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REVIEW

Toward Understanding Molecular Mechanisms of Abiotic Stress Responses in Rice

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Abstract Plants have evolved delicate mechanisms to cope with environmental stress. Following exposure to environmental stimuli, extracellular signals are perceived and transmitted through signal transduction cascades. Upon receipt and transmission of the signals, a number of stress-related genes are induced, leading to stress adaptation in plant cells. Rice, which is a critical food grain for a large portion of the world's population, is frequently impacted by several abiotic stressors, the most important of which are drought, salinity, and cold. Exposure to environmental conditions outside of acceptable tolerance ranges can negatively affect rice growth and production. In this paper, a review of rice responses to abiotic stress is presented, with particular attention to the genes and pathways related to environmental stress tolerance. It is apparent that, while progress has been made in identifying genes involved in stress adaptation, many questions remain. Understanding the mechanisms of stress response in rice is important for all research designed to develop new rice varieties with improved tolerance.

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Plant growth and productivity can be adversely affected by abiotic stress. Plants are exposed to any number of potentially adverse environmental conditions such as water deficit, high salinity, extreme temperature, and submergence. In response, plants have evolved delicate mechanisms, from the molecular to the physiological level, to adapt to stressful environments.

Rice is the staple food for more than half of the world's population. Evolved in a semi-aquatic, low-radiation habitat, rice exhibits distinct tolerance and susceptibilities to abiotic stresses among domesticated cereal crops [92]. Rice thrives in waterlogged soil and can tolerate submergence at levels that would kill other crops, and is moderately tolerant of salinity and soil acidity but is highly sensitive to drought and cold [92]. Cultivated over a broad region between 45° north and south latitudes, rice plants are faced with low temperature in temperate regions, submergence in tropical regions, water deficit in humid tropics, and other stressors [109].

Arabidopsis is a good model in plant molecular biology and genetics research, and the majority of studies examining the impacts of abiotic stress have employed this plant [37, 85, 165, 183, 193]. The signaling pathways and regulatory network in *Arabidopsis* have been well characterized and well reviewed. Although progresses were also made on rice, reviews were less focused on this most important crop because of little functional genes characterized. Recent years, multiple genes contributing to abiotic stress responses in rice were identified by using genetics, reverse genetics, and molecular biology method. Here, we

present a summary to display those progresses so as to better understand genetics and molecular mechanisms of rice response to abiotic stress.

Signal perception

Signal perception is the first step of plant response to environmental stress. A stress sensor can detect environmental variables and specifically transmit the initial stress signals to cellular targets. Some of the two-component histidine kinases (HK) function as stress sensors in bacteria and yeast. For example, the cyanobacterium Hik33 [166] and the *Bacillus subilis* DesK [6] are thermosensors that induce gene expression in response to low temperature. The *Saccharomyces cerevisiae* histidine kinase SLN1 is an osmosensor that activates the HOG1 mitogen-activated protien kinase (MAPK) pathway [110]. In the cyanobacterium *Synechocystis*, at least five HKs are involved in the perception of osmotic stress [127].

Each environmental stimulus provides plant cells with specific yet related information. Given a large number of potential stimuli, it is possible that plants may monitor the unique attribute of stress signals through different kinds of sensors [183]. To date, most of the stress sensors remain unidentified. Urao et al. [175] reported that the temperature-sensitive osmosensing-defective *sln1* yeast mutant, *sln1-ts*, is lethal because the HOG1 MAPK cascade is constitutively activated at 37°C and *Arabidopsis* histidine kinase AHK1/ATHK1 can nullify this mutation. Moreover, expression of *AHK1/ATHK1* in the yeast double mutant *sln1Δ sho1Δ*, which lacks two osmosensors, activates the HOG1 pathway and confers high-osmolarity tolerance to the double mutant [175]. These results suggest that *Arabidopsis* AHK1/ATHK1 can act as an osmosensor in yeast. Microarray analysis reveals that AHK1/ATHK1 functions upstream of several stress-responsive transcription factors, such as AREB1, ANAC, and DREB2A, and is a positive regulator of drought and salt stress responses through both abscisic acid (ABA)-dependent and ABA-independent signaling pathways [171]. In *Arabidopsis*, four of six nonethylene receptor histidine kinases, AHK1/ATHK1, AHK2, AHK3, and AHK4/CRE1, are stress-responsive. However, unlike AHK1/ATHK1, AHK2, AHK3, and AHK4/CRE1 are negative regulators in ABA signaling, and AHK2 and AHK3 are negative regulators of osmotic stress responses [171]. AHK2, AHK3, and AHK4/CRE1 also function in cytokinin signaling [54, 122].

The two-component system, which typically contains two conserved proteins—a histidine protein kinase and a response regulator (RR) protein—plays an important role in the perception and integration of various extracellular and intracellular signals in prokaryotes, lower eukaryotes, and plants [14, 160, 173]. When activated by environmental stimuli, the histidine kinase autophosphorylates the conserved histidine residue within its transmitter domain. The phosphoryl group is subsequently transferred to an aspartate residue in the response regulator protein, resulting in a conformational change that activates a downstream signaling cascade [160]. The *Arabidopsis* RRs are classified into two distinct subgroups, type A RRs and type B RRs. Type B RRs, including 11 members, have a phosphorylatable receiver domain at their N terminus and a GARP DNA-binding domain in the middle, and function as DNA-binding transcriptional factors [63, 67, 146]. The type A RRs, including ten members, contain only the receiver domain with no DNA-binding domain [67, 68, 80]. Results from overexpression and mutant plants reveal that type A RRs are negative regulators of cytokinin signaling, while type B RRs are positive regulators [63, 80, 146]. But their roles in abiotic stress signaling remain unknown.

There are at least 14 histidine kinase genes, 15 type A RR genes, and seven type B RR genes identified in rice genome [30, 71, 73, 128], while most of them have not been intensively studied. As a result of alternative splicing, 14 genes encode 22 putative histidine kinases in *Oryza sativa* ssp. *japonica*, including at least seven members of the OsHK family that demonstrate a close relationship with AHK1/ATHK1 [128]. The induction of *OsRR6* in response to salinity, dehydration, and low temperature indicates its role in both abiotic stress and cytokinin signaling [73]. In rice, the best studied two-component system protein is Early heading date 1 (Ehd1), a type B RR. Edh1 promotes flowering by inducing *FT*-like gene expression under short-day conditions, indicating that the two-component system is involved in photoperiodic flowering pathway in rice [28]. Two-component systems are also thought to be involved in sensing abiotic stress in rice, although their biological roles are not well understood.

Signal transduction

Once an extracellular stimulus is perceived, second-messenger molecules, e.g., Ca^{2+}, inositol phosphates, and reactive oxygen species (ROS), are immediately generated. Second messengers subsequently activate a downstream signal cascade that phosphorylates transcription factors that regulate the expression of a set of genes or proteins involved in stress adaptation [183]. Signaling can also bypass second messengers in the early signaling steps [183]. Phosphorylation by protein kinases is the most common and important regulatory mechanism in signal transduction. CBL-CIPK, CDPK, and MAPK pathways have been identified as being involved in plant stress signaling [105, 106, 169].

CBL–CIPK pathway

In plant cells, the concentration of cytosolic free Ca^{2+} rises transiently during early-stage stress response as a reaction to nearly all abiotic stresses [84, 150]. The Ca^{2+} oscillation is generated through the opening of Ca^{2+}-permeable channels that allow the downhill flow of Ca^{2+} from a compartment in which the ion is present at relatively high electrochemical potential to one in which Ca^{2+} is at lower potential (reviewed by [151]). The intracellular increase in calcium, due either to an influx from external sources or release from internal stores [47, 84], is perceived by various calcium-binding proteins, such as calcineurin B-like protein (CBL), and Ca^{2+}-dependent protein kinase (CDPK) [105, 106, 151].

In *Arabidopsis*, the Ca^{2+} oscillation elicited during salt stress can be perceived by a Ca^{2+} sensor, SOS3/CBL4. SOS3 is an EF-hand-type calcium-binding protein whose amino acid sequence shares significant similarities with the yeast calcineurin B subunit and animal neuronal calcium sensors [100]. Calcineurin is a heterodimer consisting of a catalytic subunit A and a regulatory subunit B. Loss-of-function mutations in the calcineurin B subunit cause increased sensitivity of yeast cells to Na^+ and Li^+ [113, 119]. Although SOS3 has a low affinity for binding Ca^{2+}, calcium binding is essential for the dimerization of SOS3, which leads to a change in the global shape and surface properties of the protein that is of sufficient magnitude to transmit the salt stress-induced Ca^{2+} signal [69, 149].

In the presence of Ca^{2+}, SOS3 interacts physically with the regulatory domain of a calcineurin B-like-interacting protein kinase (CIPK), SOS2/CIPK24 [51]. *SOS2* encodes a serine/threonine protein kinase with an N-terminal catalytic domain that is very similar to those of the yeast SNF1 and mammalian AMPK kinase, and a C-terminal regulatory domain that is unique to the CIPK family kinases [101]. Under normal conditions, the regulatory domain interacts with the catalytic domain to inhibit kinase activity by blocking substrate access to the catalytic site [48]. The binding of SOS3 to SOS2, which is mediated by the 21 amino acid residue FISL motif in the SOS2 regulatory domain, releases the catalytic domain that subsequently activates the substrate phosphorylation activity of SOS2 [48]. SOS3 is myristoylated at its N terminus, and the myristoylation is important for recruiting SOS2 to the plasma membrane and for phosphorylation of the Na^+/H^+ antiporter SOS1 [69, 132, 154] (Fig. 1).

The SOS pathway is highly conserved in rice. Mimicking their *Arabidopsis* homologs, OsSOS3/OsCBL4, OsSOS2/OsCIPK24, and OsSOS1 functionally reconstitute the SOS pathway in yeast mutants that lack endogenous Na^+ transporters and impart NaCl tolerance to those mutants [112, 134]. OsSOS3/OsCBL4 and OsSOS2/OsCIPK24 can

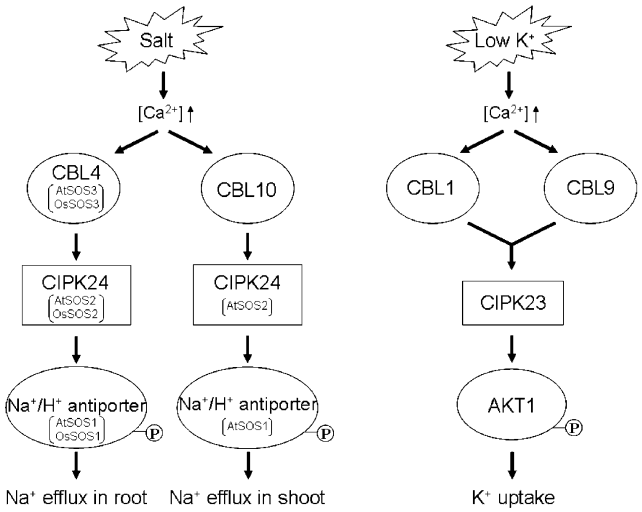

Fig. 1 CBL–CIPK pathway for maintaining ion homeostasis under high salinity and low-K^+ conditions. Salt and low-K^+ environmental conditions are perceived by unknown sensors, triggering different cytosolic Ca^{2+} signals. CBL4, CBL10, CBL1, and CBL9 perceive related Ca^{2+} signals; the first two proteins interact with CIPK24, while CBL1 and CBL9 interact with CIPK23. Plasma membrane Na^+/H^+ antiporter SOS1 is phosphorylated and activated by CBL4–CIPK24 in roots and by CBL10–CIPK24 in shoots, subsequently transporting Na^+ out of the cell. The CBL1/9–CIPK23 complex phosphorylates K^+ channel AKT1, which enhances K^+ uptake under K^+ deficient conditions. Only CBL4–CIPK24 pathway has been confirmed in rice. At, *Arabidopsis*; Os, rice.

be exchanged with their *Arabidopsis* counterparts to form heterologous protein kinase modules that activate both OsSOS1 and AtSOS1, and suppress the salt sensitivity of *sos3* and *sos2 Arabidopsis* mutants, respectively [112]. The conservation among the SOS proteins from *Arabidopsis* and rice implicates that the SOS machinery may also function in other cereals.

Studies have shown that there are at least ten CBLs and 25 CIPKs in *Arabidopsis* [105], and ten CBLs and 30 CIPKs in rice [88]. Because each CBL protein may interact with more than one CIPK protein and vice versa [88, 105], functional diversification of the CBL–CIPK pathways that are relevant for stress signaling deserve further study. Recent evidence has revealed SOS3–SOS2 complex functions in root tissues, whereas CBL10 responds to salinity by activating and recruiting SOS2 in the shoot [133]. Two independent studies have shown that the CBL1/9–CIPK23 pathway enhances K^+ uptake by activating K^+ channel AKT1 in *Arabidopsis* in response to K^+-deficient conditions [96, 184].

Despite the data gathered by several recent investigations, the functional identification of all rice CBL proteins is still in its infancy, except for some reports on the functions of mouse calcineurin in rice and OsCBL2 in aleurone cells. The protein phosphatase 2B (PP2B) calcineurin plays a central role in the signaling pathway that

regulates Na^+ and K^+ homeostasis [143]. Deletion of the C-terminal autoinhibitory domain from the mouse calcineurin A subunit constitutively activates phosphatase activity. Expression of this truncated calcineurin A subunit in rice enhances salt stress tolerance by limiting Na^+ accumulation in roots [107]. Among ten genes, only *OsCBL2* is up-regulated in aleurone by gibberellic acid (GA); other *OsCBLs* are not induced by GA and ABA in the aleurone layer or vegetative tissues [64]. OsCBL2 targets to the aleurone tonoplast and promotes vacuolation in aleurone cells through the GA-signaling pathway [64].

CIPKs have been identified as having a diverse role in different stress responses in rice. Analysis of the expression profile shows that drought, salinity, cold, polyethylene glycol (PEG), and ABA induce expression of 20 *OsCIPK* genes [180]. Most of the drought- or salt-inducible genes are also induced by treatment with ABA but not by cold [180]. Transcripts of *OsCIPK12/OsPK7* increase during drought or exposure to PEG and ABA, regardless of light, nutrient, and cytokine status [124, 180]. OsCIPK3/OsCK1, whose expression is induced by cold, salt, light, sugar, cytokinin, and calcium, interacts with AtCBL3 through the C-terminal regulatory region [82]. The truncated form of OsCIPK3/OsCK1 (without the C-terminal) has normal substrate phosphorylation activity but decreased autophosphorylation activity [82]. Overexpression of *OsCIPK3*, *OsCIPK12*, and *OsCIPK15* in rice improves cold, drought, and salt tolerance, respectively [180].

CDPK pathway

Another well-studied class of calcium-binding protein in the Ca^{2+} signaling pathway is CDPK. CDPKs, which contain a calmodulin-like domain to which Ca^{2+} can be bound and a Ser/Thr kinase domain, can sense and transmit calcium signals by a single protein [52, 138, 151]. CDPKs constitute one of the largest subfamilies of plant-specific protein kinase [106]. Availability of the whole genome sequence allows identification of 34 and 31 CDPK genes in *Arabidopsis* [23, 58] and in the rice genome [9, 135], respectively.

Expression analyses of different plant *CDPKs* provide evidence for their diverse functions in plant signal transduction [106]. Twelve *OsCDPK* genes exhibit cultivar- and tissue-specific expression [177], and 31 *OsCDPK* genes were found to express during the vegetative, panicle, and seed developmental stages [135]. Expression of *OsCPK9* is increased in plants infected with rice blast [9]. *CDPKs* are also involved in a plant's response to abiotic stresses. Seven *OsCDPK* genes have been found to accumulate differentially during cold, salt, and desiccation stress [135]. *OsCDPK7* [19, 145], *AtCDPK1* and *AtCDPK2* [174] are induced by salt; *OsCDPK7* [145], *OsCDPK13* [1], and *ZmCDPK1* [12] are induced by cold; *OsCDPK2* [16], *CpCPK1* [32], *ZmCDPK7*, and *ZmCDPK9* [144] are down-regulated by light; *OsCDPK2* is down-regulated by anoxic treatment [16].

Functional analyses using transgenic plants have revealed the biological function of some *CDPK* genes in higher plants. The *NtCDPK2*-silenced tobacco plants show a reduced and delayed hypersensitive response (HR) to the fungal Avr9 elicitor [139]. Overexpression of cold- and salt-inducible *OsCDPK7* results in enhanced tolerance to cold, salt, and drought, suggesting a function for this gene in the corresponding signaling pathways [145]. At the transcript level, *OsCDPK13* responds to various abiotic stresses as well as to hormone levels. OsCDPK13 gene expression and protein accumulation are enhanced in response to cold and GA_3 treatment but suppressed under drought, salt and ABA exposure, and brassinolide treatment [1]. Sense *OsCDPK13* transgenic lines are resistant to cold stress; antisense lines show the dwarf phenotype, which suggest that OsCDPK13 has a role in both abiotic stress tolerance and leaf sheath elongation [1].

The activation of CDPKs is dependent upon Ca^{2+} binding. Activated CDPKs relay signals through phosphorylation of specific substrates, many of which have been described [52]. Sucrose synthase is a substrate for CDPK in maize [62], soybean [189], and rice [10]. An *OsCDPK* gene, *Spk*, also called *OsCPK23* [9], is specifically expressed in developing rice seeds [78]. SPK phosphorylates a Ser residue in sucrose synthase, which catalyzes the initial step in starch biosynthesis from sucrose [10]. Phosphorylation is important for sucrose synthase activity in the degradation of sucrose. Transgenic plants containing the antisense *Spk* gene are defective in starch accumulation, producing a water-rich seed rather than one containing starch granules [10]. In the common ice plant, *Mesembryanthemum crystallinum*, McCDPK1 phosphorylates CSP1, a pseudo-response regulator-like protein, in vitro in a Ca^{2+}-dependent manner [129]. McCDPK1 co-locates with CSP1 in the nucleus under salt stress. However, while McCDPK1 is induced by salt and drought, CSP1 is not [129]. Several OsCDPKs show a response to abiotic stress, but information regarding the targets of each individual gene is limited.

MAPK pathway

Mitogen-activated protein kinase (MAPK) pathways are highly conserved among yeast, animals, and plants [179]. MAPK protein phosphorylation cascades are typically comprised of three sequentially acting protein kinases, a MAPK kinase kinase (MAPKKK), a MAPK kinase (MAPKK), and a MAPK. These three-component modules link a variety of extracellular stimuli to cellular and nuclear

response. In plants, MAPK cascades play important roles in responding to hormones, cell division, development, and biotic and abiotic stresses [75, 169].

The *Arabidopsis* genome encodes 60 MAPKKKs, ten MAPKKs, and 20 MAPKs [111]. Based on yeast two-hybrid analysis and functional complementation tests of yeast mutants related to the MAPK cascade, a putative MAPK cascade, MEKK1–MEK1/MKK2–MPK4, has been identified [65, 117]. Genetic and biochemical evidence indicate that MEKK1–MKK2–MPK4/MPK6 mediate cold and salt stress signaling in *Arabidopsis* [167] (Fig. 2). Transcription of MAPK kinase kinase *MEKK1* increases markedly in response to cold, salt, and drought stress [116]. MEKK1 specifically phosphorylates and activates MAPK kinase MKK2; MKK2 then directly targets and activates the downstream MAPK MPK4 and MPK6 in vivo [167]. *MKK2*-overexpressing plants exhibit constitutive MPK4 and MPK6 activity, and improved cold and salt tolerance [167]. Another *Arabidopsis* MAPK cascade composed of MEKK1–MKK4/MKK5–MPK3/MPK6 functions in innate immunity [8], indicating the existence of biotic and abiotic stress-signaling cross-talk among MAPK modules.

Although little is known about the composition and function of classical three-component modules in rice, several MAPKs implicated in abiotic stress signal transduction have been identified [5]. Salt, cold, and sugar starvation induce the expression of *OsMAPK4*, which is differentially expressed at different development stages [35]. A MAPK gene, *OsMAP1* (also named *OsMAPK5*, *OsMSRMK2*, *OsMAPK2*, and *OsBIMK1*), is induced by multiple biotic and abiotic stresses such as pathogen infection, low temperature, salinity, drought, and ABA [4, 61, 159, 178, 182]. OsMAP1 can inversely modulate abiotic stress tolerance and broad-spectrum disease resistance. Plants overexpressing OsMAP1 exhibit increased kinase activity and elevated tolerance to cold, salt, and drought. Interestingly, rice lines that suppress OsMAP1 show reduced resistance to abiotic stress but significantly increased resistance to fungal and bacterial pathogens [182].

Only a few upstream components, MAPKKK, and MAPKK, have been investigated in rice. Expression analysis reveals that MAPKKK OsEDR1, an ortholog of *Arabidopsis* AtEDR1, is probably associated with development and the defense/stress response [81]. The expression pattern of MAPK kinase *OsMEK1* is similar to that of *OsMAP1* under abiotic stress [178]. Both *OsMEK1* and *OsMAP1* messenger RNA levels are induced by treatment at a moderately low temperature (12°C) but not at 4°C. Two-hybrid analysis reveals that OsMEK1 interacts with OsMAP1. The OsMEK1–OsMAP1 pathway, therefore, may be involved in moderately low-temperature signaling in rice [178].

Heavy metals such as cadmium, copper, and zinc induce the activation of several OsMAPKs [98, 187, 188]. A common response to abiotic stress is the production and accumulation of reactive oxygen species in plant cells. In *Arabidopsis*, hydrogen peroxide (H_2O_2) can specifically induce a MAPKKK, ANP1, which leads to the activation of AtMPK3 and AtMPK6 [89]. In rice roots, Zn-induced activation of 40- and 42-kDa MAPK was suppressed by treatment with a ROS scavenger, suggesting that second messenger ROS may mediate a Zn-triggered MAPK pathway [98]. However, information regarding the downstream factors of MAPK pathway is still limited in rice.

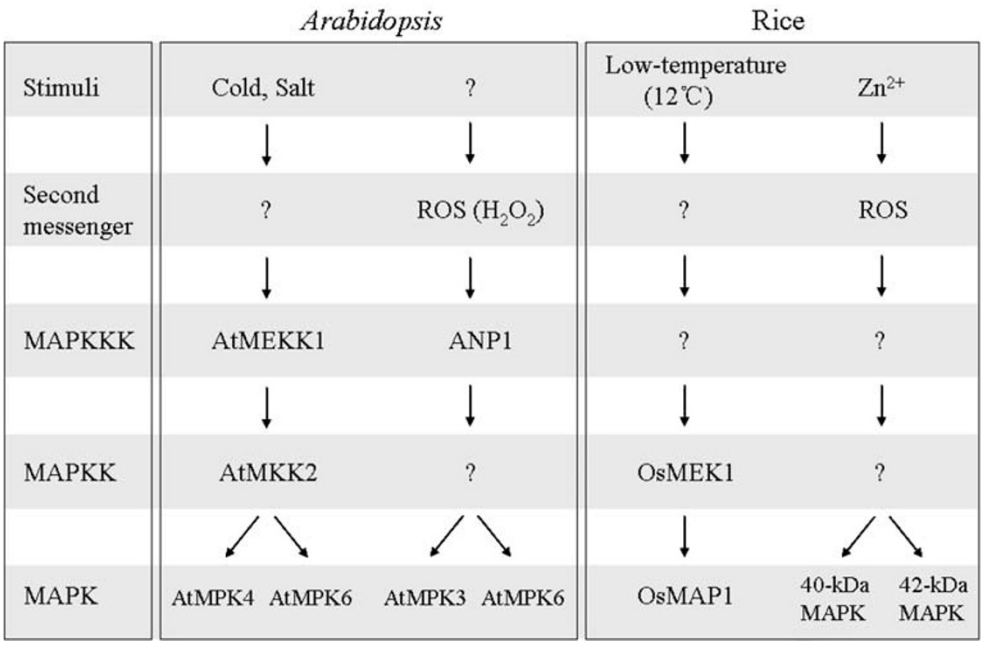

Fig. 2 Schematic illustration of MAPK pathways for abiotic stress signaling in *Arabidopsis* and rice. The general tiers of the MAPK signal pathway are shown in the *far left column*. The *arrows* indicate activation of downstream components. A *question mark* indicates unidentified components.

The duration and magnitude of MAPK activation may be regulated at many locations along the signaling pathway, but a major point occurs at the MAPK level [79]. Dual-specificity MAPK phosphatases (MKPs) are negative-feedback regulators of the MAPK cascade that dephosphorylate both threonine and tyrosine residues and inactivate MAPKs. OsMKP1 has been shown to be a negative regulator of the wound response in rice. Among five putative rice *MPKs*, only the expression of *OsMPK1* is rapidly induced by wounding [77]. In contrast to the normal phenotype of the *Arabidopsis atmkp1* mutant, *osmkp1* loss-of-function plants show a semi-dwarf phenotype. In *osmkp1* mutants, both the activities of two stress-responsive MAPKs and the expression of wounding-inducible genes are elevated, resulting in constitutive activation of the wound response [77].

ABA signaling

ABA is the most important phytohormone for plant coping with abiotic stress, especially drought and salt stresses. There are at least two effects of ABA on plant response to abiotic stress: inducing stomata closure and regulating expression of a big part of abiotic stress responsive genes. Identification of ABA receptors is a breakthrough for ABA signaling. So far, three ABA receptors were reported [103, 136, 153], and a G protein coupled-receptor was proven to mediate both effects above of ABA [103]. As similar proteins have been found in rice genome (unpublished data), similar mechanisms of ABA perception may also exist in rice.

In addition to the perception of ABA signaling, ABA signal transduction was also better understood because of characterization of some sucrose non-fermenting 1-related protein kinase 2 (SnRK2s). Recent studies in both *Arabidopsis* and rice have shown that SnRK2s can be activated by both ABA and abiotic stress [15, 18, 36, 86, 87]. The activated SnRK2s phosphorylate and activate AREB/ABF/ABI5, and subsequently activate expression of AREB/ABF/ABI5 target genes [15, 18, 36, 86]. It is known that ABA-mediated stomata closure involves reactive oxygen (for example, H_2O_2), but the detailed process is till unknown. However, an ABA-induced transcription factor, SNAC1 (described below), may be an important downstream factor for the process, given *SNAC1* is dominantly expressed in the stoma and overexpression of SNAC1 leads to stomata closure [60].

Transcriptional regulation network

It has been estimated that about 10% of the yeast genes are transcriptically affected by salt stress [192]. Although the proportion of affected genes in higher plants seems lower, based on published expression profile data, the actual number should be even higher than that in yeast, considering that higher plants are composed of several highly differentiated tissues and cells. For example, the abiotic stress-affected genes in roots and shoots, and in guard cells and mesophyll cells are quite different [19, 90, 95]. The transcriptional regulation networks of higher plants, therefore, are likely to be much more complex. To date, multiple regulons involved in reprogramming of abiotic stress have been identified (Fig. 3). Although current data are inadequate to provide a clear picture of the functional stress response pathways in higher plants, ongoing progress will continue to expand our understanding of the complex mechanisms that are involved.

CBF/DREB pathway

The CBF/DREB pathway was one of the first identified through transcriptional regulation research of abiotic stress and, now, is the best documented [25, 26, 170, 186, 191]. CBF/DREB is an ERF/AP2 family transcription factor and specifically binds CRT/DRE elements and activates responding genes with those elements [186]. There are multiple CBFs/DREBs in *Arabidopsis* that respond to different abiotic stresses [50, 102, 161, 186]. Among these, *DREB1A/CBF3*, *DREB1B/CBF1*, and *DREB1C/CBF2* are specifically induced by cold, and *DREB2A* and *CBF4* mainly respond to salt and drought stress [50, 102, 161, 186].

The CBF/DREB pathway is vital in the abiotic stress response in plants. Overexpression of CBFs/DREBs or modified CBFs/DREBs in *Arabidopsis* or rice significantly enhanced their tolerance of abiotic stress [31, 70, 72, 102, 148]. These data also suggested that the CBF/DREB pathway is conserved in rice. Actually, five DREB homologs, *OsDREB1A*, *OsDREB1B*, *OsDREB1C*, *OsDREB1D*, and *OsDREB2A*, were identified in rice [31]. The expression patterns of these genes are similar to their homologs in *Arabidopsis*, that is, *OsDREB1A* and *OsDREB1B* are induced by cold and *OsDREB2A* is induced by salt and drought [31]. Overexpression of these genes also enhanced the tolerance of *Arabidopsis* and rice to abiotic stress [31, 70, 123]. There are, however, some differences between OsDREBs and their orthologs in *Arabidopsis*. OsDREBs specifically bind the DRE/CRT core sequence GCCGAC [31], while AtDREBs show equal affinity to GCCGAC and ACCGAC [102, 161]. This implies that the abiotic stress tolerance mechanisms continued to evolve after the divergence of dicotyledons and monocotyledons.

Recent researches have been successful in identifying the upstream factors of this pathway by screening EMS-mutated *Arabidopsis* with the CRT/DRE element or *CBF/DREB* promoter-driven reporter gene [25, 26, 191]. ICE is

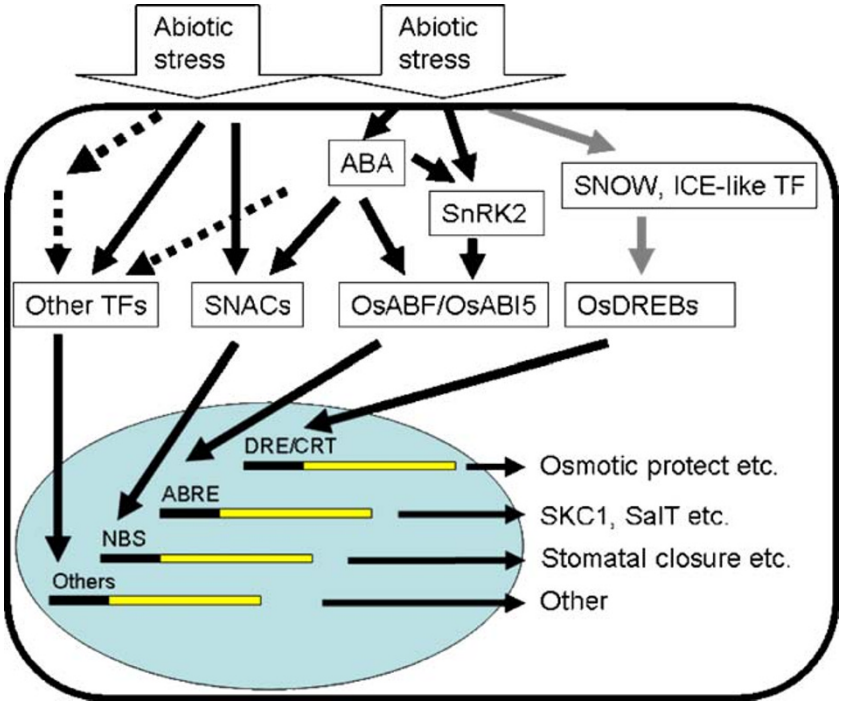

Fig. 3 Transcriptional regulation network under abiotic stress in rice. At least three transcriptional pathways, involving three kinds of transcription factors (*TFs*) as indicated, have been identified in rice. Based on knowledge from rice and/or *Arabidopsis*, upstream components and target genes or outputs of these TFs are also displayed. *Black solid arrows* indicate pathways with evidence from rice, *grey solid arrows* indicate pathway with evidence from *Arabidopsis*, and *broken arrows* indicate pathways without direct evidence. *NBS* NAC-binding site.

the first *trans*-factor that was found to bind the ICE box in the promoter of *CBF/DREB* and control the expression of CBFs/DREBs [27, 94]. It also can control the expression of other transcription factors involved in plant stress tolerance, suggesting a key role in transcriptome reprogramming under environmental stress [94]. Another protein, named SNOW, has also been tentatively identified as being involved in transcription control of CBF/DREB by serving as an ICE partner (unpublished, http://www.faculty.ucr.edu/~jkzhu/). Other *Arabidopsis* factors, such as HOS1 and SIZ1, that control ICE steady state by regulating its ubiquitination and sumolylation respectively were also identified [29, 115]. In rice, some putative proteins show high similarities with ICE1, HOS1, and SIZ1 in sequences (unpublished data). Although their functions remain to be characterization, a similar pathway in rice is expected.

AREB/ABF/ABI5/bZIP

Abiotic stress-induced genes also can be induced by ABA. The *cis*-elments responding to ABA were identified as ABRE (ABA-responsive element) and MYBRS/MYCRS (MYB/MYC recognition sequence) [24, 156, 170]. The transcription factors binding these *cis*-elements are AREB/ABF/ABI5 [38, 172] and MYB/MYC [2, 3], respectively. AREB/ABF is a bZIP-type transcription factor, which can bind the ABRE *cis*-element. *ABI5*, a mutation that leads to *Arabidopsis* plants that were insensitive to ABA, was also found to encode a bZIP transcription factor and belong to the *AREB* family [33]. Rice *ABI5*, which was recently identified, is also transcriptically regulated by ABA and multiple abiotic stresses. Knockdown of *OsABI5* enhanced salt tolerance in rice and affected expression of some salt-stress-responsive genes (for example, *SKC1* and *SalT*), indicating that the ABRE/ABF/ABI5 pathway also exists in rice [194].

NACs

Some dehydration-induced genes in *Arabidopsis*, *ERD1*, for example, have no DRE/CRT elements in their promoter region and yet are regulated like those that do contain DRE/CRT elements [83, 120, 158]. Studies have demonstrated that a MYC-like site, NACRS, and its binding factors—NAC family transcription factors—are required for induction of these genes [158].

There are also numerous genes that encode NAC transcription factors in the rice genome [126]. Some of them are also induced by abiotic stress [19, 59, 60, 121, 125], suggesting that the NAC regulation pathway is conserved in rice. Overexpression of two rice *NAC* genes, *SNAC1* and *SNAC2*, significantly enhanced rice tolerance to abiotic stress, including cold, drought, and salt [59, 60]. *SNAC1* is dominatively expressed in rice guard cells, and its overexpression promoted stomatal closure [60]. It is believed, therefore, that SNAC1 functions in stoma movement under dehydration stress. Transcriptome analysis of overexpression lines of these two genes showed that their target genes are not rich with NACRS in the promoter regions [59, 60], suggesting that they are different from the

Arabidopsis NACs that are involved in dehydration tolerance [158]. Furthermore, there are few of the *SNAC1* and *SNAC2* target genes, suggesting that multiple NAC pathways are associated with abiotic stress response.

Other TFs

Other kinds of transcription factors also play vital roles in transcriptional regulation during stress conditions, although little information is available about their upstream regulators or direct targets. It has been demonstrated that Sub1A-1, an ethylene-response-factor (ERF), is the major genetic determinant for submergence tolerance in rice [185]. Sub1A-1 finely modulates acclimation responses to sudden and total inundation to maintain the capacity of regrowth when water subsides. For example, Sub1A-1 inhibits leaf elongation by suppressing the expression of expansin-encoding genes and restrains carbohydrate consumption by reducing the expression of α-amylose genes and sucrose synthase genes [39].

Although multiple *cis*-elements and *trans*-factors for transcriptional regulation under abiotic stress have been identified and characterized, a clear explanation of the complex transcription network and the huge number of abiotic stress responsive genes remains elusive. For example, it was found that only 12% of the cold responsive genes in *Arabidopsis* are regulated by CBF/DREB [34]. In addition, some of the CBF/DREB-regulating genes have no DRE/CRT element in their promoters [34]. It is very likely that these genes are controlled by CBF/DREB-regulating transcriptional factors (e.g., *RAP2.1*) [34]. Chen et al. [22] used transcription factor microarray analysis to demonstrate that at least 30 transcription factors in *Arabidopsis* were induced by abiotic stress. A similar situation exists in rice. Microarray analysis revealed that transcription factor genes are rich within the group of the earliest salt-responsive genes [19]. Considering the spatial and temporal expression pattern of the abiotic stress responsive genes, it is highly likely that many transcription factors and regulatory pathways related to abiotic stress remain to be identified.

Functional proteins

Plant stress tolerance depends on the correct regulation of physiological mechanisms. This is achieved by multiple functional proteins participating in developmental, biosynthetic, and metabolic pathways. Based on changes at the transcript or/and activity level, functional proteins protect cells from stress by the removal of toxic elements, restoration of cellular homeostasis, and eventual recovery of normal growth patterns. For this review, we focused on enzymes associated with ROS scavenging and biosynthesis of compatible solutes and sodium transporters.

ROS scavenging system

ROS, including singlet oxygen (O_2^1), superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (HO^-), are generated during aerobic metabolism and abiotic stress conditions. They are capable of unrestricted oxidation of various cellular components and can lead to membrane lipid peroxidation, protein oxidation, and enzyme inhibition [114]. Plant cells remove excess ROS produced during stress conditions by enzymatic and non-enzymatic mechanisms.

ROS-scavenging enzymes include superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione peroxidase (GPX), and catalase [7]. APX and GPX are the most studied scavenging enzymes in rice [76, 97, 168]. They belong to the plant peroxidase superfamily and catalyse the conversion of H_2O_2 to H_2O. Because ROS also function as second messengers, their generation and removal are tightly regulated in different cellular components. There are eight APX enzymes in rice: two cytosolic (OsAPX1 and OsAPX2), two peroxisomal (OsAPX3 and OsAPX4), one mitochondrial (OsAPX6), and three chloroplastic isoforms (OsAPX5, OsAPX7, and OsAPX8) [168]. OsGPX1 and other plant GPX enzymes, on the other hand, are cytosolic [7, 76]. Under salt stress, *OsAPX2, OsAPX7*, and *OsAPX8* show altered transcript levels [168], but only *OsAPX8* is induced in roots [55]. NaCl, ABA, and H_2O_2 can enhance the expression of *OsAPX8* in rice roots, while the NaCl-induced expression of *OsAPX8* is mediated through the accumulation of ABA but not H_2O_2 [55]. Even isoforms with the same subcellular location may have distinct functions. Expression analysis reveals that *OsAPX2* is up-regulated by salt [168]. *Arabidopsis* plants expressing *OsAPX2* exhibit higher ROS-scavenging activity and salt tolerance than those expressing *OsAPX1* [104].

Non-enzymatic antioxidants include the major cellular redox buffers ascorbate and glutathione, as well as carotenoids and tocopherol [7]. Alleviation of oxidative injury by the use of antioxidants can enhance plant resistance to abiotic stress. Guo et al. [49] found that feeding rice roots with L-ascorbic acid and its immediate precursor protected plants against oxidative damages, suggesting that manipulation of ascorbic acid biosynthesis could be a strategy for improving stress tolerance. During the antioxidation process, ascorbate itself is oxidized to dehydroascorbate; dehydroascorbate reductase (DHAR) re-reduces the oxidized ascorbate. A high ratio of reduced to oxidized ascorbate is important for ROS-scavenging efficiency. Ushimaru et al. [176] reported that overexpression of rice *DHAR1* in *Arabidopsis* increases ascorbate levels, which leads to increased salt tolerance.

Compatible solute

Severe osmotic stress induced by drought, high salinity, and low temperature disrupts normal cellular activities [181]. Physiological studies have shown that a group of soluble organic compounds accumulate and function as osmoprotectants during osmotic stress [11]. Accumulation of compatible solutes such as amino acids (e.g., proline), quaternary and other amines (e.g., glycine betaine and polyamines), sugars (e.g., raffinose, sucrose, and trehalose), and sugar alcohols (e.g., mannitol) decrease the osmotic potential in the cytoplasm, thus protecting cellular function or maintaining the structure of cellular components [152].

In rice, physiological responses to the accumulation of several compatible solutes, as well as the transcript level of genes encoding enzymes for their synthesis, have been investigated under stress conditions [20, 21, 43, 66, 91, 130]. Manipulation of genes in the metabolic pathways is a common strategy to increase plant stress tolerance. For example, improved tolerance has been found in transgenic rice plants harboring genes involved in metabolism of compatible solutes such as proline [162, 190], glycine betaine [118, 147, 157, 163], polyamines [17, 141, 140], and trehalose [45, 46, 74].

Modulating multiple steps in the same pathway can result in a more efficient strategy. In *Escherichia coli*, trehalose-6-phosphate synthase (TPS, encoded by *OstA*) synthesizes trehalose-6-phosphate from glucose-6-phosphate and UDP-glucose. Trehalose-6-phosphate phosphatase (TPP, encoded by *OstB*) then catalyzes the formation of trehalose by removing the phosphate from trehalose-6-phosphate. Overexpression of a bifunctional fusion gene of TPS and TPP from *E. coli* in rice increases the trehalose level and stress tolerance without growth inhibition, probably resulting from reducing levels of deleterious trehalose-6-phosphate [74].

Sodium transporters

Sodium is a micronutrient in plant cells. Under high salinity, excessive accumulation of Na^+ in cytosol disrupts enzymatic and photosynthetic functions and causes ion toxicity. Both Na^+ efflux and vacuolar sequestration contribute to a lower cytosolic Na^+ concentration. Na^+/H^+ antiporters catalyze the exchange of Na^+ for H^+ across the membranes in order to maintain ion homeostasis, as well as cytoplasmic pH and cell turgor [56]. In *Arabidopsis*, extruding Na^+ out of cell is mediated by the plasma membrane Na^+/H^+ antiporter SOS1 [154], whose activity is regulated by the SOS3–SOS2 complex in roots and by the CBL10–SOS2 complex in shoots [132, 133]. Biochemical and genetic analyses have demonstrated that OsSOS1 is a functional homolog of SOS1. Plasma membrane preparations from yeast expressing OsSOS1 show

Table 1 Effect of Selected Rice Genes on Abiotic Stress Tolerance

Gene (Product)	Phenotype (approach)	Reference
Component of signal transduction pathway		
OsCIPK3 (calcineurin B-like-interacting protein kinase)	Cold tolerance (o)	[180]
OsCIPK12 (calcineurin B-like-interacting protein kinase)	Drought tolerance (o)	[180]
OsCIPK15 (calcineurin B-like-interacting protein kinase)	Salt tolerance (o)	[180]
OsCDPK7 (Ca^{2+}-dependent protein kinase)	Cold, drought and salt tolerance (o)	[145]
OsCDPK13 (Ca^{2+}-dependent protein kinase)	Cold tolerance (o)	[1]
OsMAP1/OsMAPK5 (mitogen-activated protein kinase)	Cold, drought and salt tolerance (o); Cold, drought and salt sensitivity (r)	[182]
Transcription factor		
OsDREB1A, *OsDREB1B* (DRE-binding protein)	Cold, drought and salt tolerance (o)	[31, 70]
OsABI5 (bZIP transcription factor)	Salt tolerance (a); Salt sensitivity (o)	[194]
SNAC1 (stress-responsive NAC 1)	Drought and salt tolerance (o)	[60]
SNAC2 (stress-responsive NAC 2)	Cold and salt tolerance (o)	[59]
Sub1A-1 (ethylene-response-factor)	Submergence tolerance (n, o)	[39, 185]
Functional protein		
OsAPX1, *OsAPX2* (ascorbate peroxides)	Salt tolerance (o)	[104]
DHAR1 (rice dehydroascorbate reductase)	Salt tolerance (o)	[176]
OsTPP1 (trehalose-6-phosphate phosphatase)	Cold and salt tolerance (o)	[46]
OsSOS1 (plasma membrane Na^+/H^+ antiporter)	Salt tolerance (o)	[112]
OsNHX1 (tonoplast Na^+/H^+ antiporter)	Salt tolerance (o)	[41]
SKC1 (rice HKT-type Na^+ transporter)	Salt tolerance (n, o)	[137]

a anti-sense expression, *n* near-isogenic line, *o* overexpression, *r* RNA interference

greater capacity for Na^+/H^+ exchange, and OsSOS1 confers salt tolerance to the yeast mutant AXT3K (*Δena1–4 Δnha1 Δnhx1*) and the *Arabidopsis sos1* mutant [112]. Na^+ in cytosol can also be sequestered into vacuoles by the Na^+/H^+ antiporter OsNHX1 located in the tonoplast [41, 40]. The overexpression of OsNHX1 improves salt tolerance in transgenic rice plants, without adversely affecting Na^+ and K^+ levels or plant growth [41].

A high K^+/Na^+ ratio is essential for normal cellular functions. There is growing evidence that supports the idea that the capacity of plants to maintain a high K^+/Na^+ ratio correlates with salt tolerance [108]. Identification of a major quantitative trait locus (QTL) for shoot K^+ content and salt tolerance revealed that *SKC1* encodes a HKT-type Na^+-selective transporter, OsHKT8 or OsHKT1;5 according to the new nomenclature [99, 131, 137]. *SKC1* is preferentially expressed in parenchyma cells surrounding xylem vessels and up-regulated by salinity in roots. SKC1 functions to recirculate Na^+ back to the roots by unloading Na^+ from xylem sap, thereby maintaining shoot K^+ homeostasis and enhancing salt tolerance [137]. In *Arabidopsis*, SOS1 [155] and AtHKT1;1 (or AtHKT1) [13, 164] also reduce shoot Na^+ concentration through the vascular system, although the mechanisms are different from SKC1 [42].

High-affinity Na^+ uptake has been reported in K^+-starved seedlings of wheat [93], rice [44], and barley [53]. However, there is no direct evidence that a channel/transporter functions in Na^+-selective uptake in plant roots. Studies using *oshkt2;1* null mutants demonstrated that OsHKT2;1 (or OsHKT1) takes up Na^+ under K^+-starvation conditions [57]. Due to a dramatically reduced influx of Na^+ in roots, *oshkt2;1* mutants accumulate less Na^+ in roots and shoots. They exhibit growth inhibition only under K^+-starvation and low-Na^+ conditions [57]. Unlike *Arabidopsis* containing one *HKT* gene, seven *HKT* genes have been identified in rice cv. Nipponbare [44]. Given this large number of genes, rice may be a better model for understanding the role of HKTs in regulating Na^+ transport [142].

Perspective

Abiotic stress is one of the primary factors limiting global crop yields. Genetic and molecular approaches are powerful tools in the identification of a multitude of genes involved in abiotic stress response and tolerance. Combining these approaches with high throughput technologies, such as microarray/genechip, allows for the identification of novel, stress-responsive genes and signaling cross-talk on a genome-wide basis. Moreover, the accessibility of the rice genome and various mutant libraries should accelerate the identification of regulatory components and functional proteins in this crop.

Although substantial progress has been made, breeding and genetic modulation of rice plants in order to improve abiotic stress tolerance is still a challenge. One major limitation to progress is the lack of knowledge of the functions and interactions of tolerance-related genes. While many genes have been identified with great potential for abiotic-stress engineering, most of them, more or less, affect rice morphology when they are constitutively over-expressed. Utilization of some of these genetic characteristics, therefore, while producing desirable stress-related results, may have concomitant negative impacts. Quantifying the advantages and disadvantages of breeding may take some time. However, it is desirable to generate plants with gene expression driven by a controllable promoter so that the gene products are not produced unless under stress conditions. So far, some reports that used a stress-inducible promoter to express foreign genes have shown increased abiotic stress tolerance with normal plant growth [140, 141, 162, 163]. Combined with other genetic and molecular approaches, the exploitation of rice stress-responsive genes (Table 1) for engineering breeding will certainly accelerate.

In addition, abiotic stress tolerance is a quantitative trait loci characteristic, influenced by a large number of genes; modulation of one or several genes is limited with regard to favorable abiotic-stress engineering. In the last few decades, QTL mapping studies allowed, at least in part, identification of specific chromosome segments that carry these QTLs or candidate genes. As QTL mapping is a challenging task, only two major QTLs for stress tolerance, *SKC1* and *Sub1*, have been successfully cloned by now. Because a number of minor QTLs may also be responsible for a large portion of phenotypic variation, these minor QTLs can be integrated together with the major QTL by a QTL-pyramiding breeding strategy. QTL pyramiding can assemble tolerant genes together for one specific trait or for two or more different traits by using marker-assisted selection. More knowledge about the genetics and molecular basis of related traits will be helpful in this direction. In conjunction with these efforts, characterization of the genetic and functional interactions of more abiotic stress-related genes is necessary.

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