Chapter 16
The Gene Network That Regulates Salt Tolerance in Rice

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Abstract Rice is one of the glycophytes and its yield and grain quality is threatened by salinity. During the past decades, great progresses have been made on molecular mechanisms of rice dealing with salt stress. Taking advantage of genetics, transcriptome studies, and forward genetics, hundreds of genes involved in salt tolerance or salt stress response have been identified. According to their functions, these genes could be divided into at least three types: signaling components, transcriptional factors, and downstream functional molecules including transporters, enzymes for compatible solute synthesis, and ROS scavengers. Based on these knowledges and those obtained from *Arabidopsis thaliana*, this review summarizes these findings and tries to draw a rough picture of the gene networks controlling salt tolerance of rice.

Keywords Rice · Salt tolerance · Gene network · Ion homeostasis · Osmotic adjusting solutes · Transporters · ROS scavengers · Transcriptional factors · Signaling components

16.1 Introduction

The salinization of irrigated farmland is becoming increasingly detrimental to plant biomass production and agricultural productivity, because most plant species are sensitive to high concentrations of Na^+. Rice (*Oryza sativa*) is a glycophyte (as opposed to a halophyte), and as little as 30 mM NaCl (electronical conductivity,~2–3 dSm^{-1}) is able to significantly inhibit the growth of rice seedlings. Salt stress affects plant growth and development mainly by (1) disturbing ion homeostasis and (2) by producing osmotic stress. However, plants respond to salt stress

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through various biological processes, such as stomatal movement, osmotic adjustment, ion transporter activation, cell wall modification, protection of the photosynthetic reaction centers, ROS scavenging, and developmental reprograming. These processes involve a large number of functional genes, as well as many transcription factors (TFs) and signaling components. Many of these genes have been identified and characterized over the past two decades, providing insight into the primary framework of the gene networks that regulate plant salt tolerance. Although this knowledge was mainly acquired from studies on *Arabidopsis thaliana,* progress has also been made in the most important model crop species, rice, using both forward and reverse genetics approaches. In this chapter, we will summarize the current understanding of the gene networks involved in salt tolerance in rice. Based on their functions, the salt tolerance-related genes can be divided into three groups: (1) downstream functional genes such as transporters, enzymes that catalyze the synthesis of osmotic adjusting solutes, and ROS scavengers, (2) TFs that reprogram the rice transcriptome in response to salt stress, and (3) signaling components that activate the functions of downstream genes and TFs. We will attempt to draw a conceptual picture of the gene networks that control salt tolerance in rice based on research progress made in recent decades (Fig. 16.1).

16.2 Genes Responsible for Ion Homeostasis Under Ionic Stress

High concentrations of Na^+ not only change the cytoplasmic ion strength that is essential for cellular metabolism but also disturb the homeostasis of other mineral elements such as K^+. Therefore, limiting the entrance of Na^+ into the cell cytoplasm or compartmentalization of Na^+ in the vacuole is required for salt tolerance in plants. Furthermore, different cell types and tissues play different roles during the plant life cycle and are distinctively sensitive to ionic stress. Thus, the distribution of Na^+ in different cell types and tissues is also regulated for better adaptation to salt stress. For example, the shoot is more sensitive to salt than is the root, and limiting root-to-shoot transport of Na^+ is an important mechanism for salt tolerance in rice. Several Na^+ transporters have been identified as being responsible for Na^+ homeostasis during these processes.

The vacuolar sequestration of Na^+ is mainly mediated by a type of Na^+/H^+ antiporter localized on the tonoplast. The role of this type of transporter in plant salt tolerance was revealed by overexpression and knockout of the *NA*$^+$/*H*$^+$ *EXCHANGER 1* (*AtNHX1*) gene in *Arabidopsis thaliana* (Apse et al. 1999, 2003). There are five NHX-type Na^+/H^+ antiporter genes in the rice genome that are inducible by salt stress (Fukuda et al. 2011). Complementation in yeast confirmed that at least four of these function as Na^+/H^+ antiporters, and overexpression of *OsNHX1* was shown to enhance salt tolerance in rice (Amin et al. 2016; Fukuda et al. 2004, 2011). Interestingly, these genes are differentially expressed in different

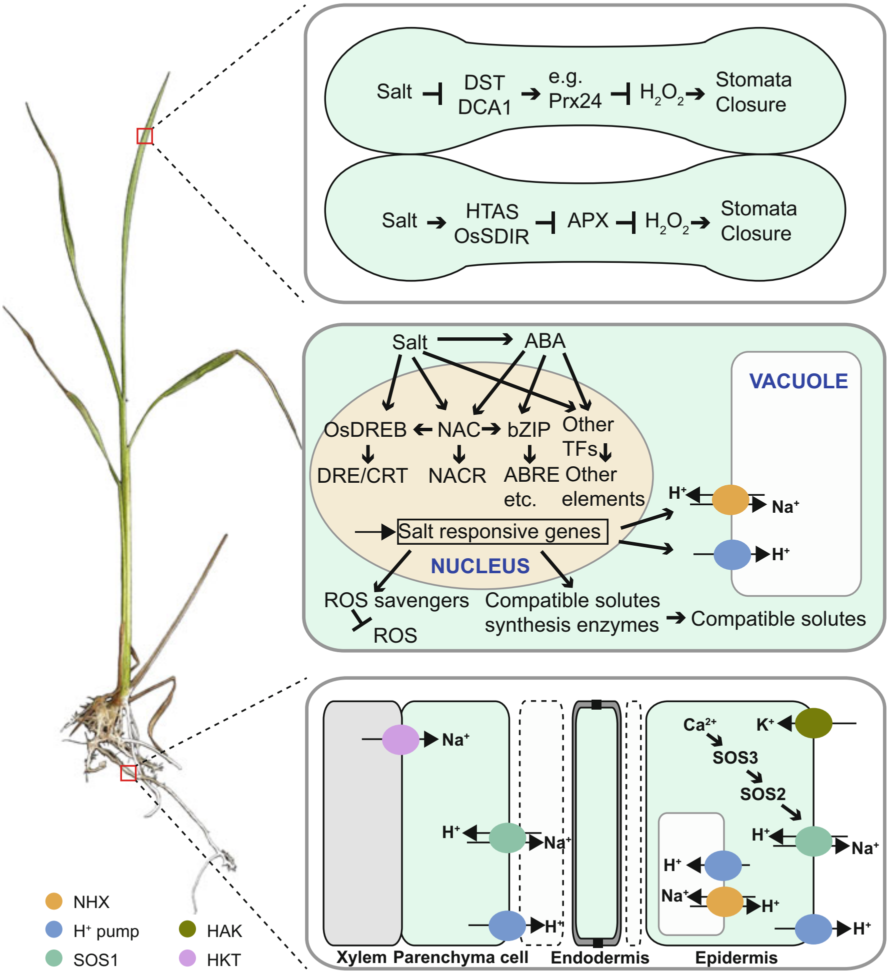

Fig. 16.1 The gene networks controlling salt tolerance of rice. The transporters are presented by ovals with different colors as indicated at the lower left corner

tissues and cell types, suggesting that the rice NHX genes play important roles in salt tolerance that differ depending on the cell type.

The other type of Na^+/H^+ antiporter, *SALT OVERLY SENSITIVE 1* (*SOS1*), also plays an essential role in plant salt tolerance by mediating Na^+ redistribution at the cellular level. The *SOS1* gene was first identified in *A. thaliana* by screening for mutants that were overly sensitive to salt stress (Shi et al. 2000). The SOS1 protein is localized on the plasma membrane (PM) of the root tip epidermis cells and xylem parenchyma cells and functions in the efflux of Na^+ into the rhizosphere and apoplastic spaces of the roots under salt stress (Shi et al. 2002). The rice genome also contains a homolog of *SOS1*, which was named *OsSOS1*. Similar to

SOS1, OsSOS1 functions in the efflux of Na^+, indicating that rice and *A. thaliana* share a common mechanism mediated by SOS1.

Whether they are located on the tonoplast or the PM, Na^+/H^+ antiporters require a H^+ gradient to drive the efflux of cytosolic Na^+. Proton pumps are therefore important in salt tolerance. Overexpression of proton pumps on either the tonoplast or PM will enhance plant salt tolerance (Gaxiola et al. 1999, 2001; Gevaudant et al. 2007), while reduced H^+-ATPase activity results in hypersensitivity to salt stress (Hubbs et al. 2007). In rice, activities of both tonoplast and PM proton pumps were observed to be upregulated by salt treatment, suggesting that the H^+-ATPase genes also play a role in rice salt tolerance (Pons et al. 2011; Shen et al. 2011).

While the Na^+/H^+ antiporters that mediate exclusion or compartmentalization of Na^+ are very important in salt tolerance, a type of protein known as the high-affinity K^+ transporter (HKT) was also found to be essential for salt tolerance in plants because it controls the Na^+ distribution between different tissues. The HKT1 protein was initially identified to function as a Na^+/K^+ cotransporter in wheat (*Triticum aestivum*) (Schachtman and Schroeder 1994). Its homologs *AtHKT1;1* and *SKC1*/*OsHKT1;5* were then shown to control natural variation in shoot Na^+ content and salt tolerance in *A. thaliana* and rice, respectively (Ren et al. 2005; Rus et al. 2006). Unlike TaHKT1, however, both AtHKT1;1 and OsHKT1;5 only transport Na^+. These genes are predominantly expressed in root xylem parenchyma cells and function in retrieving Na^+ from the transpiration stream (Ren et al. 2005; Sunarpi et al. 2005). Interestingly, the *SKC1* gene was cloned via a QTL analysis of shoot K^+ content under salt stress, indicating that *SKC1*/*OsHKT1;5* indirectly affects K^+ homeostasis (Ren et al. 2005). A similar phenotype was also observed in the null mutant *athkt1-1* (Sunarpi et al. 2005), suggesting that the K^+ deficiency caused by increased Na^+ is a disastrous effect of salt stress.

Unlike *A. thaliana*, which has only a single *HKT* gene, *AtHKT1;1*, the rice genome contains nine *HKT* genes (including one pseudogene). Based on protein sequence alignment, these nine genes can be divided into two subfamilies. The most important difference between the two subfamilies is a glycine/serine change in the first pore loop, because it determines the ion selectivity of HKT proteins (Garciadeblas et al. 2003; Maser et al. 2002). The members of Subfamily 1 have a serine at this position and function as specific Na^+ transporters, while the members of Subfamily 2 have a glycine at the same position and function as Na^+-K^+ cotransporters. Both AtHKT1;1 and OsHKT1;5 are members of Subfamily 1, and other Subfamily 1 members in rice have also been found to play a role in salt tolerance. *OsHKT1;4* is the closest homolog of *OsHKT1;5* in the rice genome. Knocking down the expression of *OsHKT1;4* demonstrated that this gene is involved in salt tolerance at the reproductive stage because it functions in Na^+ unloading in the xylem of leaf sheaths and stems (Suzuki et al. 2016). The other *HKT* family member, *OsHKT1;1*, is also required for salt tolerance in rice, possibly by mediating recirculation of Na^+ in the phloem as well as unloading Na^+ from the xylem (Wang et al. 2015). Recently, a genome-wide association study (GWAS) of rice salt tolerance identified a locus that controls root Na^+ content on chromosome 4, which was then named *Root* Na^+ *Content 4* (*RNC4*). Both *OsHKT1;4* and

OsHKT1;1 localize to the candidate region of *RNC4*, and further evidence confirmed that *OsHKT1;1*, but not *OsHKT1;4*, drives the natural variation in root Na^+ content in rice during salt stress (Campbell et al. 2017). This finding is consistent with the role of *OsHKT1;1* in Na^+ recirculation.

The range of substrates utilized by Subfamily 2 HKT proteins is wider than that of Subfamily 1. In addition to Na^+, members of HKT Subfamily 2 also can transport K^+ and Ca^{2+} (Garciadeblas et al. 2003; Lan et al. 2010). OsHKT2;1, a Subfamily 2 HKT protein, mediates Na^+ uptake in the rice root when exposed to conditions of K^+ starvation and was found to be rapidly downregulated in response to salt stress (Horie et al. 2007), indicating that OsHKT2;1 plays a negative role in salt tolerance in rice. Similarly, OsHKT2;2 also mediates the influx of K^+ and Na^+, and the induction of *OsHKT2;2* in the salt-tolerant rice variety "Nona Bokara" was observed to be suppressed by salt treatment, suggesting that *OsHKT2;2* also plays a role in rice salt tolerance.

One of the toxic effects of Na^+ is to disturb homeostasis of other elements, especially K^+. Therefore, other metal transporters and channels are also involved in salt tolerance in rice. The *Oryza sativa* contains 27 members of high-affinity K^+ transporters (HAKs), and at least OsHAK1, OsHAK5, and OsHAK21 have found to mediate specific K^+ influx and are inducible in response to salt stress (Chen et al. 2015; Shen et al. 2015; Yang et al. 2009, 2014). Reverse genetic analysis established that *OsHAK1*, *OsHAK5*, and *OsHAK21* all play important roles in rice salt tolerance by activating K^+ uptake, thus maintaining high K^+/Na^+ ratios under salt stress conditions (Shen et al. 2015; Yang et al. 2014). Recently, a magnesium transporter OsMGT1 was also found to be required for salt tolerance in rice (Chen et al. 2017), possibly by regulating the transporter activity of OsHKT1;5.

In addition to specific transporters, the Casparian strips and suberin lamellae of the cell exo- and endodermis also play essential roles in preventing water loss and limiting the entrance of Na^+ into the transpiration stream. A recent study showed that high concentrations of Na^+ can enhance the disposition of suberin through activation of the ABA pathway (Barberon et al. 2016). Though little is known about the gene network regulating Casparian strips and suberin lamellae in rice in response to salt stress, the bypass flow of Na^+ via the apoplastic pathway has long been known to be a significant contribution of shoot Na^+ accumulation to salt stress (Horie et al. 2012; Krishnamurthy et al. 2009; Yeo et al. 1987). Rice homologs of the genes that regulate Casparian strips and suberin lamellae in *A. thaliana* might be involved in limiting apoplastic Na^+ bypass and salt tolerance in rice.

16.3 Genes Involved in Osmotic Adjustment

In addition to ionic stress, high concentrations of Na^+ also cause severe osmotic stress in plants. To deal with osmotic stress, plants can activate at least three mechanisms, including adjusting water uptake, synthesizing compatible solutes, and preventing water loss. The most efficient means of water uptake is through water channel aquaporins. However, when high concentrations of Na^+ are present on the root surface, the extracellular osmotic potential (ψ_{osm}) can be lower than the cellular ψ_{osm} and could immediately trigger water efflux from the roots. Therefore, one of the rapid responses of the root is to shut down the water channels, a phenomenon that is widely observed in *A. thaliana*, corn, and barley. This process can be completed at the transcriptional level or the posttranscriptional level and can include protein modification (Horie et al. 2011) and subcellular redistribution (Boursiac et al. 2005, 2008; Maurel et al. 2008).

The rice genome contains 33 aquaporin genes, and several of them, such as *OsPIP2;3*, *OsPIP2;5*, and *OstTIP2;1*, have been shown to be predominantly expressed in the root (Sakurai-Ishikawa et al. 2011; Sakurai et al. 2005, 2008). Similar to the observations in *A. thaliana,* corn, and barley, a series of *OsPIP* and *OsTIP* genes were also found to be downregulated by salt stress in rice (Guo et al. 2006; Kawasaki et al. 2001). These results suggest that aquaporin genes might also play important roles in salt stress.

Accumulation of osmotic adjustment solutes helps decrease the cellular ψ_{osm} and thus promotes water influx under conditions of salt stress. A group of organic compounds, such as proline, glycinebetaine, trehalose, and polyols (such as myo-inositol), are synthesized by plants, especially some species from extreme environments, during salt and drought stress (Bohnert et al. 1995; Hasegawa et al. 2000). These nontoxic organic compounds are called compatible solutes, and they reduce the cellular ψ_{osm} and protect protein activities during osmotic stress. Considerable efforts have been directed toward the application of these compatible solutes or the expression of exogenous enzymes producing these solutes to improve salt tolerance in rice (Garg et al. 2002; Sobahan et al. 2009); however, there is very little evidence to show that native rice genes are involved in the synthesis of compatible solutes.

Transcriptome studies of rice under salt stress revealed that quite a few of the genes involved in trehalose synthesis are upregulated (Chao et al. 2005; Kawasaki et al. 2001), which is consistent with the observation that trehalose accumulates in salt-stressed rice roots (Garcia et al. 1997). Overexpression of either *OsTPP1* or *OsTPS1*, two genes encoding enzymes for trehalose synthesis, can promote salt tolerance in rice (Ge et al. 2008; Li et al. 2011). However, the trehalose does not accumulate to high enough levels to function as a compatible solute either in *OsTPP1* or *OsTPS1* overexpressing plants, and it was thus hypothesized to be a signal component in the salt response or to play a regulatory role in carbon metabolism under salt stress (Ge et al. 2008; Li et al. 2011).

Another compatible solute, myoinositol, was found to play an important role in a halophytic wild rice, *Porteresia coarctata* (also known as *Oryza coarctata*), in adaptation to salt stress (Sengupta and Majumder 2010). Expression of the *P. coarctata L-myo-inositol-1-phosphate synthase* (*PcINO1*) gene remarkably enhanced salt tolerance in tobacco, indicating that genes involved in synthesis of myoinositol and its derivates are vital for salt tolerance in this species (Das-Chatterjee et al. 2006; Ghosh Dastidar et al. 2006; Majee et al. 2004). Rice cultivars also have *INO1* genes, but their roles in salt tolerance are unclear at present (Ray et al. 2010).

Endodermis suberization and stomatal closure are two major mechanisms by which plants prevent water loss during salt stress. As mentioned above, the molecular basis for endodermal suberization of rice in response to salt stress remains unknown. Stomatal movement is controlled by a complicated gene network, and the genes involved in salt-stressed stomatal closure are described below.

16.4 Genes Involved in Stomatal Movement During Salt Stress

Stomatal closure in response to salt stress is mediated by the phytohormone ABA and reactive oxygen species (ROS), which function as signaling molecules (Song et al. 2014). Some of the genes involved in this process have been characterized in rice. The RING-finger ubiquitin E3 ligase-encoding gene *HEAT TOLERANCE AT SEEDLING STAGE* (*HTAS*) is inducible by ABA and multiple abiotic stresses including salt stress; overexpression of this gene enhances stomatal closure, while knockdown of *HTAS* expression inhibits stomatal closure (Liu et al. 2016). Further study indicated that *HTAS* might mediate the degradation of an ascorbate peroxidase, thus promoting ROS-mediated stomatal closure (Liu et al. 2016). Similarly, another salt-inducible RING-finger E3 ligase, *Oryza sativa* SALT-AND DROUGHT-INDUCED RING FINGER 1 (OsSDIR1), was also found to be involved in stomatal closure during salt stress, because overexpression of *OsSDIR1* enhanced stomatal closure and salt tolerance in rice (Gao et al. 2011). Although the molecular mechanisms underlying the involvement of *OsSDIR1* in stomatal movement require further investigation, studies on its homolog in *A. thaliana* revealed that *SDIR1* activates the ABA pathway through its target gene *SDIRIP1* (*SDIR-INTERACTING PROTEIN 1*) (Zhang et al. 2015).

A well-established stomatal movement pathway found in rice is the DST-mediated pathway. *DST* (*Drought and Salt tolerance*) encodes a zinc finger type of TF, and mutation of this gene improves drought and salt tolerance in rice (Huang et al. 2009). Further study showed that DST can bind to the promoters of a series of genes encoding ROS scavengers such as peroxidase 24 and then activate them. When exposed to salt or drought stress, expression of *DST* in guard cells is downregulated within 30 min. This suppression of *DST* expression reduces the levels of ROS scavengers and allows H_2O_2 to accumulate, subsequently resulting in stomatal closure (Huang et al. 2009). This process requires not only DST but also its partner DCA1 (DST coactivator). DST and DCA1 form a heterologous tetramer which promotes the expression of peroxidase 24 (Cui et al. 2015). In addition to peroxidase 24, a leucine-rich repeat (LRR)-RLK gene named *Leaf Panicle 2* (*LP2*) was also found to be downstream of *DST*. *LP2* is also required for stomatal closure in response to salt stress by regulating H_2O_2 (Wu et al. 2015a), indicating that *DST* controls H_2O_2 levels via multiple mechanisms.

16.5 Genes Involved in ROS Scavenging

ROS are important signaling components in stomatal movement as well as in some other physiological processes, but they are also deleterious to many essential molecules, such as nucleic acids, proteins, membrane lipids, and components of the photosynthetic apparatus. The production of ROS is induced by biotic and abiotic stresses, and their levels need to be well-regulated. To cope with this, plants have evolved complicated gene networks, including those encoding peroxidase (POD), superoxide dismutase (SOD), catalase, dehydroascorbate reductase (DHAR), and a series of proteins involved in catalyzing and regulating the synthesis of antioxidants.

As in other abiotic stresses, salt stress also enhances the production of ROS. Many independent studies have identified a series of salt tolerance-related genes that function in ROS scavenging in rice. Ascorbic acid is an important cellular antioxidant, and the synthesis of ascorbic acid in plants involves the enzyme GDP-D-mannose pyrophosphorylase (GMPase) (Conklin et al. 1999). A recent study showed that knockdown of the GMPase gene *OsVTC1-1* in rice resulted in the overaccumulation of ROS and a decrease in salt tolerance (Qin et al. 2016). Interestingly, a monocot-specific microRNA, miRNA528, that targets a gene encoding ascorbic acid oxidase (AAO), was also found to be required for salt tolerance in rice (Yuan et al. 2015). Overexpression of miRNA528 reduced AAO activity and improved salt tolerance in rice, indicating the involvement of miRNA528 in salt tolerance through its regulation of *AAO* expression (Yuan et al. 2015).

Glutathione is another important antioxidant in plants. Transcriptome studies have indicated that the expression of several genes related to glutathione metabolism is reprogramed during salt stress (Chao et al. 2005; Kawasaki et al. 2001; Rabbani et al. 2003; Walia et al. 2005). Reverse genetics showed that a mitochondrial glutathione peroxidase, GPX1, is required for salt tolerance in rice, and knockdown of this gene induces accumulation of ROS that impairs photosynthesis during salt stress (Lima-Melo et al. 2016). The mitochondrion is an important source of ROS, and the genes required for maintenance of mitochondrial functions are thus also important in salt tolerance. It has been reported that overexpression of the fertility restorer gene *Rf5* can improve salt tolerance in transgenic rice plants, because the Rf5 protein can suppress translation of the *orfh79* mRNA, thus restoring mitochondrial function that was impaired by the accumulation of ORFH79, a cytoplasmic male sterility protein (Yu et al. 2015). Peroxisomes are as important as mitochondria in the production of ROS and thus play a vital role in a number of biological processes, including the abiotic stress response. A peroxisomal biogenesis factor, OsPEX1, was recently reported to be associated with salt tolerance in rice, because overexpression of *OsPEX1* activates antioxidant enzymes and decreases lipid peroxidation during salt stress (Cui et al. 2016). In addition to mitochondria and peroxisomes, plasma membrane NADPH oxidases also play a key role in the production of ROS under stress conditions. *OsRbohA*, a rice plasma membrane NADPH oxidase, was recently shown to mediate ROS regulation and tolerance to abiotic stresses including high salt levels (Wang et al. 2016).

Several other genes related to ROS-scavenging have also been reported to contribute to salt tolerance in rice, but detailed descriptions of their actions will require further investigation. For example, some rice jasmonic acid (JA) biosynthesis mutants were shown to be salt tolerant. Further analysis showed that these JA mutants were impaired in allene oxide cyclase (AOC) function, which improved ROS scavenging and promoted salt tolerance (Hazman et al. 2015). Interestingly, two DNA/RNA helicases, OsSUV3 and PDH45, were shown to be involved in salt tolerance and the regulation of ROS homeostasis in rice, but the underlying mechanism remains unclear (Nath et al. 2013, 2016). In addition, a rice cyclophilin gene, *OsCYP2*, also acts as a regulator of ROS homeostasis and contributes to salt tolerance in rice, but an understanding of its mode of action will require further investigation (Ruan et al. 2011).

16.6 TFs Involved in Salt Tolerance in Rice

When exposed to salt stress, plants have to alter their development to adapt to the new environment. This process requires transcriptome reprogramming that is initiated by a series of TFs. In the past 15–20 years, a milestone achieved in the field of abiotic stress research was the discovery and characterization of the DREB (DRE-binding protein)/CBF (DRE/CRT-binding factor)-mediated regulatory pathway. Early studies revealed that many of the genes induced by abiotic stresses contain a DRE (dehydration-responsive element)/CRT (C-repeat) element with a core sequence A/GCCGAC (Yamaguchi-Shinozaki and Shinozaki 1994). Two groups independently identified the TFs that target the DRE/CRT cis-element by using yeast one-hybrid assays and found that they belong to a large family of AP2 (APETALA)/ERF (ethylene-responsive element-binding) TFs (Liu et al. 1998). These TFs are rapidly induced and activated by different abiotic stresses, and they trigger the expression of downstream genes containing the DRE/CRT element, such as *LEA* (Late-Embryogenesis Abundant) and *COR* (cold-responsive) genes. In addition, subsequent research has identified additional genes in the CBF/DREB pathway, such as *ICE1* (Inducer of CBF expression 1) and *CAMTA1* (calmodulin-binding transcription activator) (Chinnusamy et al. 2003; Pandey et al. 2013).

Based on sequence analysis, the rice genome contains at least ten *DREB1*-type genes and four *DREB2*-type genes. Overexpression of *OsDREB1A* and *OsDREB1B* either in *A. thaliana* or rice enhances salt tolerance in the transgenic plants (Dubouzet et al. 2003; Ito et al. 2006). Interestingly, the retarded growth phenotype caused by the overexpression of *AtDREB1* was also observed in plants overexpressing *OsDREB1A* and *OsDREB1B*. In addition, the target genes of *AtDREB1* and *OsDREB1A* were found to largely overlap, providing evidence for the functional conservation of *DREB1* in *A. thaliana* and rice. Overexpression of another two salt inducible DREB1-type genes, *OsDREB1F* and *OsDREB1G*, was also shown to improve salt and/or drought tolerance in rice and *A. thaliana* by activating downstream genes containing DRE/CRT elements (Chen et al. 2008; Wang et al. 2008). Similarly, the OsDREB2-type genes *OsDREB2A* and *OsDREB2B* are also induced by abiotic stresses including high salinity (Matsukura et al. 2010). Overexpression of *OsDREB2B* in either rice or *A. thaliana* improved osmotic stress tolerance, suggesting that it might be also involved in the salt stress response (Chen et al. 2008; Matsukura et al. 2010). In addition to DREB/CBF TFs that bind DRE/CRT elements, other AP2/ERF-type TFs, such as AP37 (Oh et al. 2009) and OsERF922 (Liu et al. 2012), also act as regulators of salt responsive genes.

The ABRE (ABA response element) that contains the core sequence ACGT is another well-known cis-element that is present in the promoters of stress- and ABA-induced genes (Guiltinan et al. 1990). The TFs that bind to the ABRE were identified as a group of bZIP (basic leucine zipper)-type proteins and were named AREB (ABRE-binding protein) or ABF (ABRE-binding factor) (Choi et al. 2000; Uno et al. 2000). Both ABRE and AREB/ABF proteins are important for transcriptome reprograming in response to abiotic stresses including high salt conditions. Many *AREB*/*ABF*-homologous genes are also regulated by salt stress and contribute to salt tolerance in rice. For example, knocking out the salt-inducible rice gene *OsABF2* resulted in a hypersensitive phenotype to salt stress (Hossain et al. 2010). Some other bZIP-type TFs related to the salt stress response and salt tolerance were also identified in rice. *OsbZIP23*, *OsABL1*, and *OsABI5* are three *bZIP* genes that are all induced in response to salt stress. Overexpression of *OsbZIP23* and *OsABL1* promotes salt tolerance, while overexpression of *OsABI5* suppresses salt tolerance in rice (Xiang et al. 2008; Yang et al. 2011; Zou et al. 2008), suggesting that functional differentiation exists among the different bZIP TFs. Interestingly, an extensive analysis of gene expression in 89 rice bZIP TFs showed that at least 37 of them are responsive to abiotic stresses (Nijhawan et al. 2008), indicating that bZIP family TFs are widely involved in abiotic stresses.

In addition to the DREB/CBF and bZIP regulons, the NAC (NAM, ATAF, and CUC)-type TFs are also essential for transcriptome reprograming during salt stress. Using yeast one-hybrid assays, Tran et al. (2004) isolated three NAC-type TFs (ANAC019, ANAC055, and ANAC072) drive expression of the salt- and drought-inducible gene *ERD1*. Further transcriptomic analyses of the transgenic plants overexpressing the *NAC* genes confirmed that these types of TFs control the expression of many salt- and drought-responsive genes (Tran et al. 2004). Soon after the identification of the NAC regulon in *A. thaliana*, the rice NAC homolog SNAC1 was also found to play an important role in rice salt tolerance. *SNAC1* is inducible by numerous abiotic stresses including salt, and the overexpression of *SNAC1* significantly improved salt and drought tolerance in rice without any visible adverse effects (Hu et al. 2006). In addition to *SNAC1*, many other *NAC* genes have been shown to be induced by salt stress and to be involved in salt tolerance in rice.

These genes include *SNAC2/OsNAC6* (Hu et al. 2008; Nakashima et al. 2007), *OsNAC5* (Takasaki et al. 2010), *OsNAC10* (Jeong et al. 2010), *ONAC106* (Sakuraba et al. 2015), *ONAC022* (Hong et al. 2016), *OsNAC2* (Shen et al. 2017), and *ONAC045* (Zheng et al. 2009).

Overexpression of these *NAC* genes is useful not only for improving rice salt tolerance but also provides genetic tools for studying downstream genes. For example, based on transcriptome changes in the overexpressing plants, *ONAC106* was demonstrated to induce expression of *OsNAC5*, *OsDREB2A*, *OsbZIP23*, and *OsLEA3* (Sakuraba et al. 2015); *ONAC022* also targets *OsDREB2A*, *OsLEA3*, and *OsbZIP23*, as well as other TF- and stress-responsive genes (Hong et al. 2016); and *OsNAC2* was found to mainly regulate ABA-dependent stress-responsive genes (Shen et al. 2017).

The DREB/CBF, bZIP, and NAC are three major groups of TFs that are involved in transcriptome reprogramming in rice exposed to salt stress. However, many other types of TFs also play roles in this process. These TFs belong to nine protein families: zinc finger, MYB, ARR-B, TCP, CPP, NIN-like, bHLH, WRKY, and TIFY. The salt tolerance-related TFs in the zinc finger family include DST, ZFP252, ZFP179, and ZFP185. DST was discussed above concerning its role in stomatal movement. ZFP252 was demonstrated to trigger expression of *OsDREB1A*, and its overexpression increased salt stress tolerance in rice (Xu et al. 2008). Overexpression of *ZFP179* promoted the accumulation of compatible solutes, such as proline and soluble sugars, and thus improved salt tolerance in rice (Sun et al. 2010). ZFP185 is an A20-/AN1-type zinc finger protein that is involved in crosstalk between the GA and ABA signaling pathways, but it lacks transcription activation potential and plays a negative role in the response to abiotic stresses (Zhang et al. 2016). The MYB-type TF OsMYB3R-2 was shown to increase the expression of *OsDREB2A* and to improve cold, drought, and salt tolerance in rice (Dai et al. 2007), while the R2R3-type MYB protein OsMYB91 regulates expression of *SLR1*, a rice homolog of DELLA genes required for coordinating plant growth and abiotic stresses, to control salt tolerance in rice (Zhu et al. 2015). Interestingly, the expression of *OsHKT1;1* is also controlled by another MYB-type TF, OsMYBc, which probably functions together with the ARR-B-type TF OsRR22 (Ismail and Horie 2017). It has been shown that OsMYBc is able to bind the AAANATNY motif in the *OsHKT1;1* promoter, and loss-of-function of *OsMYBc* results in decreased salt tolerance in rice and a reduced level of expression of *OsHKT1;1* under salt stress (Wang et al. 2015). In contrast to *OsHKT1;1*, the Na^+/H^+ transporter gene *OsNHX1* is regulated at the transcriptional level by five TFs that belong to the TCP-, CPP-, and NIN-like protein families (Almeida et al. 2017). The transcription factor that controls another salt tolerance-related ion transporter, OsHAK21, was identified as the bHLH-type TF OsbHLH062 (Wu et al. 2015b). The roles of stress-induced TFs, including the WRKY-type OsWRKY45 and the TIFY-type OsTIFY11a, were also characterized by reverse genetics (Tao et al. 2011; Ye et al. 2009).

16.7 Rice Genes Involved in Salt Response Signaling

The first step of a plant's response to salt stress is to perceive and translate the Na^+ and osmotic signals into a cascade of biochemical reactions that alter the cell status at the transcriptional and posttranscriptional levels to adapt to the environmental change. Although the identities of the sensors that perceive Na^+ and osmotic stress remain elusive, some signaling components in this process have been identified in model plants such as *A. thaliana* and rice. The most well-known signaling pathway is the SOS (or CIPK/CBL) pathway. In the SOS (salt-overly-sensitive) pathway, the Na^+/H^+ antiporter SOS1 can be phosphorylated by the SOS2/SOS3 complex after the complex is activated by increased cytosolic Ca^{2+} (Hasegawa et al. 2000; Zhu 2002). The *SOS3* gene encodes a member of the calcineurin B-like protein family (CBL) and SOS2 belongs to the CBL-interacting protein kinase family (CIPK). When plants are exposed to salt stress, the increased cytosolic Ca^{2+} binds to SOS3 and then promotes the formation of the SOS2-SOS3 complex. The binding of SOS3 releases the catalytic domain of SOS2 that is then able to phosphorylate SOS1 (Qiu et al. 2002; Zhu 2002). The SOS pathway was characterized in *Arabidopsis* but is conserved in rice. In addition to the cloning of *OsSOS1*, the *OsSOS2*/*OsCIPK24* and *OsSOS3*/*OsCBL4* genes were also cloned from rice based on sequence similarity, and their functions and relationships were studied in yeast and *A. thaliana* (Martinez-Atienza et al. 2007). The results showed that the three rice proteins are able to functionally replace their homologs in *A. thaliana*, indicating that the SOS pathway is conserved between monocots and dicots.

In addition to the CIPK/CBL pathway, the CDPK (calcium-dependent protein kinase) proteins were also found to be essential for rice salt tolerance. Either of the CDPK genes *OsCPK21* or *OsCPK12* can enhance salt tolerance in rice. Overexpression of *OsCPK21* upregulated ABA- and salt stress-inducible genes, while overexpression of *OsCPK12* was shown to upregulate genes encoding ROS scavenging enzymes such as OsAPx2 and OsAPx8 (Asano et al. 2011, 2012). Several other genes that encode kinases were also studied for their roles in salt tolerance, including the receptor-like protein kinase gene *OsRPK1* and the phosphoglycerate kinase gene *OsPGK2*. Overexpression of these genes in *A. thaliana* or tobacco showed that they also contribute to salt tolerance in plants (Joshi et al. 2016; Shi et al. 2014).

There are other salt stress signaling pathways that have been identified in *A. thaliana*, such as the MAPK and phospholipid pathways (Zhu 2002), but their existence in rice requires further investigation. However, several studies have suggested that there are many signaling components that regulate salt tolerance in rice. The rice phospholipase Dα was found to be important in the activation of H^+-ATPase and salt tolerance (Shen et al. 2011), and a phospholipase C, OsPLC1, can elicit stress-induced Ca^{2+} signals and controls Na^+ accumulation in the leaf (Li et al. 2017), supporting the idea that the phospholipid pathway is also important for rice salt tolerance. Additionally, a rice calmodulin-like gene, *OsMSR2*, and a G-protein-encoding gene, *OsYchF1*, were also suggested to be involved in signaling in the rice salt stress response (Cheung et al. 2013; Xu et al. 2011).

16.8 Perspective

In the past several decades, researchers have identified numerous genes involved in salt tolerance in rice, and several of them have been used to engineer salt-tolerant rice varieties. However, most of this progress was achieved through reverse genetics, and the basic knowledge was acquired from studies conducted in *A. thaliana*. Because rice is a monocot crop and *A. thaliana* is a dicot weed, differences in the molecular mechanisms underlying salt tolerance between these two diverse species could very well be extensive. We therefore postulate that a large number of salt tolerance-related genes remain to be identified in rice. However, our current knowledge of the genes and pathways that regulate salt tolerance is still very limited, and a clear picture of the gene networks involved has yet to emerge. In the future, we believe that more and more related genes will be identified and functionally characterized. Particularly, the development of phenomics and deep-sequencing technology will accelerate this process (Al-Tamimi et al. 2016; Takaqi et al. 2015). These progresses will not only greatly improve our understanding of the molecular and genetic basis of rice salt tolerance but also contribute to fast breeding of salt-tolerant rice varieties.

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