

SiMYB19

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SiMYB19 is tentatively localized to the nucleus and activates transcription. It enhances salt tolerance in transgenic rice at the germination and seedling stages. SiMYB19 overexpression increased shoot height, grain yield, and salt tolerance in field- and salt pond-grown transgenic rice. SiMYB19 overexpression promotes abscisic acid (ABA) accumulation in transgenic rice and upregulates the ABA synthesis gene OsNCED3 and the ABA signal transduction pathway-related genes OsPK1 and OsABF2.

high salt stress

MYB transcription factor

MYB19

1. Introduction

Salt stress adversely affects plant growth and development and has a serious impact on crop yield and quality. Eight hundred million hectares of soil worldwide are affected by salinity according to FAO data. Soil salinity affects over 20% of all arable land globally. This rate is expected to continue to increase ^[1]. Therefore, the selection of salt-tolerant crops is vital to the maintenance of grain production in saline-alkali soil, the expansion of cultivable land, and the assurance of food security. Foxtail millet (*Setaria italica* L.) belongs to the Gramineae family. It originated in China and has strong natural abiotic stress resistance ^[2], a small genome, and a short growth cycle. Therefore, it is an ideal model crop to study abiotic stress resistance in gramineous crops ^[2]. However, very little research has been conducted to date on the functional genome of foxtail millet. Furthermore, its stress-related regulatory network is poorly understood. Identification of the key stress resistance genes in foxtail millet and especially those with important practical field application may help facilitate the improvement of stress resistance in this plant and the other gramineous crops.

MYB-like transcription factors perform various functions during plant growth and development. They regulate anthocyanidin biosynthesis and accumulation, lateral root and pollen development, and phytohormones ^[3]. *Arabidopsis* induces the expression of *AtMYB2* and *AtMYB15* by regulating ABA content under drought and high salt conditions ^{[4][5]}. *GAMYB* in rice is also an important regulator of gibberellin signal transduction ^[6]. The foregoing genes also play important roles in stress adaptation. The rice R2R3-MYB transcription factor (TF) *OsMYB2* is strongly induced in response to salt and cold stress. *OsMYB2* overexpression enhances tolerance to different abiotic stressors in *OsMYB2* transgenic plants ^[7]. In *Arabidopsis*, certain R2R3-MYB TFs such as *AtMYB2*, *AtMYB20*, *AtMYB44*, *AtMYB73*, and *AtMYB74* are induced by salt stress and regulate salt tolerance ^[8]. *ZmMYB3R* is a positive regulator of salt and drought resistance. Its ectopic expression significantly enhances transgenic plant tolerance to drought and salt stress ^[9]. The alfalfa TF *MYB4* is activated by DNA methylation and/or histone modification in response to salt stress ^[10]. The poplar MYB TF *PtrSSR1* enhances salt stress

tolerance in transgenic plants [11]. Apple *MdMYB88* and its homolog *MdMYB124* regulate root xylem development and cell wall cellulose accumulation under drought conditions. Therefore, these genes regulate water transport under drought stress [12]. Several studies have reported on the roles of MYB TFs in abiotic stress response. However, it is difficult to regulate the strength of abiotic stressors such as salinity because of the long duration of field trials. Hence, most of the foregoing data were obtained from laboratory or greenhouse experiments. There is a lack of field trial data demonstrating the influences of MYB-like TFs on abiotic stress resistance in field crops. Functional evaluation of stress-related genes in field crops may help establish whether they merit further investigation and should be applied in practical breeding research.

2. SiMYB19 Is a Positive Regulator That Modulates Field Crop Salt Stress Tolerance

SiMYB19 overexpression significantly improves salt tolerance in transgenic rice grown in the greenhouse and field. Salinization seriously affects crop growth, yield, and total agricultural production [13][14]. The current global area of salinized land is ~954 million hm², accounts for 7% of the total land area worldwide, and is distributed mainly in Africa, western North America, and Eurasia [15]. In China, the area of saline-alkali land is ~36.66 million hm² [16], and most of it has neither been developed nor utilized [17]. Moreover, it is constantly expanding, severely reduces crop growth and grain yield, and threatens the environment and food security. Salt stress may impede crop growth at different developmental stages. The plant growth cycle cannot proceed normally when the soil salt concentration is >200 mM [18][19]. *SiMYB19* overexpression increased salt tolerance in field-grown transgenic rice subjected to 0.3% (w/v) and 0.5% (w/v) NaCl. Under these conditions, the transgenic rice could grow and develop normally and had significantly superior grain yield and salt tolerance compared to the WT plants. *OsMYB91*, *OsMYB2*, and *OsMLD* (with MYB TF domain) genes were overexpressed in rice [7][20][21]. The results showed that MYB TF had a positive regulatory effect on salt stress, and the newly identified transgenic line OE-6 also showed similar salt stress resistance. Therefore, this study may provide germplasm resources for improving crop salt tolerance. *SiMYB19* has potential value in practical cereal crop breeding research. This gene can improve salt tolerance and increase yield in saline-alkali soil. The stable application of *SiMYB19* may be validated by multi-year field experiments. If these trials are successful, then *SiMYB19* could help expand the global range of arable land.

3. SiMYB19 Confers Salt Stress Tolerance through an Aba-Dependent Pathway

The four categories of MYB family proteins are MYB-related, R2R3-MYB, 3R-MYB (R1R2R3-MYB), and 4R-MYB [22][23]. Abiotic stress can induce MYB-related genes. Overexpression of the latter in transgenic plants can increase drought and salt stress resistance. Several R2R3-like MYB TFs participate in stress tolerance [7][24]. Here, the researchers found that *SiMYB19* belongs to the R2R3-MYB subgroup. A phylogenetic tree identified genes with the highest homology, namely, *ZmLAF1*, *OsMYB19*, *TaMYB18*, *SiMYB18*, and *AtMYB45* in maize, rice, wheat, foxtail millet, and *Arabidopsis*, respectively. The foregoing genes belong to the R2R3-MYB TF family. *SoMYB18* is a sugarcane R2R3-MYB TF that improved salt and drought tolerance in tobacco [25]. *MYB15* overexpression

improved drought and salt resistance in *Arabidopsis* by enhancing its ABA sensitivity [26]. Therefore, the R2R3-MYB TF *SiMYB19* identified herein may also confer abiotic stress resistance in other plants.

MYB-related genes regulate ABA-related pathways and enable plants to contend with various stressors. ABA reduces water loss from cells in response to osmotic stress [27]. The genes regulating abiotic stress response are involved in both ABA-dependent and ABA-independent signaling pathways [28][29]. In the former, the class A protein phosphatase PP2Cs represses *SnRK2s* [30], and the ABA signaling pathway is closed. Under stress conditions, ABA production is upregulated, and the phytohormone binds the receptor protein PYR/PYL/RCARs [31] to form a receptor complex with PP2Cs. The *SnRK2s* is released and is automatically phosphorylated and self-activated [32][33]. It then phosphorylates downstream ABA TFs and regulates the expression of ABA-responsive genes. Here, the expression levels of ABA synthesis signal transduction genes such as *NCED3*, *ABF2*, and *PK1* were higher in *SiMYB19* transgenic plants than in the WT. The high expression levels of these genes observed in OE-8 may be explained by the fact that the plants were sampled at the early stages of salt stress treatment. *SiMYB19* confers salt and drought tolerance in field-grown transgenic rice through the ABA pathway. Previous studies reported that *AtMYB44* and *AtMYB96* control plant drought and ABA responses through the ABA-dependent signaling pathway [34][35]. *OsMYB6* overexpression affected neither the growth nor the development of transgenic rice but increased its ABA sensitivity and enhanced its resistance to drought and salt stress [36]. Overexpression of the MYB19-like protein *TaMYB19-B* from *Triticum aestivum* improved stress tolerance in transgenic *Arabidopsis*. *TaMYB19-B* was induced by both abiotic stress and exogenous ABA treatment [37]. *TaMYB19-B* overexpression upregulated *RD29A*, *RD22*, and *MYB2* in transgenic *Arabidopsis*. *RD29A* plays a role in an ABA-independent pathway while *RD22* and *MYB2* act through an ABA-dependent pathway [38][39]. No detailed functional analysis of *TaMYB19-B*-mediated stress tolerance has been performed, and its specific association with ABA is unknown. The present study revealed that the action of *SiMYB19* in salt stress tolerance is mediated through ABA synthesis and signal transduction. *SiMYB19* is regulated through an ABA-dependent pathway. Nevertheless, the specific mechanism by which *SiMYB19* regulates the ABA pathway merits further investigation.

4. SiMYB19 Modulates Drought Stress

Drought and salt stress negatively influence plant growth and crop productivity [40]. The improvement of crop drought tolerance is vital to food security [41][42]. Here, the researchers found that 10% (w/v) PEG also induced *SiMYB19*. To clarify the regulatory roles of *SiMYB19* on other types of abiotic stress, the researchers conducted a drought tolerant analysis on OE-6 transgenic rice. After 15 d drought stress and 7 d recovery, the survival rate of OE-6 was higher than that of the WT. Therefore, the roles that *SiMYB19* plays in other types of abiotic stress remain to be determined.

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