3MYBS: SR-R2R3MYBs usually acting as a key knot integrate a diversity of pathways including metabolic, SOS, signal transduction pathways etc. forming a sophisticated network in respond to various stresses (Fig. 3). TaPIMP1 enable wheat to resist *B. sorokiniana* and drought stresses by orchestrating ABA- and SA-signaling pathway cross-talk (Zhang *et al.*, 2012d). Seo *et al.* (2009) reported that AtMYB96 acts as a molecular link that mediates ABA-SA crosstalk, resulting in an increase in plant disease resistance (Seo *et al.*, 2010). At the same time, this gene can also affect lateral roots growth under drought condition through mediating ABA-IAA crosstalk (Seo *et al.*, 2009). In addition, ABA is able to affect wax biosynthesis via AtMYB96 in response to drought (Seo *et al.*, 2011). These findings show that different SR-R2R3MYBs play different roles in waving tress-related network. Besides TaPIMP1 and AtMYB96, a large amount of other SR-R2R3MYBs, such as AtMYB102, OsMYB4 and JAmyb, also serve as regulatory component that integrate the pathways related to dehydration, osmotic, salinity stress, and wound-signaling etc, to enhance plant tolerance or resistance. However, to date, no one clear and complete schematic of the stress-responsive network weaved by R2R3MYBs was drawing out.

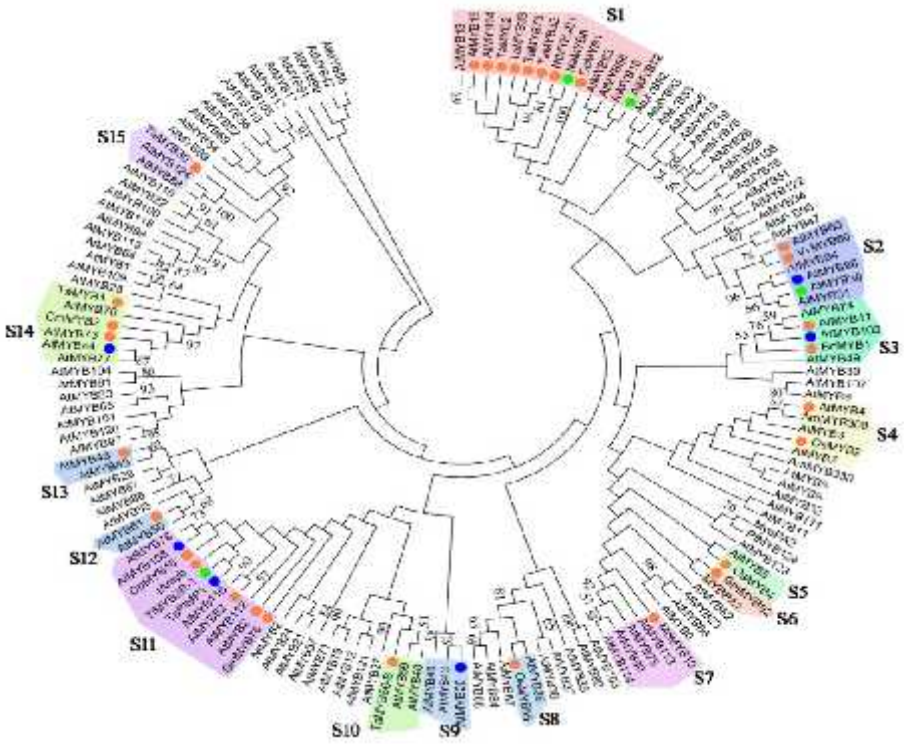

Figure 1 Phylogenetic relationship of *Arabidopsis* R2R3-MYB proteins and stress-respective R2R3-MYBs from other plant species was clustered using MEGA 5.0 (NJ, bootstrap=1000). The R2R3-MYBs responsive to abiotic and biotic stresses are highlighted by orange and green dot, respectively, and those concurrently responsive to abiotic and biotic stresses are emphasized by blue dot. All of them have been directly tested in vivo.

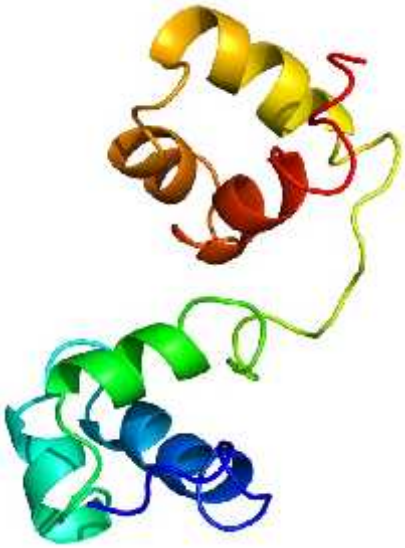

Figure 2 The three-dimensional (3D) structure of the MYB domain of a citrus R2R3-MYB identified from clementina genome (http://www. phytozome.org), referred as to CitMYB79. This 3D structure was constructed by Phyre2 (http://www.expasy.org/proteomics/protein_structure). The schematic was colored by rainbow from N to C.

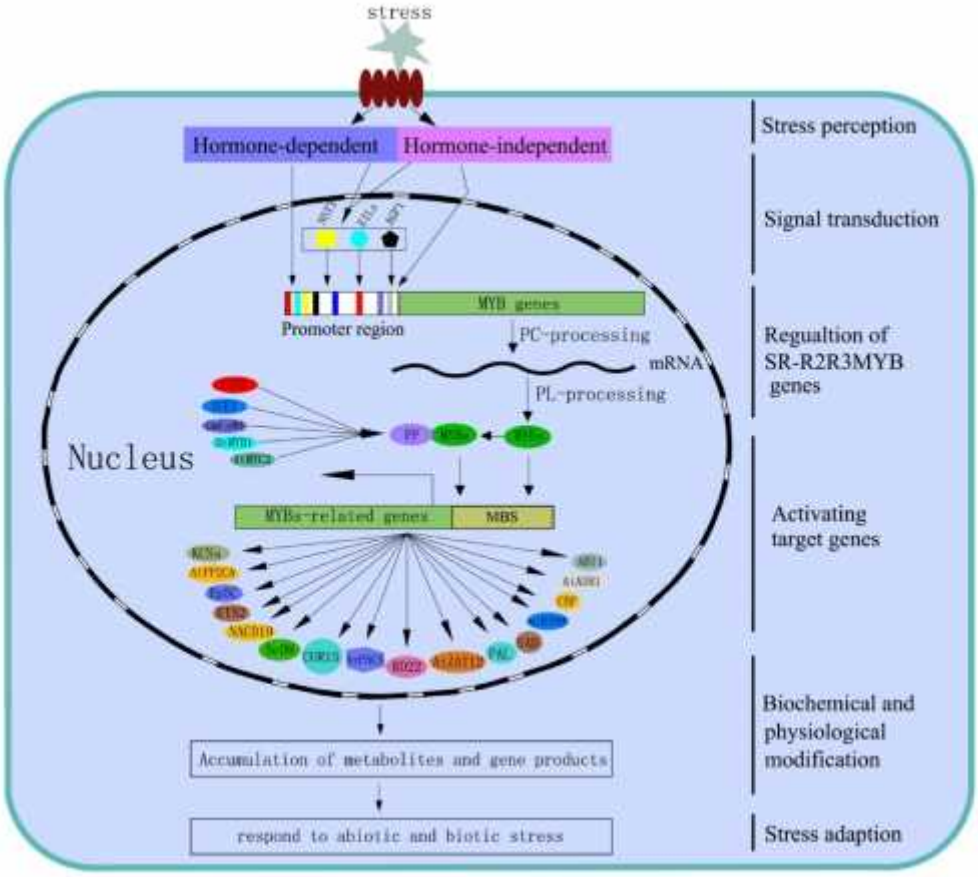

Figure 3 A schematic of SR-R2R3MYB TFs as key components in transcriptional regulation of gene expression during abiotic and biotic stresses. Abbreviations: PP, partner protein; MBS, MYB binding site; PC, post-transcriptional processing; PL, post-translational processing.

Table 1 Summary of stress-associated *R2R3-MYB* genes and their corresponding biologic functions

Transgenic plant	Genotype	Result/phenotype	Negative traits of thansgenics	Target genes	References
A. thaliana	CaMV 35S-*AtMYB60* overexpression	Promoted root mess and negatively controlled stomatal aperture under draught dress	By overexpression, increased sensitivity to drought	The auxin-responsive *DR5*, *PAP1*, *PAP2*, *flavanon-3ß-hydroxylase*	Oh *et al.*, 2011
	CaMV 35S-*AtMYB15* overexpression	Decreased *CBF* genes expression, enhanced salt and drought tolerance	Reduces freezing tolerance	***CBF1, CBF2, CBF3***, *ABI3*,*AtADH1*, *RD22 etc.*	Agarwal *et al.*, 2006; Ding *et al.*, 2009
	CaMV 35S-*AtMYB30* overexpression	*MYB30* positively regulated pathogen resistance for different bacterial pathogens and a biotrophic fungal pathogen, *Cercospora nicotianae*	-	*hsr203*, *hsr511 Athsr3*, *PR-1*, *PR-5*	Vailleau *et al.*, 2002
	CaMV 35S-*TaMYB30-B* overexpression	Improved drought stress		*RD29A*, *ERD1*	Zhang *et al.*, 2012a
	CaMV 35S-*AtMYB2* overexpression	Improved Stress Tolerance, and Pi uptake	Showed a dwarf phenotype and reduced primary root lenght	***rd22, AtADH1,*** *Cor6.6*, *rd20*, *US1*,*VSP2*,*BG1*,*TGG2*, ***miR399f*** **,** *PSI*	Abe *et al.*, 2003; Baek *et al.*, 2013
	AtMYB14 knock-down/overexpression	Negative regulator of low temperature tolerance	-	*CBF1*, *CBF2*, and *CBF3*	Chen *et al.*, 2013
	CaMV 35S-*AtMYB41* overexpression	Enhanced sensitivity to desiccation	Showed a mild dwarf phenotype	*AtRd29a*, *AtCor15a*, *AtKin1*, *AtDreb2a etc.*	Cominelli *et al.*, 2008
	CaMV 35S-*AtMYB44* overexpression	Showed enhanced resistance to *Pseudomonas syringae* pv. tomato DC3000 and to draught, salt and cold stresses	Showed a mild dwarf phenotype; delayed flowing time; small seeds	*PR1*, *ABI1*, *ABI2*, *AtPP2CA*, *HAB1*, *HAB2* etc.	Jung *et al.*, 2008; Zou *et al.*, 2012
	CaMV 35S-*TaMYB73* overexpression	Enhanced salinity tolerance		***AtCBF3, AtABF3,*** *AtRD29A*, *AtRD29B*	He *et al.*, 2012
	CaMV 35S-*TaMYB32* overexpression	Tolerance to salt stress	-	-	Zhang *et al.*, 2012b
	CaMV 35S-*MdMYB10* overexpression	Tolerance to osmotic stress	-	*chs*, *chi*, *f30h*, *c4h* and *fls*	Gao *et al.*, 2011
	CaMV 35S-*CmMYB2* overexpression	Tolerance to drought and salt stress	Delayed in flowering	*RD22*, *RD29A*, *RAB18*, *COR47*, *ABA1*, *ABA2*, *CO*, *FT*, *SOC1*,*LFY* and *AP1*	Shan *et al.*, 2012
	AtMYB46 mutant	Showed enhanced resistance to *B. cinerea*		***Ep5C***	Ramírez *et al.*, 2011
	AtMYB72 knockouts		impaired the ability against a broad spectrum of pathogens		Katiyar *et al.*, 2012
	CaMV 35S –*TaMYB33* overexpression	Enhanced resistance to drought and salt stresses		*AtP5CS*, *AtZAT12*, *AtAAO3*, *AtABF3*, *AtABI1*	Qin *et al.*, 2012
	CaMV 35S-*TaMYB56-B* overexpression	Enhanced resistance to freezing and salt stresses		DREB1A/CBF3 and COR15a	Zhang *et al.*, 2012c
	CaMV 35S-*OsMYB4* overexpression	Enhanced resistance to freezing and chilling stresses	Resulted in dwarf phenotype	***PAL2***, ***COR15a***, *COR78*	Vannini *et al.*, 2004

	CaMV 35S-*AtMYB15* overexpression	resulted in activation of the shikimate pathway genes in response to wounding		*DHS, DHQase-SDH, EPSPS* ect.	Chen *et al.*, 2006b
	CaMV 35S-*AtMYB62* overexpression	delayed senescence,	resulted in a characteristic gibberellic acid (GA)-deficient phenotype, leading to decreased total Pi content in leaf	*AtCPS, AtKO, AtGA3ox1, AtKS.*	Devaiah *et al.*, 2009
	CaMV 35S-*JAmyb* overexpression	Enhanced resistance to high-salinity	-	*AtPS, GPAT5, bHLH3* etc	Yokotani *et al.*, 2013
	AtMYB102 knockout	Increased susceptibility to *P. rapae*	-	*AtTHI2.1, AtVSP1*, etc.	Vos *et al.*, 2006
	Bos1 mutant	Hypersentitive to multiple abiotic and biotic stress	-	-	Mengiste *et al.*, 2003
	CaMV 35S-AtMYB20 overexpression	Enhanced resistance to salinity	-	***ABI1, AtPP2CA***	Cui *et al.*, 2013
	CaMV 35S-AtMYB96 overexpression	Enhanced resistance to drought; promoted accumulation of epicuticular wax	Resulted in dwarfed growth with reduced lateral roots	***CH3，KCS1, KCS2, KCS6, KCR1, CER3, WSD1 ,*** *RD22*	Seo *et al.*, 2009, 2011
	CaMV 35S-*TaMYB2A* overexpression	Enhanced tolerance to drought, salt, freezing tresses	-	*DREB1A, RD29A, COR15*, ect.	Mao *et al.*, 2011
	CaMV 35S-*DwMYB2* overexpression	hypersensitive to iron limitation.	Negatively affected size and morphology of rosette leaves	*AtFRO2, AtIRT1, AtIRT2* ect.	Chen *et al.*, 2006a
	CaMV 35S-AtMYB4 mutant	Enhanced resistance to UV-B light		*C4H*	Jin *et al.*, 2000
N.tabacum	CaMV 35s-*NtMYBJS1* overexpression	Accumulated more dark-colored phenolics, when stressed		***Phenylalanine ammonia-lyase***, *4-counarate:CoA ligase*	Gális *et al.*, 2006
	CaMV 35s-*TaPIMP1* overexpression	Tolerance to drought, salt, oxidative stress and *Ralstonia solanacearum*			Liu *et al.*, 2011
	CaMV 35s-*TaPIMP1* silencing	Decreased in tolerance to drought	leaves exhibited severe downward curling and abnormal growth of blades along the main veins	*NbACD1, NbACD2, NbASMDC, NbCAT, NTH20, KNOX*	Huang *et al.*, 2013
	AtMYB73 mutant	Enhanced adaptation to salt stress		*SOS1, SOS3*	Kim *et al.*, 2013
O. sativa	CaMV 35S-*OsMYB2* overexpression	Cold, salt and dehydration tolerance	By overexpression, increased sensitivity to ABA.	*OsLEA3, OsRab16A, OsDREB2A* ect.	Yang *et al.*, 2012
	Ubiquitin-*OsMYB2P-1* overexpression	Enhanced adaptation to low the low-Pi environment	Showed retarded growth in high level of Pi.	*(OsSQD, OsPAP10, OsIPS1, OsmiR399a, and OsmiR399j*	Dai *et al.*, 2012
T. aestivum	Ubiquitin-*TaPIMP1* overexpression	enhanced resistance to *Bipolaris sorokiniana* and drought stresses,		*RD22, dehydrin 6, ABAI, GLP4, GST22, PAL5, PR1a, PR2, and TLP4*	Zhang *et al.*, 2012d
	Ubiquitin-*TiMYB2R-1* overexpression	enhanced resistance take-all disease		*PR1a, PR17c, Chit2, Chit3, nsLTP1, GST22*	Liu *et al.*, 2013
G. max	CaMV 35S-*AtMYB2* overexpression	Tolerance to drought, salt stress	Showed a dwarf phenotype throughout the growth period		Seo *et al.*, 2012
M. pumila Mill.	CaMV 35S-*OsMYB4* overexpression	Enhanced resistance to draught and cold stress	Showed a dwarf phenotype		Pasquali *et al.*, 2008
H. vulgare	Cor 15a- *OsMYB4* overexpression	Enhanced resistance to frost and hypoxic stess	Showed a slight retarded growth, but not a dwarfism		Soltész *et al.*, 2012

Summary: Plants are sessile organisms and are frequently exposed to fluctuating environmental stress, such as drought, low temperature and pathogen that adversely affect plant growth and agricultural production. R2R3MYBs play an important role in plant adaptation to numerous stresses, recently receiving considerable attention. Overexpressing stress-responsive *R2R3-MYB* genes can modify the expression of stress-related genes, leading to an increase or a decrease in plant resistence. Some of them show the great potential for crop improvement. A growing body of R2R3MYBs has been identified from different plant species and their partial roles in stress tolerance also have been elucidated. However, there still have numerous questions remaining to be answered. Concerning these questions, further researches are needed to detailedly explore the *R2R3-MYB* sequence structure how to decide its biologic functions, the specificity to activate target gene, and the stress-responsive network waved by *R2R3-MYBs*. Unraveling the role of *R2R3-MYBs* in plant adaptation will ultimately contribute to the development and/or selection of crops with high productivity and quality under adverse environment conditions.

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