MYB转录因子在植物盐胁迫调控中的研究进展

陈娜[1], 迟晓元[1,2], 潘丽娟[1], 陈明娜[1], 禹山林[1,*]
[1]山东省花生研究所, 山东青岛266100; [2]农业部油料作物生物学与遗传育种重点实验室, 中国农业科学院油料作物研究所, 武汉430062

摘要: 盐胁迫是影响植物生长、发育及作物产量的重要环境因子。在植物响应高盐胁迫的过程中, 许多基因被激活, 并产生了许多抵御盐胁迫的蛋白。这些胁迫诱导基因的表达大多由转录因子调控。MYB转录因子广泛存在于真核生物中, 是一类数量较多、功能多样的转录因子家族。MYB蛋白在包括盐胁迫在内的植物非生物胁迫调控中有重要作用。MYB转录因子在结构上具有多样性, 因此对植物盐胁迫的调控机制较为复杂。近年来, 随着研究手段的提高, MYB家族转录因子, 尤其是R2R3-MYB, 在盐胁迫调控中的作用机制得到了较为深入的研究。此外, 越来越多的MYB-related蛋白也被证实参与了植物盐胁迫的调控。本文论述了MYB转录因子的结构特征和不同类型MYB蛋白在盐胁迫调控中的功能及作用机制, 以期为MYB转录因子的研究和利用提供参考。

关键词: 植物; 盐胁迫; MYB转录因子

Advances in MYB Transcription Factors during Salt-Stress Regulation in Plants

CHEN Na[1], CHI Xiao-Yuan[1,2], PAN Li-Juan[1], CHEN Ming-Na[1], YU Shan-Lin[1,*]
[1]Shandong Peanut Research Institute, Qingdao, Shandong 266100, China; [2]Key Laboratory of Biology and Genetic Improvement of Oil Crops, Ministry of Agriculture, Oil Crops Research Institute, Chinese Academy of Agricultural Sciences, Wuhan 430062, China

Abstract: Salt stress is a major environmental factor that affects plant growth, development and crop yields adversely. During plant response and adaptation to salt stress, many genes are activated, leading to accumulation of numerous proteins involved in resistance to salt stress. The expression of stress-induced genes is largely regulated by specific transcription factors (TFs). The MYB transcription factor family is large, functionally diverse and represent in all eukaryotes. MYB proteins function in a variety of plant-specific processes and they are proved to be key factors in regulatory networks controlling abiotic stresses including salt stress. Because of the structure diversity of MYB TFs, the regulation mechanisms of MYB are very complicated during salt stress regulation. In recent years, with an increase in research methods, the function mechanisms of MYB transcription factors, especially the R2R3-MYB members, have been studied deeply in plant salt stress regulation. Additionally, an increasing number of MYB-related proteins have also been demonstrated to be involved in the regulation of plant salt stress. In this review, we describe the structure of MYB proteins and summarize the research progress in different types of MYB TFs in plant salt stress regulation. We focus on the function and mechanism of this diversity transcription factor family so as to provide reference for further study and utilization.

Key words: plant; salt stress; MYB transcription factor

1 MYB转录因子结构特征

MYB蛋白主要特征是它们均具有高度保守的DNA结合结构域——MYB结构域。该结构域通常包含1~4个甚至更多的不完全重复序列(R), 这些序列在调控DNA结合或蛋白互作中可以协同地或独立地发挥作用。每个MYB重复序列由大约52个氨基酸组成, 序列中均匀分布的3个色氨酸残基形成一个疏水核心(Kanei-Ishii等1990)。每个MYB重复可形成3个α-螺旋结构, 第2和第3个螺旋与3个均匀分布的色氨酸残基形成螺旋-转角-螺旋结构(Ogata等1996)。每个重复的第3个螺旋是“识别螺旋”, 能

收稿 2015-05-05 修定 2015-07-29
资助 国家产业体系(CARS-14)、山东省自然科学基金(ZR2011-CQ036、ZR2012CQ031、ZR2014YL011、ZR2014YL012)、国家自然科学基金(31000728、31200211)、青岛市科技计划[12-1-4-11-(2)-jch、14-2-3-34-nsh]、农业部油料作物生物学与遗传育种重点实验室开放课题基金(2014010)。
* 通讯作者(E-mail: yshanlin1956@163.com; Tel: 0532-87626830)。

够直接与DNA接触并嵌入其大沟里(Jia等2004)。在与DNA接触的过程中, 2个MYB重复序列紧密结合于DNA大沟中, 使2个“识别螺旋”协同作用, 结合到特定的DNA序列上(Jia等2004)。

根据MYB重复序列数目的不同, MYB家族蛋白可以分为4种类型: 4R-MYB含有4个重复序列; 3R-MYB (R1R2R3-MYB)含有3个连续的重复序列; R2R3-MYB含有2个重复序列; MYB-related类型通常(但不一定)只包含1个单一的MYB重复序列(Rosinski和Atchley 1998; Jin和Martin 1999; Dubos等2010)。所有4种类型的MYB转录因子在植物中均有发现。

2 MYB转录因子在植物盐胁迫下的表达

许多MYB家族蛋白参与了植物对不利生长环境的响应, 其中一部分与植物盐胁迫调控密切相关。全基因组分析结果表明, 拟南芥和水稻中分别至少存在197个和155个MYB基因; 表达分析表明水稻中有14个(9.03%) MYB基因的表达在盐胁迫下上调, 而拟南芥MYB基因中35.02%和56.85%的基因在盐胁迫下分别上调和下调(Katiyar等2012)。Zhang等(2011a)在小麦中鉴定到60个MYB基因, 其中14个基因表达受盐胁迫诱导, 2个基因表达受盐胁迫抑制。Liao等(2008)在大豆中鉴定出156个*GmMYB*基因, 其中43个基因在脱落酸(abscisic acid, ABA)、盐、干旱或低温胁迫下表达量发生改变。陈嘉贝等(2014)发现, 甜瓜幼苗在盐胁迫下有6个MYB基因的表达量发生了明显变化。本研究组在花生中鉴定出30个MYB基因, 通过荧光定量PCR证明至少8个基因在花生根中受盐胁迫诱导表达(Chen等2014)。其他植物中许多MYB基因如*BcMYB1*、*PScMYBAS1*、*MdSIMYB1*等也参与了对盐胁迫的响应(Chen等2005; Prabu和Prasad 2012; Wang等2014)。

已有研究表明, 大部分盐胁迫响应MYB基因为R2R3类型。3R-MYB蛋白在植物中是一个较小的亚家族, 至今发现只有少数3R-MYB基因(包括*OsMYB3R-2*和*TaMYB3R1*)参与了植物盐胁迫调控(Dai等2007; Cai等2011)。MYB-related蛋白在植物中是一个较大的亚家族, 然而该家族蛋白在植物盐胁迫调控中的功能研究很少。已知受盐胁迫诱导表达的MYB-related基因主要有*OsMYB48-1*、*AtMYBL*和*LcMYB1* (Xiong等2014; Zhang等2011b; Cheng等2013)。最近, 小麦和花生中的一些MYB-related基因也被证明受盐胁迫诱导表达(Zhang等2011a; Chen等2014)。

3 MYB转录因子在植物盐胁迫调控中的功能

功能研究表明MYB蛋白能够影响转基因植株的耐盐能力, 并且大部分参与植物盐胁迫调控的MYB蛋白为R2R3类型。拟南芥的R2R3-MYB基因如*AtMYB44/AtMYBR1*、*AtMYB41*、*AtMYB15*和*AtMYB20*在mRNA水平上均对盐胁迫有响应, 在拟南芥中超表达均能够提高转基因植株对盐胁迫的抗性(Jung等2008; Lippold等2009; Ding等2009; Cui等2013)。小麦的R2R3-MYB基因*TaMYB32*、*TaMYB33*、*TaMYB56-B*和*TaMYB73*在小麦中均受盐胁迫诱导表达, 超表达这些基因的转基因拟南芥植株耐盐能力均有所增强(Zhang等2011a, 2012; He等2012; Qin等2012)。其他植物中的一些R2R3-MYB基因, 如水稻的*OsMYB2*、苹果的*MdSIMYB1*、甘蔗的*PScMYBAS1*及毛竹的*PeMYB2*, 在植物中超表达均能够提高转基因植株的耐盐能力(Yang等2012; Wang等2014; Prabu和Prasad 2012; 肖冬长等2013)。此外, Dai等(2007)发现水稻中一个3R-MYB基因*OsMYB3R-2*也参与了水稻盐胁迫调控。

与R2R3-MYB不同, MYB-related蛋白已被证明主要参与了昼夜节律(Wang和Tobin 1998; Kuno等2003)和细胞形态(Schellmann等2002; Kirik等2004)的调控, 在植物非生物胁迫调控中的研究很少。但是近年来一些MYB-related蛋白也被证明参与了植物盐胁迫调控。高盐胁迫能够激活拟南芥MYB-related基因*AtMYBL*的表达, 在拟南芥中超表达该基因能够提高转基因种子在盐胁迫下的萌发率(Zhang等2011b)。白骨壤的AmMYB1是只含有1个MYB重复的MYB蛋白, 其在转录水平受盐和ABA的诱导, *AmMYB1*在烟草中超表达能够提高转基因烟草对盐胁迫的耐受性(Ganesan等2012)。羊草中的R1-MYB基因*LcMYB1*表达受盐胁迫的诱导, 并能够提高转基因拟南芥对盐胁迫的抗性(Cheng等2013)。水稻的*OsMYB48-1*也是一个MYB-related基因, 其表达受盐胁迫的轻微诱导, 但在水稻中超表达该基因能够显著提高转基因植株

耐盐能力(Xiong等2014)。MYB-related蛋白在植物中是一个较大的亚家族, 随着研究的深入, 越来越多该亚家族成员将被证明参与植物非生物胁迫的调控。

另外, 一些MYB蛋白可能对植物盐胁迫抗性有负调控作用。例如, 拟南芥的*AtMyb73*在拟南芥中的表达受盐胁迫的诱导, 但*atmyb73*缺失突变体植株在盐胁迫下的存活率高于野生型植株。这表明AtMyb73在拟南芥盐胁迫调控中可能是一个负调控因子(Kim等2013)。

4 MYB转录因子在植物盐胁迫调控中的作用机制

尽管不同的MYB蛋白氨基酸序列相似, 但其在植物中的作用机制不尽相同。一些MYB蛋白通过依赖ABA的方式行使功能, 这些蛋白包括AtMYB44、CmMYB2、TaMYB33等(Jung等2008; Shan等2012; Qin等2012)。在拟南芥中超表达*AtMYB44*和*AtMYB15*, 转基因植株对ABA诱导的气孔闭合反应比野生型植株更敏感, 说明超表达这两个基因增强了转基因植株对ABA的敏感性(Jung等2008; Ding等2009)。*AtMYB44*和*AtMYB20*在拟南芥中超表达能够降低ABA信号负调控因子蛋白磷酸酶2C (protein phosphatase 2C, PP2Cs)基因的表达, 从而增强转基因植株耐盐能力(Jung等2008; Cui等2013)。*TaMYB33*在拟南芥中超表达能够增强*abscisic-aldehyde oxidase 3* (*AtAAO3*)的表达, 同时降低*ABA responsive elements-binding factor 3* (*AtABF3*)和*ABA insensitive 1* (*AtABI1*)的表达, 表明转基因植株中ABA合成途径增强, 而信号途径减弱, TaMYB33通过重建渗透平衡, 清除活性氧自由基而增加转基因植株在盐胁迫下的抗性(Qin等2012)。其他R2R3-MYB成员如水稻的OsMYB2和菊花的CmMYB2在植物盐胁迫调控中均通过依赖ABA的方式行使功能(Yang等2012; Shan等2012)。MYB-related蛋白OsMYB48-1也是通过依赖ABA的方式发挥作用(Xiong等2014)。还有一些MYB蛋白不依赖ABA途径行使功能, 而是通过激活DREB/CBF (dehydration-responsive element-binding protein/C-repeat binding factor)信号途径下游一些非生物胁迫相关基因的表达而提高转基因植株的耐盐能力。例如, *TaMYB56-B*在拟南芥中超表达能够提高一些冷响应基因如干旱响应元件结合蛋白基因*DREB1A*和低温调控蛋白基因*COR15a* (*cold-regulated protein 15a*)的表达, 表明TaMYB56-B可能以不依赖ABA的方式调控植物的盐胁迫适应性(Zhang等2012)。毛竹*PeMYB2*基因在拟南芥中超表达能够提高转基因植株耐盐能力, 表达分析表明盐胁迫响应的标记基因包括*NXH1* (*Na^+/H^+ exchanger*)、*SOS1* (*salt overly sensitive 1*)、*RD29A* (*responsive to dehydration 29A*)和*COR15A*在转基因植株中盐胁迫下表达量均比野生型高(肖冬长等2013)。研究表明, 还有一些MYB蛋白可以通过依赖和不依赖ABA两条路径行使功能。例如, 大豆的*GmMYB76*和*GmMYB177*均能够增强转基因拟南芥对盐胁迫的耐受性, 转基因植株对ABA的敏感性降低, 表明这两个*GmMYB*基因是ABA信号途径的负调控因子; 同时这两个*GmMYB*基因也能够提高*DREB2A*、*RD17*、*RD29B*、*COR78*、*ERD10* (*early response to dehydration*)和*P5CS* (*pyrroline-5-carboxylate synthase*)基因的表达(Liao等2008)。超表达*TaMYB73*的拟南芥植株在高盐和ABA处理下萌发率均有所增强, 转基因植株中两种信号途径基因包括*AtCBF3*和*AtABF3*均有所增强, 表明TaMYB73可能分别以依赖和不依赖ABA方式调控基因表达(He等2012)。Dai等(2007)研究发现, 水稻中3R-MYB蛋白OsMYB3R-2也是以依赖和不依赖ABA两种方式调控植物对盐胁迫的抗性。

由于MYB家族蛋白功能的多样性, MYB转录因子对植物盐胁迫的调控还存在其他作用机制。对拟南芥*atmyb73*缺失突变体的研究表明, 300 $mmol \cdot L^{-1}$ NaCl处理下SOS路径相关基因*SOS1*和*SOS3*在突变体中表达量增加, 表明AtMyb73在拟南芥对盐胁迫的响应中是SOS调控路径的负调节因子(Kim等2013)。羊草*LcMYB1*超表达能够增强*P5CS1*的表达, 但是抑制盐胁迫响应路径中一些标记基因的表达, 说明LcMYB1对植物盐胁迫的调控方式与传统DREB1A介导的信号途径不同(Cheng等2013)。红树*AmMYB1*在烟草中超表达能够减轻盐胁迫下叶片及整株植物的枯萎、变黄, 从而提高转基因烟草对盐胁迫的抗性(Ganesan等2012)。Zhang等(2011b)报导, AtMYBL通过调控叶片衰老来调节拟南芥对非生物胁迫的响应。Lippold等

(2009)研究表明, AtMyb41以依赖ABA的方式响应渗透胁迫, 并参与渗透胁迫下特定的细胞过程如初级代谢及转录负调控等。Cheng等(2013)报导, 盐胁迫下*IbMYB1*转基因马铃薯中二苯代苦味酰基自由基[2,2-diphenyl-1-(2,4,6-trinitrophenyl) hydrazyl, DDPH]的清除能力增强, 光系统II (PSII)光化学效率升高, 表明*IbMYB1*表达量升高后影响了植物的次级代谢, 从而使转基因植株抗性增强。芯片杂交分析结果表明, *JAmyb*超表达能够激活防御反应和JA途径相关基因的表达, 说明JAmyb可能通过JA介导的信号途径调控水稻对非生物胁迫的响应(Yokotani等2013)。

近年来人们对MYB蛋白的调控因子也进行了研究。Persak和Pitzschke (2014)提出一个胁迫抗性调控中丝裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)-MYB介导的提高植物抗氧化能力的模型, 该模型指出, AtMYB44是MPK3的底物, 被MPK3磷酸化后成为盐胁迫信号途径中的正调节因子。Prabu和Prasad (2012)对*ScMYBAS1*启动子区进行了分析, 发现该启动子区能够对干旱、盐、低温、伤害、赤霉素(gibberellic acid, GA)、水杨酸(salicylic acid, SA)和茉莉酸甲酯(methyl jasmonate, MeJA)响应, 表明ScMYBAS1可能介导多种信号途径。Nagaoka和Takano (2003)发现耐盐蛋白(salt tolerance protein, STO)能够与MYB转录因子结合, 进而增加拟南芥对盐胁迫的抗性。

5 小结与展望

土壤盐化已经成为全球农业一个持续加剧的问题。了解盐胁迫响应途径的关键成员, 通过对这些成员的基因操控, 可以获得耐盐能力增强的转基因植株(吴运荣等2014)。MYB转录因子是一类多功能蛋白, 在植物盐胁迫中有重要功能, 近年来对其作用机制的研究获得了较大进展。然而, 由于MYB蛋白功能复杂, 对所有MYB蛋白在不同植物调控网络中的功能研究还有很多工作要做。此外, MYB-related蛋白在植物盐胁迫中的功能及作用机制研究处于起步阶段, 随着研究的深入, 将会有更多参与植物盐胁迫及其他非生物胁迫的该亚家族成员被挖掘出来。

参考文献

陈嘉贝, 张芙蓉, 黄丹枫, 张利达, 张屹东(2014). 盐胁迫下两个甜瓜品种转录因子的转录组分析. 植物生理学报, 50: 150~158

吴运荣, 林宏伟, 莫肖蓉(2014). 植物抗盐分子机制及作物遗传改良耐盐性的研究进展. 植物生理学报, 50: 1621~1629

肖冬长, 张智俊, 徐英武, 杨丽, 张凤雪, 王超莉(2013). 毛竹MYB转录因子*PeMYB2*的克隆与功能分析. 遗传, 35: 1217~1225

Cai H, Tian S, Liu C, Dong H (2011). Identification of a MYB3R gene involved in drought, salt and cold stress in wheat (*Triticum aestivum* L.). Gene, 485: 146~152

Chen BJ, Wang Y, Hu YL, Wu Q, Lin ZP (2005). Cloning and characterization of a drought inducible MYB gene from *Boea crassifolia*. Plant Sci, 168: 493~500

Chen N, Yang Q, Pan L, Chi X, Chen M, Hu D, Yang Z, Wang T, Wang M, Yu S (2014). Identification of 30 MYB transcription factor genes and analysis of their expression during abiotic stress in peanut (*Arachis hypogaea* L.). Gene, 533: 332~345

Cheng L, Li X, Huang X, Ma T, Liang Y, Ma X, Peng X, Jia J, Chen S, Chen Y et al (2013). Overexpression of sheepgrass R1-MYB transcription factor *LcMYB1* confers salt tolerance in transgenic *Arabidopsis*. Plant Physiol Bioch, 70: 252~260

Cheng YJ, Kim MD, Deng XP, Kwak SS, Chen W (2013). Enhanced salt stress tolerance in transgenic potato plants expressing *IbMYB1*, a sweet potato transcription factor. J Microbiol Biotech, 23: 1737~1746

Cui MH, Yoo KS, Hyoung S, Nguyen HT, Kim YY, Kim HJ, Ok SH, Yoo SD, Shin JS (2013). An *Arabidopsis* R2R3-MYB transcription factor, AtMYB20, negatively regulates type 2C serine/threonine protein phosphatases to enhance salt tolerance. FEBS Lett, 587: 1773~1778

Dai X, Xu Y, Ma Q, Xu W, Wang T, Xue Y, Chong K (2007). Overexpression of an R1R2R3 MYB gene *OsMYB3R-2*, increases tolerance to freezing, drought, salt stress in transgenic *Arabidopsis*. Plant Physiol, 143: 1739~1751

Ding Z, Li S, An X, Liu X, Qin H, Wang D (2009). Transgenic expression of *MYB15* confers enhanced sensitivity to abscisic acid and improved drought tolerance in *Arabidopsis thaliana*. J Genet Genomics, 36: 17~29

Dubos C, Stracke R, Grotewold E, Weisshaar B, Martin C, Lepiniec L (2010). MYB transcription factors in *Arabidopsis*. Trends Plant Sci, 15: 573~581

Ganesan G, Sankararamasubramanian HM, Harikrishnan M, Ganpudi A, Parida A (2012). A MYB transcription factor from the grey mangrove is induced by stress and confers NaCl tolerance in tobacco. J Exp Bot, 63: 4549~4561

He Y, Li W, Lv J, Jia Y, Wang M, Xia G (2012). Ectopic expression of a wheat MYB transcription factor gene, *TaMYB73*, improves salinity stress tolerance in *Arabidopsis thaliana*. J Exp Bot, 63: 1511~1522

Jia L, Clegg MT, Jiang T (2004). Evolutionary dynamics of the DNA-binding domains in putative R2R3-MYB genes identified from rice subspecies *indica* and *japonica* genomes. Plant Physiol, 134: 575~585

Jin H, Martin C (1999). Multifunctionality and diversity within the plant MYB-gene family. Plant Mol Biol, 41: 577~585

Jung C, Seo JS, Han SW, Koo YJ, Kim CH, Song SI, Nahm BH, Choi YD, Cheong J (2008). Overexpression of *AtMYB44* enhances stomatal closure to confer abiotic stress tolerance in transgenic *Arabidopsis*. Plant Physiol, 146: 623~635

Kanei-Ishii C, Sarai A, Sawazaki T, Nakagoshi H, He DN, Ogata K, Nishimura Y, Ishii S (1990). The tryptophan cluster: a hypothetical structure of the DNA-binding domain of the myb protooncogene product. J Biol Chem, 265: 19990~19995

Katiyar A, Smita S, Lenka SK, Rajwanshi R, Chinnusamy V, Bansal KC (2012). Genome-wide classification and expression analysis of MYB transcription factor families in rice and *Arabidopsis*. BMC Genomics, 13: 544

Kim JH, Nguyen NH, Jeong CY, Nguyen NT, Hong SW, Lee H (2013). Loss of the R2R3 MYB, AtMyb73, causes hyper-induction of the *SOS1* and *SOS3* genes in response to high salinity in *Arabidopsis*. J Plant Physiol, 170: 1461~1465

Kirik V, Simon M, Huelskamp M, Schiefelbein J (2004). The *ENHANCER OF TRY AND CPC1* gene acts redundantly with *TRIPTYCHON* and *CAPRICE* in trichome and root hair cell patterning in *Arabidopsis*. Dev Biol, 268: 506~513

Kuno N, Moller SG, Shinomura T, Xu XM, Chua NH, Furuya M (2003). The novel MYB protein EARLY-PHYTOCHROME-RESPONSIVE1 is a component of a slave circadian oscillator in *Arabidopsis*. Plant Cell, 15: 2476~2488

Liao Y, Zou HF, Wang HW, Zhang WK, Ma B, Zhang JS, Chen SY (2008). Soybean *GmMYB76*, *GmMYB92*, and *GmMYB177* genes confer stress tolerance in transgenic *Arabidopsis* plants. Cell Res, 18: 1047~1060

Lippold F, Sanchez DH, Musialak M, Schlereth A, Scheible W, Hincha DK, Udvardi MK (2009). AtMyb41 regulates transcriptional and metabolic responses to osmotic stress in *Arabidopsis*. Plant Physiol, 149: 1761~1772

Nagaoka S, Takano T (2003). Salt tolerance-related protein STO binds to a Myb transcription factor homologue and confers salt tolerance in *Arabidopsis*. J Exp Bot, 54: 2231~2237

Ogata K, Kanei-Ishii C, Sasaki M, Hatanaka H, Nagadoi A, Enari M, Nakamura H, Nishimura Y, Ishii S, Sarai A (1996). The cavity in the hydrophobic core of Myb DNA binding domain is reserved for DNA recognition and *trans*-activation. Nat Struct Biol, 3: 178~187

Persak H, Pitzschke A (2014). Dominant repression by *Arabidopsis* transcription factor MYB44 causes oxidative damage and hypersensitivity to abiotic stress. Int J Mol Sci, 15: 2517~2537

Prabu G, Prasad DT (2012). Functional characterization of sugarcane MYB transcription factor gene promoter (*PScMYBAS1*) in response to abiotic stresses and hormones. Plant Cell Rep, 31: 661~669

Qin Y, Wang M, Tian Y, He W, Han L, Xia G (2012). Over-expression of TaMYB33 encoding a novel wheat MYB transcription factor increases salt and drought tolerance in *Arabidopsis*. Mol Biol Rep, 39: 7183~7192

Rosinski JA, Atchley WR (1998). Molecular evolution of the Myb family of transcription factors: evidence for polyphyletic origin. J Mol Evol, 46: 74~83

Schellmann S, Schnittger A, Kirik V, Wada T, Okada K, Beermann A, Thumfahrt J, Jürgens G, Hülskamp M (2002). *TRIPTYCHON* and *CAPRICE* mediate lateral inhibition during trichome and root hair patterning in *Arabidopsis*. EMBO J, 21: 5036~5046

Shan H, Chen S, Jiang J, Chen F, Chen Y, Gu C, Li P, Song A, Zhu X, Gao H et al (2012). Heterologous expression of the chrysanthemum R2R3-MYB transcription factor *CmMYB2* enhances drought and salinity tolerance, increases hypersensitivity to ABA and delays flowering in *Arabidopsis thaliana*. Mol Biotechnol, 51: 160~173

Wang RK, Cao ZH, Hao YJ (2014). Overexpression of a R2R3 MYB gene *MdSIMYB1* increases tolerance to multiple stresses in transgenic tobacco and apples. Physiol Plantarum, 150: 76~87

Wang ZY, Tobin EM (1998). Constitutive expression of the *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*) gene disrupts circadian rhythms and suppresses its own expression. Cell, 93: 1207~1217

Xiong H, Li J, Liu P, Duan J, Zhao Y, Guo X, Li Y, Zhang H, Ali J, Li Z (2014). Overexpression of *OsMYB48-1*, a novel MYB-related transcription factor, enhances drought and salinity tolerance in rice. PLoS ONE, 9: e92913

Yang A, Dai X, Zhang W (2012). A R2R3-type MYB gene, *OsMYB2*, is involved in salt, cold, and dehydration tolerance in rice. J Exp Bot, 63: 2541~2556

Yokotani N, Ichikawa T, Kondou Y, Iwabuchi M, Matsui M, Hirochika H, Oda K (2013). Role of the rice transcription factor JAmyb in abiotic stress response. J Plant Res, 126: 131~139

Zhang L, Zhao G, Jia J, Liu X, Kong X (2011a). Molecular characterization of 60 isolated wheat MYB genes and analysis of their expression during abiotic stress. J Exp Bot, 63: 203~214

Zhang L, Zhao G, Xia C, Jia J, Liu X, Kong X (2012). Overexpression of a wheat MYB transcription factor gene, *TaMYB56-B*, enhances tolerances to freezing and salt stresses in transgenic *Arabidopsis*. Gene, 505: 100~107

Zhang X, Ju H, Chung M, Huang P, Ahn S, Kim CS (2011b). The R-R-type MYB-like transcription factor, AtMYBL, is involved in promoting leaf senescence and modulates an abiotic stress response in *Arabidopsis*. Plant Cell Physiol, 52: 138~148