

## Advances in Understanding Cold Sensing and the Cold-Responsive Network in Rice

Qi Zhang<sup>1#</sup>, Nan Jiang<sup>1#</sup>, Guo-Liang Wang<sup>1,2</sup>, Yahui Hong<sup>1\*</sup>, Zhilong Wang<sup>1\*</sup><sup>1</sup>Hunan Provincial Key Laboratory of Crop Germplasm Innovation and Utilization, College of Biological Science and Technology, College of Agronomy, Hunan Agricultural University, Changsha, Hunan 410128, China<sup>2</sup>Department of Plant Pathology, Ohio State University, Columbus, Ohio 43210, USA<sup>#</sup>These authors contributed equally to this work

### Abstract

Cold stress reduces the growth and production of many crops including rice (*Oryza sativa* L.), which is a staple food crop and model monocot plant. During the past two decades, significant progresses have been made in understanding the cold-responsive network in rice. Various genes and gene products functioning in cold sensing and transcriptional regulation and post-transcriptional processing of the response to cold have been identified and these include *OsDREBs*, *OsNACs*, *OsMAPs*, *OsCDPKs*, miR-171, and miR-444a. The important roles of calcium, Reactive Oxygen Species (ROS) and Abscisic Acid (ABA) in cold sensing and signaling during both vegetative and reproductive stages have also been revealed. The new findings summarized in this review will facilitate the breeding of cold tolerance in rice and will also be useful for studying and understanding cold sensing and signaling in other crops.

**Keywords:** Cold stress; Sensing; Responsive network; Rice

### Introduction

Temperature severely affects plant growth and basically determines the geographical distribution of plants. The changes in mean annual temperatures predicted by climate change models will affect both soil organic matter turnover and cropping patterns in agriculture [1,2]. Rice is one of the most important stable crops globally and also a monocot model plant for molecular research. Like other plant species originating in tropical or sub-tropical areas, rice is sensitive to low temperatures with prolonged exposure resulting in chilling injury [3]. In tropical areas, especially in Indonesia and Malaysia, cold stress rarely occurs and is not the major problem for rice breeding in those areas. Nevertheless, rice is cultivated well beyond tropical environments to temperate and high altitude areas. In these areas, temperatures fluctuate greatly across seasons and rice is often exposed to temperatures below 20°C during the most sensitive stages of development (i.e., germination, seedling, and reproduction) [4]. Low temperature impairs seed germination, reduces seedling vigor, weakens photosynthetic ability by inducing leaf discoloration, reduces plant height, produces degenerated spikes, delays days to heading, reduces spikelet fertility, causes irregular grain maturity, and poor grain quality [5]. About 30.7 million ha of rice in China are grown over a wide area from 53°27'N to 18°90'N, and almost the entire area can be harmed by cold injury caused by low temperatures. Annual losses are 3-5 million tonnes. Low temperature during the reproductive stage of rice in the Republic of Korea caused 17, 78, and 20% damage to the total rice area in 1971, 1980, and 1993, respectively, with maximum yield loss of milled rice of 3.9 t/ha in 1980. Yield loss of 1-2 t/ha due to low temperature during the reproductive stage in 1995-96 was also reported in Australia and an annual yield loss of 3-5 million tons was recorded in China [5,6]. The mechanisms of cold stress in rice have been extensively investigated in the past two decades, and cold-responsive strategies that differ from those in other plant species such as *Arabidopsis* and tomato have been detected in rice. The identification of QTLs for cold stress shows that different loci are involved in cold tolerance at different growth stages in rice [7,8]. And these findings are useful to facilitate the selection and development of improved cold-tolerant genotypes with high percent seed set for their cultivation in temperate environments and high-altitude areas. According to common cold-responsive network in various plants,

previous reviews provide useful information, but the review which specifically focuses on the studies in crops, especially in rice, is scarce. In this review, we summarize recent advances on cold sensing and transcriptional regulation in rice. In addition, we discuss intriguing findings on the role of post-transcriptional regulation in chilling and/or freezing tolerance in rice.

### Cold sensing

Plant cells can sense cold stress based on changes in membrane rigidity, changes in the physical state of membrane proteins, and changes in the concentrations of metabolites. At low temperatures, an increase in electrolyte leakage (EL) commonly occurs in rice cultivars because of increased membrane rigidity [9-11]. Ca<sup>2+</sup> influx into the cytosol is an important and early event caused by cold stress, an influx which may be mediated by membrane rigidification-activated mechano-sensitive or ligand-activated Ca<sup>2+</sup> channels [12]. Subsequently, the Ca<sup>2+</sup> signatures are interpreted and amplified by calcium sensors, such as Calmodulin (CaM) and Calmodulin-like Proteins (CMLs), Calcineurin B-like Proteins (CBLs), and Calcium-Regulated Protein Kinases (CDPKs) (Figure 1). The CDPK gene *OsCDPK7* is induced by chilling in rice, and overexpression of this gene enhances cold tolerance in transgenic rice

**\*Corresponding authors:** Zhilong Wang, Hunan Provincial Key Laboratory of Crop Germplasm Innovation and Utilization, College of Biological Science and Technology, College of Agronomy, Hunan Agricultural University, Changsha, Hunan 410128, China, E-mail: [zhilongwang@126.com](mailto:zhilongwang@126.com)

Yahui Hong, Hunan Provincial Key Laboratory of Crop Germplasm Innovation and Utilization, College of Biological Science and Technology, College of Agronomy, Hunan Agricultural University, Changsha, Hunan 410128, China, E-mail: [yahuihong@vip.sina.com](mailto:yahuihong@vip.sina.com)

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[13]. Other calcium-regulated protein kinase genes such as *OsCDPK13*, *OsCBF1*, and *OsNAC5* are also cold-induced and involved in the calcium signaling pathway [14-16].

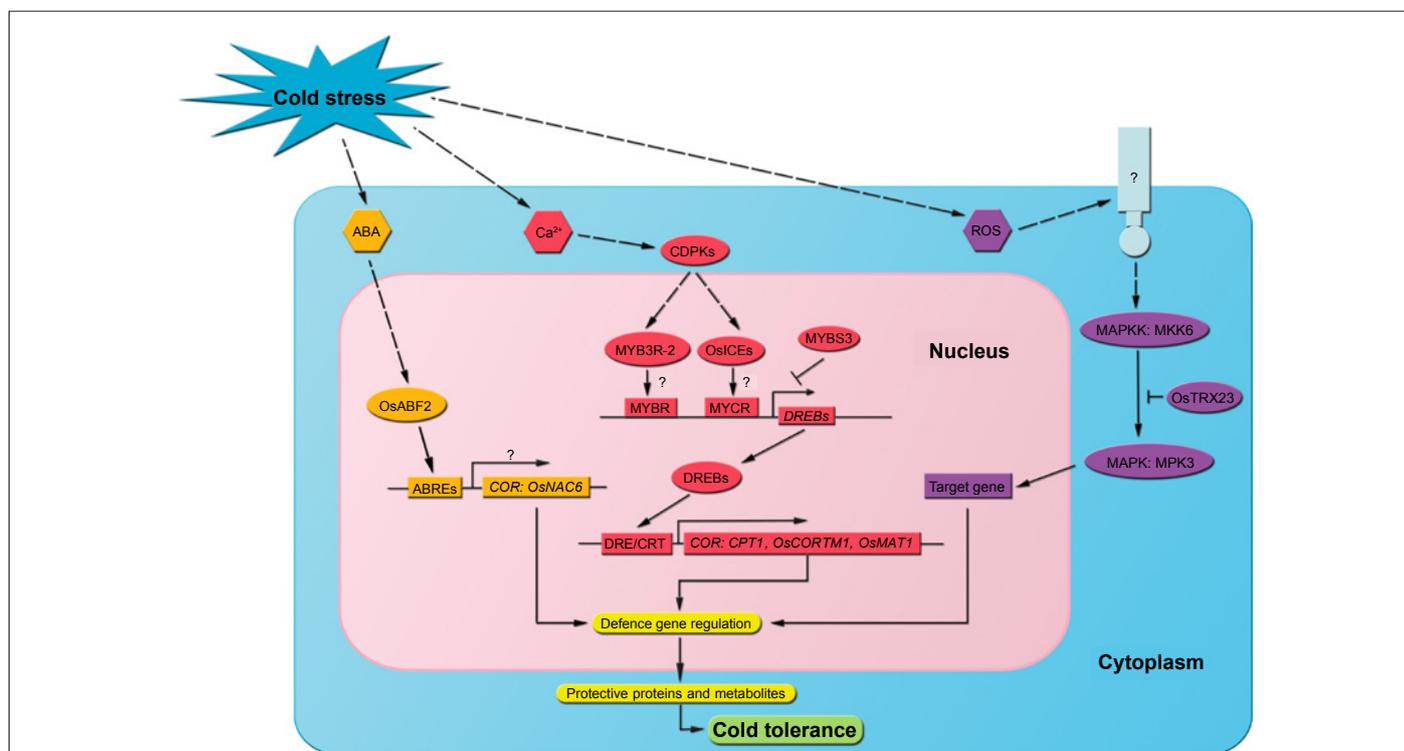
As a cold-responsive signaling in cold-stressed plants, abscisic acid (ABA) accumulates and then initiates the cold-sensing period (Figure 1) [17]. An ABRE (ABA-responsive elements)-binding bZIP transcription factor *OsABF2* plays a role in the cold response, and significantly increases at the transcriptional level [18]. In a rice mutant deficient in the ABA-responsive pathway *ABI5-Like1 (abl1)*, over one-third of the genes are down-regulated in response to cold and other abiotic stresses, indicating that ABA may play a positive and complex role in the sensing of cold stress in rice [19].

Reactive Oxygen Species (ROS) accumulate in cells when plants are challenged with biotic or abiotic stresses. ROS, which include superoxide ( $O_2^-$ ), hydrogen peroxide ( $H_2O_2$ ), and the hydroxyl radical, play two roles under cold stress: they induce ROS scavengers and initiate protective mechanisms [20]. When plants are exposed to biotic and abiotic stimuli, an increase in ROS level can damage membranes, induce alterations of cellular ion conductance, and trigger mitogen-activated protein kinase (MAPK) cascades (Figure 1) [19]. Transgenic rice overexpressing *OsAPXa* (ascorbate peroxidase) exhibits an elevated cold tolerance that is negatively correlative with the levels of  $H_2O_2$  and lipid peroxidation, which have been scavenged by increased ascorbate peroxidase activity during cold treatment [21]. Moreover, ROS regulate the *OsMKK6* (MAPK kinase)-*OsMPK3* (MAPK) pathway through redox control of *OsTRX23* [22]. Interestingly, an analysis of the

transcriptional regulatory network in japonica rice subjected to cold treatment revealed that oxidative-mediated clusters (several  $H_2O_2$ -induced gene such as *bZIP*, *ERF*, and *MYB* genes) are activated earlier than ABA-mediated clusters (factors acting on ABRE-like enriched clusters), and that the former may play a more important role in early cold sensing [8,23-25].

### CDPKs pathway

Calcium-Dependent Protein Kinases (CDPKs) belong to a family of Ser/Thr protein kinases that were first discovered in plants. By playing a central role in calcium-dependent pathways and by controlling the calcium content in the cell, CDPKs have been thought to coordinate the sensing of and responses to abiotic stress [26,27]. Expression by all 29 CDPK (CPK) genes in rice has been evaluated under various abiotic stresses. Nine CDPK genes (*OsCPK7*, *OsCPK13*, *OsCPK15*, *OsCPK17*, *OsCPK20*, *OsCPK21*, *OsCPK23*, *OsCPK24*, and *OsCPK29*) are induced by chilling temperatures in rice seedlings [28]. Moreover, *OsCDPK7* and *OsCDPK13* overexpression transgenic lines exhibit higher recovery rates after cold stress than the vector control. An *in situ* hybridization localized the expression of *RAB16A*, one of the proposed target genes regulated by the *OsCDPK7* signaling pathway. CDPKs have also been identified as downstream components in Gibberellin (GA) and Brassino Steroids (BRs) signaling pathways [29-31]. With transgenic analysis in rice, the expression of *OsCDPK13* is up-regulated in response to both GA3 and cold treatment, suggesting that *OsCDPK13* may mediate the GA-induced signaling and the  $Ca^{2+}$  influx [32]. A reduction in GA content of cold-treated *Arabidopsis*, modulated through the stimulation



**Figure 1:** In response to low temperature stress, rice upregulates the expression of protective proteins, which is initiated by the ABA signaling pathway, the DREBs pathway, and the MAPK cascade. Solid arrows indicate direct activation; broken arrows indicate indirect activation; lines ending with a bar indicate negative regulation. ABA: abscisic acid; ABRE: ABA-responsive elements; ABF: ABRE-binding factor; CDPK: calcium-dependent protein kinase; COR: cold-responsive gene; *CORTM1*: one of the cold-regulated (COR) genes in rice; *CPT*: one gene that is activated by *OsMYB3R-2*; CRT: C-repeat elements; DRE: dehydration-responsive elements; DREB: dehydration-responsive element-binding protein; MAPK (MPK): mitogen-activated protein kinase; MAPKK: MAP kinase kinase; ICE: inducer of CBF expression; MAT1: malonyltransferase 1; MYB: myeloblastosis; MKK6: MAPK kinase 6; MYB3R-2: a R1R2R3 MYB transcription factor; MYBR: MYB recognition site; MYCR: MYC recognition site; NAC: NAM-ATAF-CUC; ROS: reactive oxygen species; *OsTRX23*: *Oryza sativa* thioredoxin.

of expression of GA-inactivating GA 2-oxidase (*GA2ox*) genes is associated with the accumulation of a green fluorescent protein-tagged DELLA protein [33]. Because CBF1 acts downstream in the CDPK pathway, a question arises about whether there is a feedback regulation between CBFs, GA, and CDPKs that explains their changes in response to cold stress. Accordingly, further research in the function of the rice CDPK genes would be useful for increasing our understanding of signal transduction pathways in cold stress responses.

### OsMAPKs

The MAPK pathway is a well-characterized signal transduction cascade system in animals, yeast, and plants. The MAPK cascade consists of three subsequently interactive phosphorylation kinases: MAP kinase kinase kinase (MAPKKK), MAP kinase kinase (MAPKK), and MAPK [34,35]. MAPK, the last component of the phosphorylation cascade, is activated by MAPKK, which is in turn activated by MAPKKK. The MAPK cascade regulates cell division, development, and differentiation in response to stress stimuli in animals and yeast [36,37]. In recent years, a series of genes encoding MAPKs, MAPKKs, and MAPKKKs have been identified from different plant species. An increasing body of evidence has shown that MAPKs play important roles in signal transduction in response to drought, ROS, pathogen attack, wounding, and low temperature in plants [38-42].

Of the 20 MAPK genes in *Arabidopsis*, *AtMPK3* and *AtMPK6*, have been implicated in the tolerance to multiple abiotic and biotic stresses [39,43]. Nine MAPK genes have been identified from rice, and each MAPK encodes a distinct protein kinase that plays a role in mediating abiotic tolerance [44]. *BWMK1*, which was the first MAPK gene found in rice and which was detected in the indica-type cultivar IR36, is induced by infection by the blast pathogen (*Magnaporthe oryzae*) and by mechanical wounding [45]. Recently, a time-based transcriptional regulation mechanism controlled by *OsTRX23* has been reported for *OsMPK3/OsMAP1* and *OsMPK6/OsSIPK* which are strongly induced by low temperature treatment (12°C) at the transcriptional level [22]. In the first 24 h of cold treatment, transcripts of *OsMPK3* and *OsMPK6* rapidly increase, and then, with an increasing transcription of *OsTRX23*, they sequentially decrease, suggesting that the MAPK pathway could be a rapid stress-responsive element associated with the transient accumulation of H<sub>2</sub>O<sub>2</sub> during chilling stress. These results also indicate that some unknown late-responsive element mediated by the inhibition of *OsMPK3* and *OsMPK6* by *OsTRX23* leads to cold tolerance in rice. Recently, a yeast two-hybrid screen designed to identify partner MAPKs for *OsMKK6* revealed specific interactions of *OsMKK6* with *OsMPK3* and *OsMPK6*. A constitutively active form of *OsMKK6* and *OsMKK6DD*, showed elevated phosphorylation activity against *OsMPK3* and *OsMPK6* *in vitro*. *OsMPK3*, but not *OsMPK6*, was constitutively activated in transgenic plants overexpressing *OsMKK6DD*, indicating that *OsMPK3* is an *in vivo* target of *OsMKK6*. Chilling tolerance was enhanced in transgenic plants overexpressing *OsMKK6DD* [46]. Taken together, these data suggest that the MAPK signaling cascade is one of the low-temperature signaling pathways in rice and positively regulates cold stress tolerance.

### The transcriptional-regulatory network associated with cold response

The transcriptional regulatory network involved in low temperature response prolongs the expression of cold acclimation genes in rice. Of the 2,604 genes that are upregulated in response to chilling in japonica rice, about 6% (148) have been estimated to be Transcription Factors (TFs)

based on the classification of the Database of Rice Transcription Factors. These putative TFs include members of AP2/ERF, bZIP, MYB, WRKY, bHLH, and NAC families, and are characterized by waves of induction at different time periods. For example, the 'early rapid response' group (phase-1) is induced during the initial 6 h of cold treatment, and the 'early slow response' group (phase-2) is induced between 6 and 24 h. A few TFs exhibited 'late response' profiles (phase-3) with no significant induction until after 24 h. Most TFs that are upregulated by chilling are activated at phase-1 and phase-2, indicating that early responses are critical for cold stress tolerance and that late responses may be involved in unknown mechanisms that protect rice growth after 24 h of exposure to low temperatures [10]. In the last two decades, researchers have made significant progress in clarifying the function of key TFs responding to cold stress, as discussed in the next section.

### DREB-CRT/DRE pathway

DREBs (dehydration-responsive element-binding proteins, also known as CBFs for C-repeat binding factors) have been the most intensively studied of the TFs involved in plant responses to cold. In rice, seven members in the DREB family have been studied in depth: *OsDREB1A/CBF3*, *OsDREB1B/CBF1*, *OsDREB1C/CBF2*, *OsDREB1D*, *OsDREB1E*, *OsDREB2A*, and *OsDREB2B* [47]. Overexpression of DREBs in transgenic rice significantly increases cold tolerance; relative to wild-type plants, the transgenic plants exhibit increased survival and growth, and changes in ROS scavenging, membrane transport, hormone metabolism, proline concentration, and accumulation of sugars such as raffinose, sucrose, glucose, and fructose [14,48].

DREBs belong to the APETALA2/Ethylene response factor (AP2/EREBP) family of TFs. These TFs can bind to GCC-box and C-repeat/dehydration-responsive elements (CRT/DRE) to promote the Cold responsive (*COR*) gene. To analyze the DNA-binding specificity of *OsDREBs*, researchers have selected *OsDREB1A* as a typical *DREB1*-type gene and *OsDREB2A* as a typical *DREB2*-type gene. The ability of the *OsDREB1A* and *OsDREB2A* fusion proteins to bind the wild-type or mutated DRE sequences in the *rd29A* promoter has been identified by the gel mobility shift assay. Furthermore, the transactivating DRE-dependent transcription capability of *OsDREB1A* and *OsDREB2A* in rice cells has been determined by transactivation experiments. Protoplasts are co-transfected with a  $\beta$ -glucuronidase (*GUS*) reporter gene fused to the dimeric 75-bp fragments containing the DRE motif and the effector plasmid. The *GUS* activity is distinctly upregulated in the presence of *OsDREB1A* and *OsDREB2A* relative to the vector control, indicating that the *DREB1A* and *DREB2A* proteins act as transcription activators in rice protoplasts [49].

In *Arabidopsis*, *ICE1* (Inducer of CBF expression1), a MYC-type basic helix-loop-helix transcription factor, is a common TF that promotes the expression of *DREB1A*. *ICE1* binds to MYC recognition (MYCR) elements in the *DREB1A* promoter region and is important for the expression of *DREB1A* during cold acclimation [12]. So far, there is no evidence that any *ICE* can function as a transcriptional factor for DREBs in rice. The Basic Helix-loop-Helix (bHLH) protein gene *OrbHLH001*, encoding an *ICE1*-like protein containing multiple homopeptide repeats, has been characterized and isolated from Dongxiang Wild Rice (*Oryza rufipogon*). Overexpression of *OrbHLH001* enhances the tolerance to freezing stress in transgenic *Arabidopsis*. Examination of the expression of cold-responsive genes in transgenic *Arabidopsis* shows that the effect of *OrbHLH001* in cold response differs from that of *ICE1* and is independent of the CBF/DREB1 cold-response pathway [50]. Recently, two *ICE* homologs in

rice, OsICE1 and OsICE2, have been identified by BLAST searches with the nucleotide sequence of *Arabidopsis ICE1* in the Rice Annotation Project Data Base [51]. Unlike the increased expression of *Arabidopsis ICE1* under cold stress, the expression of *OsICE1* and *OsICE2* remains constant under cold stress as indicated by semi-quantitative RT-PCR; immunoblot with the anti-ICE specific antibody showed, however, that the levels of *OsICE1* and *OsICE2* proteins are upregulated by both cold and salt stresses. Although the expression of OsDREB1B increases under cold treatment, no evidence of a direct interaction between OsDREB1B and OsICE1/OsICE2 has been provided. There is little information available concerning the role of the MYC-type transcription factor in the DREB pathway but many genes have been found that upregulate the expression of *DREB* in rice [10,52,53]. OsMYB3R-2, a nuclear-localized R1R2R3 MYB TF, plays a role in cold response in rice [54]. *Arabidopsis* transgenic plants overexpressing *OsMYB3R-2* show increased tolerance to cold, drought, and salt stresses, and the expression of some cold-related genes such as *DREB2A* and *CBF1/2/3* is increased in the *OsMYB3R-2*-overexpression plants. These results suggest that OsMYB3R-2 acts as a master switch in cold tolerance. A more recent study has shown that overexpression of *OsMYB3R-2* in transgenic rice leads to higher transcript levels of several G2/M phase-specific genes and *OsCPT1*, which are putatively targeted by the *DREB* genes [53]. The role of R2R3-type MYB TF (OsMYB2), which is localized in the nucleus and which has transactivation activity, in tolerance to cold stress has been functionally characterized by generating overexpression and RNAi transgenic rice plants of *OsMYB2*. In the *OsMYB2*-overexpression plants, the expression of *OsDREB2A* is upregulated compared with the wild type under low temperature treatment, suggesting that OsMYB2 is an upstream regulon for *OsDREB2A* [55].

A negative regulator of the CBF regulon, MYBS3, operates via a distinct pathway to help rice plants tolerate cold stress. MYBS3 is a single DNA-binding repeat MYB TF. By using genotypes that overexpress or underexpress *MYBS3* to identify genes in the MYBS3-mediated cold signaling pathway, Su et al. [56] determined that *MYBS3* responds slowly to cold stress and enables rice seedling to tolerate 4°C for at least 1 week. Surprisingly, *MYBS3* represses the well-known *DREB1/CBF* fast-acting and short-term signaling pathway at the transcriptional level in rice [56]. By repressing the expression of the *DREB1* regulon, the slow acting *MYBS3* may prevent unnecessary expression of *DREB1*.

## NAC TFs

NAC proteins represent one of the largest families of TFs. There are at least 105 putative NAC TFs in *Arabidopsis*, 140 in rice, 205 in soybean, and 152 in tobacco (*Nicotiana tabacum*) [10]. NAC TFs are key regulators of stress sensation and developmental programs, and contain an N-terminal NAC domain. Although the NAC TF family is widely distributed in plants, it has not been found in other eukaryotes [57,58].

Analysis of the NAC domain has been conducted by database searches with a comprehensive analysis of NAC family genes both in rice and *Arabidopsis* [59]. Five subdomains, each typically ~50 amino acids long, have been identified in the DNA-binding domain of a typical NAC protein. A comprehensive *in silico* analysis of the NAC TF family in rice recently identified 36 putative motifs within the NAC family. Based on the pattern of these motifs, the NAC family of rice can be classified into 15 types (types A-O). Most rice NAC proteins (97 of 140) contain a complete NAC DNA-binding domain with five major subdomains, which are classified into types A-E [60,61]. The sequences in the 1.5 kb promoter region of *OsNAC6* include ABRES,

MYBRS, MYCRS, W-boxes, GCC boxes, and as-1 motifs [24]. ABRES, MYBRS, and MYCRS play important roles in ABA signaling and abiotic stress response. The W-boxes and GCC boxes are recognition sites for WRKY and ERF transcription factors, respectively, and are involved in the regulation of various plant-specific physiological processes such as pathogen defense and senescence. The as-1 motifs are known as oxidative stress-responsive elements. These sequences may function as abiotic and/or biotic stress-responsive cis-acting elements in the *OsNAC6* promoter, and they may sense cold stress from the upstream transcription factors induced by ABA, ROS, and other metabolite changes.

Regarding the *OsNAC5*-dependent tolerance to abiotic stress in rice, research has demonstrated that the overexpression line is more tolerant of cold stress and that the *OsNAC5* RNAi line is less tolerant of cold stress than the wild type [16,62]. Moreover, knockdown and overexpression of *OsNAC5* enhances and reduces, respectively, the accumulation of malondialdehyde and H<sub>2</sub>O<sub>2</sub>, suggesting that knockdown of *OsNAC5* renders RNAi plants more sensitive to oxidative damage. In addition, the sensitivity of seed germination to ABA is increased in overexpression plants and decreased in RNAi plants. These results indicate that *OsNAC5* is important for cold tolerance in rice and that the effect of *OsNAC5* is associated with an ABA-related transcriptional regulation network.

However, the target genes of NAC TFs in rice remain largely unknown. The rice NAC gene *SNAC1* (stress-responsive NAC 1) is predominantly induced in guard cells by drought and encodes NAC TF with transactivation activity [63]. *SNAC1*-overexpression plants show a greater sensitivity to ABA and an increased rate of stomatal closure that reduces water loss. In the field, the drought tolerance of transgenic plants is significantly greater than that of wild-type plants at anthesis, and the increased drought tolerance is not associated with other phenotypic changes or with yield reduction. The distinctive binding character of *SNAC1* suggests that a special NAC binding site exists in rice.

## Other TFs

In addition to the well-characterized rice TF genes in the cold responsive pathway that were described in the previous sections, many other genes also display changes in transcriptional expression upon low temperature treatment and are involved in the cold-sensing cascade.

Proteins with the A20/AN1 zinc-finger domain are present in all eukaryotes and are well characterized as common elements in the stress response of animals and plants [64]. The stress-associated proteins (SAPs) contain the AN1 domain, which has a dimetal (zinc)-bound alpha/beta fold and often combines with A20 zinc finger domains (SAP8) or C2H2 domains (SAP16) including ascidian posterior end mark 6 (PEM-6) protein and human AWP1 protein (associated with PRK1) [65,66]. The human AWP1 protein is expressed during early embryogenesis, and mutations in *SMUBP-2* (human immunoglobulin mu binding protein 2) cause muscular atrophy with respiratory distress type 1 [67]. *OsiSAP8* is an early cold-responsive gene in rice, and the *OsiSAP8* protein fused to GFP is specifically localized in the cytoplasm, indicating that, unlike many zinc-fingers containing proteins, *OsiSAP8* is a cytoplasmic protein. Furthermore, the A20 and AN1 type zinc-finger domains of *OsiSAP8* interact with each other in yeast two-hybrid assays, and *OsiSAP8* overexpression transgenic rice plants grow better than wild-type plants under cold stress [68]. According to a microarray analysis of the rice A20/AN1-type zinc finger genes, four

genes (*ZFP177*, *ZFP181*, *ZFP176*, *ZFP173*), two genes (*ZFP181* and *ZFP176*), and one gene (*ZFP157*) are significantly induced by cold, drought, and H<sub>2</sub>O<sub>2</sub> treatments, respectively [69]. The promoter region of *ZFP177*, which is a specific cold-induced A20/AN1-type zinc finger gene, contains no stress-associated cis-acting elements other than HSE, suggesting that the heat response of *ZFP177* might be regulated by heat shock factors but that the cold response is not directly mediated by CBF/DREB transcription factors.

The TFIIIA-type zinc finger protein was first detected in *Xenopus* oocytes [70] and contains at least one TFIIIA-type zinc finger motif with the consensus of CX<sub>2-4</sub>CX<sub>3</sub>FX<sub>5</sub>LX<sub>2</sub>HX<sub>3-5</sub>H. A number of TFIIIA-type zinc finger proteins are related to stress response [71]; for example, *Arabidopsis* STZ/ZAT10 and ZAT7 are involved in salt tolerance [72-74], soybean SCOF-1 is involved in cold tolerance [52], and *Arabidopsis* ZAT12 is involved in cold and oxidative stress [75]. The first TFIIIA-type zinc finger protein identified in rice, *ZFP245*, is involved in cold and drought tolerance [9]. Overexpression of *ZFP245* in rice leads to increased cold tolerance and increased sensitivity to exogenous ABA treatment, suggesting that *ZFP245* may play a role in the ABA signal transduction pathway during stress responses. Another TFIIIA-type zinc finger protein, *ZFP182*, helps protect cell membrane integrity under cold stress (as indicated by reduced electrolyte leakage) and is associated with the DREB pathway [76].

Recent research has also demonstrated the involvement of many other genes in the cold signal pathway, including *bHLH1*, *OsP5CS2*, *LIP19*, *OSPGYR*, *ZFP245*, *OVP1*, *bZIP52/RISBZ5*, *TEF1* and *SICZFP1*. The CBF-independent gene *OrbHLH001* from Dongxiang wild rice can enhance tolerance to low temperature, suggesting that wild rice may have a distinct stress responsive pathway that enables a perennial life history [9,23,50,77-82].

## Post-transcriptional Regulation

### mRNA processing

Pre-mRNA processing is an important mechanism of post-transcriptional regulation of gene expression in eukaryotes. For conversion into mature mRNA, pre-mRNA requires various modifications such as the addition of a 5' methyl cap and poly (A) tail and intron splicing. Precursor mRNA with more than one intron can undergo alternative splicing to produce functionally different proteins from a single gene. In plants, about 20% of genes require alternative splicing [83]. Alternative splicing affects many important processes and characteristics in plants including photosynthesis, flowering, grain quality in cereals, and stress responses. For example, the *Arabidopsis* *COR15A* gene, which encodes a chloroplast stromal protein with cryoprotective activity, plays an important role in conferring freezing tolerance to chloroplasts; the *Arabidopsis* *stabilized1* (*sta1*) mutant is defective in the splicing of the cold-induced *COR15A* pre-mRNA and is hypersensitive to chilling, ABA, and salt stress [84,85]. *STA1* encodes a nuclear pre-mRNA splicing factor and is upregulated by cold stress. *STA1* catalyzes the splicing of *COR15A*, which is necessary for cold tolerance. Furthermore, pre-mRNAs of serine/arginine-rich (SR) proteins, which are involved in the regulation or execution of mRNA splicing, also undergo alternative splicing under cold and heat stresses in *Arabidopsis*.

In rice, recent studies on the mRNA processing of *OsDREB2B*, a member of the DREB-CRT/DRE pathway, have revealed an efficient mRNA processing strategy for cold acclimation [86,87]. To recognize the two types of *OsDREB2B* transcripts, the authors of these papers

designed two primers that are specific for each transcript. In the non-stress plants, *OsDREB2B1* is approximately five times more abundant than *OsDREB2B2*. However, in the cold stress plants, *OsDREB2B2* accumulates to a level equal to or greater than that of *OsDREB2B1*. To determine whether *OsDREB2B2* is modified from *OsDREB2B1* or is spliced alternatively from the *OsDREB2B* gene, the authors introduced *OsDREB2B1* or *OsDREB2B2* fused to the synthetic green fluorescent protein (sGFP) genes into two kinds of transgenic rice plants. RT-PCR analysis did not detect *sGFP-OsDREB2B2* in the Ubi:sGFP:*OsDREB2B1* plants but did detect the accumulated endogenous *OsDREB2B2* transcript. This result indicated that *OsDREB2B2* is produced directly from the *OsDREB2B2* gene and is not modified from *OsDREB2B1*. In addition, a transcriptional analysis showed that transcription is greater for *OsDREB2B2* than for *OsDREB2A* under stress conditions. These data suggest that mRNA processing is an important regulatory strategy for *OsDREB2B* expression as part of the abiotic stress response in rice.

### Small RNAs

Small RNAs (sRNAs) are sequence-specific regulatory elements that mediate endogenous gene silencing in eukaryotes. Plant sRNAs have been divided into four classes based on their origins and structures: microRNAs (miRNAs) and three types of small interfering RNAs (siRNAs), including trans-acting siRNAs (ta-siRNAs), natural cis-antisense transcripts-derived siRNAs (nat-siRNAs), and repeat-associated siRNAs (ra-siRNAs) [88-90]. One major difference between miRNAs and siRNAs is that miRNAs result from the processing of a single-stranded hairpin precursor while siRNAs are generated from long double-stranded RNAs (dsRNAs) [91]. Plant miRNAs, a class of short non-coding RNAs (~22 nucleotides), are processed from primary miRNA transcripts through two sequential cleavages by Dicer-like1 (DCL1), and mature miRNAs are loaded into argonaute proteins to guide cleavage of target mRNAs or translational repression [92]. The biogenesis of ta-siRNAs is initiated by miRNA-mediated cleavage of non-coding transcripts. The cleaved RNAs are copied into dsRNAs by RNA-dependent RNA polymerase 6 (RDR6) and are processed by DCL4 into phased siRNAs from the end defined by miRNA-mediated cleavage. The production of ra-siRNAs requires the activity of DCL3, RDR2, and polymerase (Pol) IV, a plant-specific DNA-dependent RNA polymerase [93,94].

The rice genome contains approximately 250,000 transposable elements (TEs), constituting approximately 35% of the genome sequence [95,96]. TEs can lead to the folding of RNA sequences into hairpin structures (reminiscent of the pre-miRNAs), and many miRNAs derived from TEs have been found in rice [97]. Global expression profiling of rice miRNAs showed that 18 miRNAs respond rapidly to cold stress. Interestingly, most of these miRNAs are down-regulated, indicating that the expression of target genes controlled by these miRNAs is induced in an adaptive response to cold stress [96].

miRNAs also affect plant hormones, which regulate many important aspects of growth and development as well as responses to environmental stresses. miR-167 helps regulate the auxin signal by cleaving two auxin-response factors and might play a role in cold tolerance by affecting auxin-signaling pathways [96]. miR-171 is a large and conserved miRNA family. A microarray-based analysis has revealed that 6 h of cold stress upregulated miR-171a in *Arabidopsis* but down-regulated miR-171a in rice [98]. These results demonstrate that miRNAs belonging to the same family can display opposite patterns in response to cold stress, suggesting that they may perform different functions. The results also suggest that differences in their expression in rice vs. *Arabidopsis* may represent species-specific differences in the

response to cold stress. Generally, miRNA accumulation negatively correlates with the level of target transcripts. Two MADS-box genes, *MADS 57* and *MADS 27*, are targets of miR-444a [96,99]. How miR-444a differentially regulates the two *MADS* genes under cold stress warrants further investigation.

## Conclusion

Intensive research has greatly increased our understanding of cold sensing, transcriptional networks, post-transcriptional regulation, and other responses of rice to cold stress. Rice plants use cold-induced calcium influx and changes in levels of ABA and ROS as signals to activate a response to cold stress. The DREB-CRT/DRE pathway has an important effect on the rice response to cold, and all DREB1 and DREB2 family members in the pathway have been identified and characterized by transgenic analysis in rice. The MAP kinase pathway and ABF/AREB pathway, whose effects have been well characterized in responses to other biotic and abiotic stress such as pathogen attack, heat, hyperosmotic stress, and oxidative stress, are involved in the cascade of cold stress responses in rice. Recent microarray analysis has revealed that small RNAs are important for cold responses. The recent research on cold acclimation also indicates that these cold-relevant genes can be used for molecular-assisted selection and transgenic research [100].

However, development of breeding techniques for rice shows that breeding of cold tolerant rice is still a challenge. Although many QTLs in cold tolerant rice varieties are identified, those QTLs are mostly stage specific and only effect germination stage, vegetative stage, or reproductive stage. Concerning current breeding techniques, varieties which tolerate to cold stress in all stages are hard to breed for the reason that the convergence of those QTLs into one rice variety is time and labor consuming. It is important, therefore, to develop alternative strategies for the breeding of crops and to discover more cold tolerant varieties and put them into breeding practices, including those wild rice varieties which live in high altitude areas and have an inborn tolerance under cold stress [101]. As the cold-responsive network is complex, characterizations of key factors and components among different cold signal transduction pathways are also useful for the breeding of cold tolerance in rice.

Although the number of cold-responsive genes found continues to increase, the biological complexity underlying cold acclimation has not decreased. An increased understanding of the molecular basis of cold tolerance in rice should facilitate the development of varieties of rice and of other crops that are tolerant to cold stress.

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