Transcriptional regulation of functional genes involved in cuticular wax biosynthesis by MYB family transcriptional factors in plants

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Abstract— *MYB transcription factor family is one of the largest families in the plant kingdom, specifically characterized by a Helix-turn-helix domain in their structural configuration with two repeats of R2R3 MYB domain and are known for regulating plant stress tolerance (abiotic and biotic) through ABA dependent signaling systems. R2R3- MYB family transcription factors plays a role in the regulation of specific downstream genes of Very Long Chain Fatty Acid Biosynthesis like KCS1, KCS2, KCS6 and KCR1, related to water use efficiency traits like cuticular wax biosynthesis. Analysis of R2R3-MYB family transcription factors regulating the production of cuticular wax emphasizes the value of the family outside of traditionally accepted roles in stress tolerance. Some MYB transcription factors like MYB96, MYB94, MYB41, MYB30, MYB106 and MYB16 isolated from Arabidopsis thaliana (Col-0) are studied with respect to their role in biosynthesis of cuticular waxes under environmental stress signals. In the present review we intensely focused on the elucidation of R2R3-MYB family transcription factors MYB96, MYB94, MYB41, MYB30, MYB106 and MYB16 role in cuticular wax biosynthesis and aid in the development of transgenics for enhanced stress tolerance.*

Keywords— MYB transcription factors, cuticular wax biosynthesis, Very Long Chain Fatty Acids, KCS1 and MYB 96.

I. INTRODUCTION

The cuticle framework is provided by cutin, a plant specific lipophylic, insoluble polyester consists of C16 and C18 hydroxy and epoxy-hydroxy fatty acids and glycerol monomers [1] [2] [3] that covers the surface of aerial plant parts and protects plants from nonstomatal water loss [4], pathogen infection [5], insect attack [6] , and UV radiation [7] [8]. Cuticle is lined as intracuticular waxes and overlaid with epicuticular waxes, which consist mainly of very-long-chain fatty acids (VLCFAs; C20 to C34) and their derivatives, such as alcohols, aldehydes, alkanes, ketones, and wax esters [9] [10] [11]. The recent studies strongly support that cuticular wax accumulation is closely associated with drought resistance responses [12] [13] [14] [15].

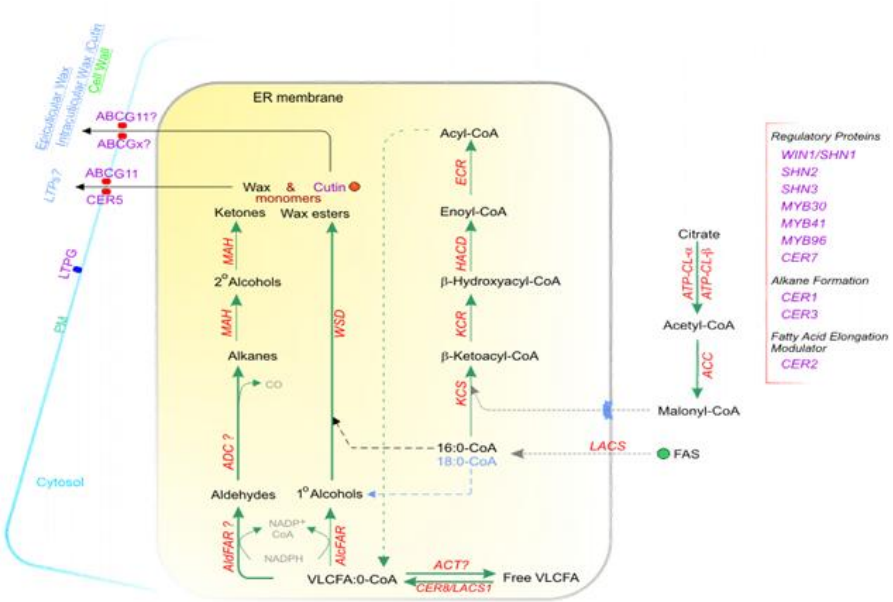

FIGURE 1: PATHWAY OF CUTICULAR WAX BIOSYTNESIS.

The above figure is deduced from internet showing the pathway of cuticular wax biosytnesis.

Wax bio-synthesis in plants starts with fatty acid synthesis in the plastid (*de novo* synthesis of C16 and C18) and elongation takes place in endoplasmic reticulum (C20–C34) with the help of four distinct enzymes 3-ketoacyl-CoA synthase (KCS), 3-ketoacyl-CoA reductase (KCR), 3-hydroxacyl-CoA dehydratese (HCD), trans-2,3-enoyl-CoA reductase (ECR). But the chain length and substrate specificity of the condensation reaction, a rate limiting step and the subsequent elongated products alkanes, aldehydes, primary alcohols, secondary alcohols, ketones and wax esters is determined by the KCS enzyme [16].

Several transcription factors are involved in cuticular wax biosynthesis like WAX INDUCER1 (WIN1)/SHINE1 (SHN1), SHN2 or SHN3 and its phylogenetic neighbours in the AP2/ERF family [12] [17] [14], homeodomain-leucine zipper (HD-ZIP) group IV transcription factors [18], OUTER CELL LAYER1 from maize (*Zea mays*)[19]. Some MYB family transcription factors [20] [21] [22] [23] [24] regulate the genes involved in biosynthesis and transport of cuticlar components. In the present review we focus on the functions of R2R3- MYB family transcription factors in relation to cuticular wax biosynthesis.

II. MYB TRANSCRIPTION FACTORS INVOLVED IN THE REGULATION OF CUTICULAR WAX BIOSYNTHESIS GENES

Several MYB transcription factors belonging to R2R3 class such as MYB30, MYB41, MYB94 MIXTA like MYBs: MYB16, MYB106, and MYB96 involved in cuticular wax biosynthesis to impart drought stress tolerance and disease resistance to crop plants.

2.1 MYB 30

MYB transcription factors are involved in the regulation of cuticle development, where the expression of these genes is affected by environmental stresses and/or developmental stages. The MYB gene MYB30 was previously identified as being activated in *Arabidopsis* plants inoculated with the strain 147 of *X. campestris pv campestris* (Xcc) [25]. AtMYB30 as a positive regulator of the signaling pathway, controls the establishment of cell death responses to pathogen attack [21]. Transient and specific activation of AtMYB30 leads to the hypersensitive cell death, after treatment with different avirulent bacterial pathogens [25].

Defense-related phenotypes of AtMYB30 transgenic plants are dependent on the VLCFA biosynthesis pathway, supporting the view that AtMYB30 modulates cell death-related lipid signaling by enhancing the synthesis of VLCFAs or VLCFA derivatives. Putative MYB30 target genes are involved in the lipid biosynthesis pathway that leads to the production of very-long chain fatty acids (VLCFAs), suggesting a role of this pathway in the control of HR and plant defense responses [22]. Ectopic expression of AtMYB30 activates genes encoding subunits of the acyl-coA elongase complex which include 3-ketoacyl-CoA synthase, 3-ketoacyl-CoA reductase, 3-hydroxyacyl-CoA dehydratase and trans-2,3-enoyl-CoA reductase, and yields the acyl-CoA elongated by two carbons [26] there by alters the VLCFA content of *Arabidopsis* leaves.

Two closely related stress-responsive MYB transcription factors, MYB30 and MYB96, activate the biosynthesis of very-long chain fatty acids (VLCFAs). Over expression of these genes induced the hyper accumulation of epidermal wax [22] [24]. AtMYB96 over expressing plants were found to be hyper sensitive to ABA, but an *Atmyb96* knock out mutant was still responsive to ABA, possibly due to functional redundancy within the MYB family [23]. AtMYB96 expression is induced by ABA and drought and the activation of some ABA-inducible genes is AtMYB96-dependent. Similar to AtMYB30, enhanced disease resistance conferred by AtMYB96 involves salicylic acid synthesis, suggesting that these two MYB transcription factors regulate cross-talks between hormone signaling pathways and contribute to the integration of Dsignals originating from various stresses [27] [28].

2.2 MYB 41

AtMYB41 gene transcriptionally regulates in response to salinity, drought, desiccation, and cold as well as the endogenous plant hormone ABA, control stress responses linked to cell wall modifications, cuticle metabolism and short-term expression of salt-responsive genes [29]. Constitutive expression of MYB41 alters permeability of leaf surface in *Arabidopsis* [20].

2.3 MIXTA-like MYBs

MIXTA-like (MML) transcription factors form the subgroup 9 of R2R3- MYBs [30] whose first characterized member was MIXTA from *Antirrhinum majus,* are required for the outgrowth of petal cells in the asteroids, *Antirrhinum* and *Petunia* [31] [32] [33]. MIXTA genes can also affect the patterning of trichomes in asterids, and heterologous expression of AmMIXTA

in tobacco promoted ectopic conical cells in leaves and trichomes in carpels [34]. MIXTA-like MYBs are common regulators of nanoridge formation and wax load as part of specialization of petal conical cells and cell elongation in filaments and siliques, which are made of non outgrown flat cells, and affect plant development through VLCFA biosynthesis; therefore, MIXTA-like MYBs act as regulators of cuticular substances that regulate surface coating and developmental signaling in the regulation of cuticle development during the differentiation of epidermal cells [35].

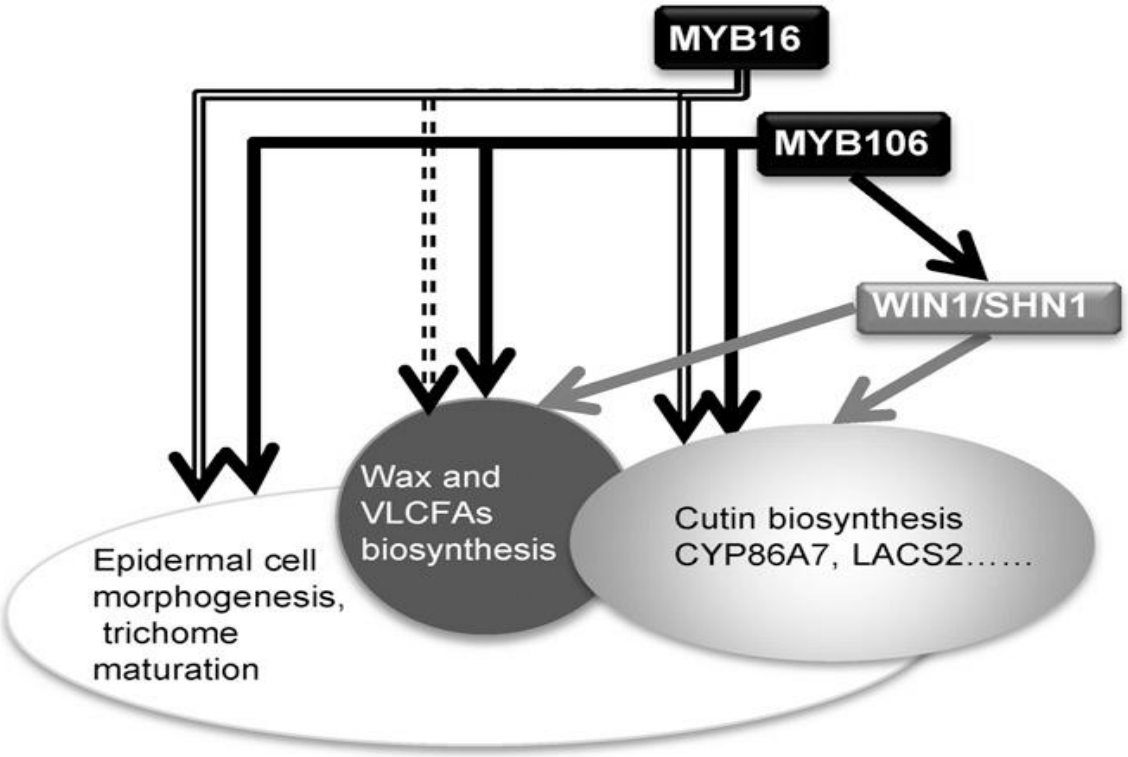

FIGURE 2: REGULATION OF CUTICLE DEVELOPMENT AND EPIDERMAL DIFFERENTIATION BY WIN1/SHN1 AND MIXTA-LIKE MYBS.

[MYB16 regulates epidermal morphogenesis and cutin biosynthesis and likely regulates wax and VLCFA biosynthesis together with MYB106. MYB106 regulates epidermal cell morphogenesis, trichome maturation, wax and VLCFA biosynthesis, cutin biosynthesis, and WIN1/SHN1 expression. WIN1/SHN1 was shown to regulate cutin and wax biosynthesis directly or indirectly [36] [37]. MYB106 regulates cutin biosynthesis via WIN1/SHN1-dependent and –independent pathways. The above figure is deduced from Oshima et al., 2013.]

2.4 MYB16

AtMYB16, proposed to control the shape of petal epidermal cells. Over expression of MYB16, an *Arabidopsis* MIXTA homolog, induced similar ectopic outgrowths in petals of *Arabidopsis* and tobacco, suggesting it has similar functions to petunia MYB1 and *A. majus* MYBML2 [33]. MYB16 activated expression from the promoters of *WIN1/SHN1* and the cutin biosynthesis gene CYP86A4 *in vivo*, indicating that it functions as a positive regulator of cuticle formation in vegetative tissues. MYB16 fused with the VP16 activation domain from herpes simplex virus infected plants had slightly shiny leaves and studies from scanning electron microscopy revealed over-accumulation of epicuticular wax-like substances. MYB16 promoter has activity in leaves and MYB16-SRDX driven by the MYB16 promoter produces an organ fusion phenotype in leaves [35].

2.5 MYB106

MYB106 belongs to MYB subgroup 9 of R2-R3 MYBs whose first characterized member was MIXTA from *Antirrhinum majus* [30]. MYB106 known to regulates the morphology of epidermal cells and acts as positive regulator of cuticle development through VLCFA biosynthesis. MIXTA-like *Arabidopsis* genes NOK/MYB106 and MYB16 participate in the regulation of cuticle biosynthesis, partially cooperating with WIN1/SHN1, in *Arabidopsis* and *Torenia fournieri*. [38].

MYB106 encodes NOK a most strongly expressed gene (among the 200) in the mature trichome transcriptome [30]. The *Arabidopsis* noeck (*nok*) mutant, which has a mutation in NOK/MYB106, exhibited over branched trichomes, suggesting that NOK/MYB106 negatively regulates trichome branch formation [39] [40]. MYB106 targets cell wall related genes [41] [42] [43]. MYB106 positively regulates cuticle formation through activation of the expression of cutin and wax biosynthetic genes and an APETALA2/ETHYLENE RESPONSE FACTOR (AP2/ERF) transcription factor, WAX INDUCER1/SHINE1, which also positively regulates cutin biosynthetic genes [12] [35] [36] [37].

2.6 MYB94

AtMYB94 transcription factor is a master transcriptional activator regulating the cuticular wax biosynthetic genes in response to drought stress [24] [44]. AtMYB94 gene expression is higher in stem epidermal peels than in stem , up-regulated in response to ABA, drought, and salinity stress [23] [45], up-regulate the transcription of cuticular wax biosynthetic genes and activate distinct target genes, WSD1, KCS2/DAISY, CER2, FAR3, and ECR genes. AtMYB94 overexpressing plants showed an increase in the total wax load in leaves, a little less in stems [45] and the rate of reduction in cuticular transpiration in leaves under drought stress [23] [45].

2.7 MYB96

The MYB96 transcription factor, a R2R3-type MYB member serves as a positive regulator of drought resistance response, enhances plant resistance to drought stress by inducing the RD22 gene. The MYB96 gene also mediates the auxin–ABA interactions during lateral root development, modulates abscisic acid (ABA)-mediated abiotic stress signals in inducing a small group of GH3 genes encoding IAA conjugating enzymes and contributes to maintenance of endogenous IAA contents at an appropriate amount under drought conditions. MYB96 transcription factor is intimately related with ABA-mediated drought stress responses, particularly during lateral root development [23]. In *Arabidopsis*, the R2R3-type MYB transcription factor MYB96, belong to the sub-group S1 and share extensive similarity in their N-terminal domain, short conserved motifs, the C-termini of sub-group S1 of MYB transcription factors are highly divergent [46]. AtMYB96 regulates lateral root meristem activation under drought conditions, possibly through an ABA–auxin signalling crosstalk, and the MYB96-knockout mutant produced more lateral roots and was more susceptible to drought stress [23]. AtMYB96-mediated ABA signaling promotes drought tolerance and resistance to the pathogen *Pseudomonas syringae* pv. tomato DC3000 infection by inducing SA biosynthesis. The ABA mediated MYB96 regulation of SA biosynthesis might be another route for balancing plant responses to pathogen infection and abiotic stresses [28].

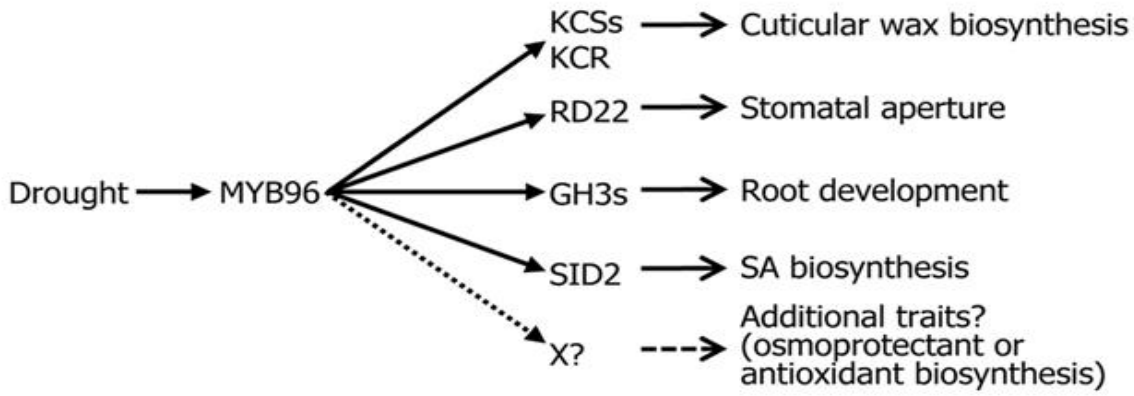

FIGURE 3

[Proposed roles of MYB96 in drought resistance response in plants. The MYB96 transcription factor induces both stomatal closure via RD 22 and cuticular wax biosynthesis by upregulating directly cuticular wax biosynthetic enzyme genes. It is also involved in modulation of root growth and development and SA biosynthesis. However, MYB96 does not seem to be related directly with biosynthesis of osmoprotectants and antioxidants. The above figure is deduced from Pil Joon Seo and Chung-Mo Park 2011.]

III. MYB96 ROLE IN CUTICULAR WAX BIOSYNTHESIS

MYB96 transcription factor regulates multiple traits, such as stomatal aperture, root development, cuticular wax accumulation and even pathogen infection [23] [28]. It serves as a molecular web that incorporates drought stress signals to promote fatty acid elongation in cuticular wax biosynthesis genes in an ABA-dependent manner. MYB96 regulates some wax-biosynthetic genes in *Arabidopsis*, suggesting it is required for drought induced cuticular wax biosynthesis [24]. MYB96 transcription factor binds directly to the promoters of genes encoding fatty acid elongation (a rate limiting step) enzymes such as KCS1, KCS2, KCS6 and KCR1 in cuticular wax biosynthesis.[47] [48]. Some mutants *myb96-1D* upregulates KCS, KCR, ECR and 3-hydroxyacyl Co A dehydratase (PAS2), CER3 (ECERIFERUM 3), CYP96A15/MAH1 (CYTOCHROME P450 96 A1) involved in decarbonylation pathway and CER4 and Wax ester synthase/diacylglycerol acyl transferase (WSD1) functions in acyl reduction pathway. ABC transporter that exports cutin monomers and waxes, are also up regulated in the mutant, indicating that MYB96 regulates both cuticular wax biosynthesis and transport [22]. Over expression of ATMYB96 confers drought resistance in *Camelina sativa* via cuticular wax accumulation [49].

IV. CONCLUSION

In the past, most studies have been focused on MYB transcription factors in plant defense against abiotic and biotic stresses; however, its role in regulating cuticular wax biosynthesis is not clearly understood. As MYB transcription factors are essential to plant-specialized metabolism, understanding their functions in cuticular wax biosynthesis will provide ways to successfully reengineer crop plants to produce higher yield. MYB transcription factors like MYB96, MYB94, MYB41, MYB30, MYB106, and MYB16 were studied in respect of their role in Bio-synthesis of cuticular waxes under environmental stress signals. Elucidating how MYBs regulate cuticular wax biosynthesis metabolism is critical not only for improving crop stress tolerance but also for increasing the productivity of crop plants. Individual expression of ATMYB96, ATMYB94, ATMYB41, ATMYB30, ATMYB106, and ATMYB16 imparted stress tolerance, by accumulating cuticular wax. But an attempt to overexpress any one of the MYB TF here MYB96, directly involved in the expression of downstream genes of Very Long Chain Fatty Acid Biosynthesis like KCS1, KCS2, KCS6 and KCR1 along with one key enzyme like KCS would be a potential option for engineering crops plants and develop transgenics for improved stress tolerance.

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