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Molecular mechanisms of salinity tolerance in rice

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ABSTRACT

Salinity is one of the major abiotic stresses which impose constraints to plant growth and production. Rice (*Oryza sativa* L.) is one of the most important staple food crops and a model monocot plant. Its production is expanding into regions that are affected by soil salinity, requiring cultivars more tolerant to saline conditions. Understanding the molecular mechanisms of such tolerance could lay a foundation for varietal improvement of salt tolerance in rice. In spite of extensive studies exploring the mechanism of salt tolerance, there has been limited progress in breeding for increased salinity tolerance. In this review, we summarize the information about the major molecular mechanisms underlying salinity tolerance in rice and further discuss the limitations in breeding for salinity tolerance. We show that numerous gene families and interaction networks are involved in the regulation of rice responses to salinity, prompting a need for a comprehensive functional analysis. We also show that most studies are based on whole-plant level analyses with only a few reports focused on tissue- and/or cell-specific gene expression. More details of salt-responsive channel and transporter activities at tissue- and cell-specific level still need to be documented before these traits can be incorporated into elite rice germplasm. Thus, future studies should focus on diversity of available genetic resources and, particular, wild rice relatives, to re-incorporate salinity tolerance traits lost during domestication.

1. Introduction

Rice (*Oryza sativa* L.) is a predominant dietary energy source and a major staple food for more than 3.5 billion people around the world, particularly across Asia. Rice has also been recognized as a model monocotyledonous plant species for molecular biological and genomic studies due to its considerable genetic diversity, its relatively small genome size, the availability of high-quality sequences, and highly efficient transformation protocols [1]. With the world population predicted to rise to 9.6 billion by 2050 [2], there is a strong imperative to increase rice production to match the increasing global food demand. This goal needs to be achieved under conditions of increasing abiotic and biotic stresses caused by climate change and increased competition for scares resources such as land and water. Among the prevalent abiotic stresses, soil salinity is one of the major factors that inhibit crop growth, development and ultimately, yield. It is estimated that more than 1000 million hectares of land is saline or sodic, and between 25% and 30% of irrigated lands (or about 70 million hectares) are salt-affected and essentially commercially unproductive [3]. Currently,

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4.03 billion people (over 50% of the world's population) live in 13 countries severely affected by soil salinity. This number is expected to increase to 5.02 billion by 2050 [4] due to inundation and sea water intrusion (sea level rise) while population pressure is simultaneously increasing.

Among the cereals, rice is the most sensitive to salinity stress, with 30 mmol L^{-1} NaCl (electrical conductivity ~ 3 dS m^{-1}) already strongly reducing the growth and yield of rice plants [5]. Above 3 dS m^{-1}, most modern, high-yielding rice varieties display a 12% reduction in yield per dS m^{-1} while 50% yield reduction have been documented at 6 dS m^{-1} [6]. Over the past few decades, significant efforts have been made worldwide to understand mechanisms of salinity tolerance and to breed salt-tolerant varieties in rice. However, owing to the complexity of plant responses to salinity, with inherent components of osmotic, ionic and oxidative stress, the task of developing salinity-tolerant rice genotypes remains challenging [7]. Further, salinity tolerance is governed by complex and interacting genetic, molecular and physiological mechanisms. Rice is relatively tolerant to soil salinity during germination and late vegetative growth, compared to the early seedling stage (3-leaf stage) and reproductive stage (pollination and fertilization). Plants at different developmental stages may employ different mechanisms to deal with salinity stress, as a very poor correlation was found between salinity tolerance at the two most salt-sensitive stages, seedling and reproductive stage. To date, numerous salinity-responsive genes have been identified in rice, but none have been successfully incorporated into commercial germplasm [8,9]. In the present review, we critically evaluate current knowledge and understanding of salinity tolerance of rice.

2. Molecular mechanisms for salt tolerance in rice: sensing and signalling

2.1. Stress sensing and signalling

Plants respond to salt stress through perceiving and transducing the osmotic and ion signals to cell interiors, followed by modification of cellular characteristics. So far, no specific sensor or receptor for Na^+ has been identified in plants [10]. However, the salt overly sensitive (SOS) signalling pathway and calcineurin B-like (CBL)/CBL-interacting kinase (CIPK) pathway has been well characterized in *Arabidopsis*. Salt-induced elevation in cytosolic Ca^{2+} activates the SOS2-SOS3 protein kinase complex, which phosphorylates and stimulates the activity of SOS1, a plasma membrane Na^+/H^+ antiporter [11]. In rice, the *OsSOS1*, *OsSOS2*/*OsCIPK24* and *OsSOS3*/*OsCBL4* genes have been isolated and the function and relationship between them investigated (Fig. 1). Among them, *OsCIPK24* and *OsCBL4* act in concert to activate *OsSOS1* [12]. The CBL10-CIPK24 complex has been suggested to constitute a novel salt-tolerance pathway that regulates vacuolar Na^+ sequestration in *Arabidopsis* [13]. The *OsCBL1-OsCIPK23* complex modulates *OsAKT1*-mediated K^+ uptake in roots [14]. It was also reported that most of the rice CBL and CIPK genes show transcriptional responses to abiotic stresses including salinity [15]. Based on the results from these studies, CBL-CIPK signalling networks in response to salinity stress should be studied in more depth.

In addition to CBLs and CIPKs, calcium-dependent protein kinases (CDPKs) also regulate the downstream components in calcium signalling pathways. A total of 29 CDPK genes have been reported in the rice genome, with some of them being involved in salt stress response. *OsCDPK7* acts as a positive regulator involved in both cold and salt/drought tolerance in rice [16]. Overexpression of *OsCPK21* promotes the expression of ABA- and salt-inducible genes including *OsLEA3*, *OsNAC6*, *OsNHX1*, and *OsSOS1*. [17]. *OsCPK12*-overexpressing (*OsCPK12*-OX) plants exhibited increased salt tolerance and decreased level of hydrogen peroxide (H_2O_2) accumulation in the leaves. Further gene expression analysis suggests that *OsCPK12* positively regulates ROS detoxification by upregulating the expression of *OsAPX2* and *OsAPX8* [18]. Several calmodulin (CaM) and CaM-like (CML) proteins including *OsCam1-1*, *OsCML4*, *5*, *8*, and *11*, and *OsMSR2* were found to be linked to salt tolerance [19–21]. A novel, *small calcium-binding protein 1* (*OsCCD1*), which is induced by osmotic stress, salt stress and calcium-mediated ABA signal, can increase the tolerance to osmotic and salt stresses in rice seedlings [22].

Other genes encoding kinases such as *receptor-like protein kinases 1* (*OsRPK1*) [23], *stress-induced protein kinase 1* and *2* (*OsSIK1*, *OsSIK2*) [24,25], and *salt-tolerance leucine-rich repeat receptor-like kinase* (*OsSTLK*) [26], *salt tolerance receptor-like cytoplasmic kinase 1* (*STRK1*) [27], and *phosphoglycerate kinase 2* (*OsPGK2*) [28] are also found to be involved in the response to salt stress in rice. Ion-specific salt stress signalling was also attributed to the operation of *monocation-induced* $[Ca^{2+}]_i$ *increases 1* (*MOCA1*) gene that is involved in the biosynthesis of glycosyl inositol phosphorylceramide (GIPC) sphingolipids and is specifically required for spikes in cytosolic Ca^{2+} [29]. Other proteins that mediate salt-induced Ca^{2+} signalling include FERONIA (FER) [30], ANNEXIN1 (ANN1) [31] and K^+ exchange antiporters (KEAs) [32]. However, all these data come from *Arabidopsis*, and their operation in stress sensing in rice and all subsequent consequences on growth and yield have not yet been demonstrated.

Soil salinity also imposes osmotic stress on roots. A hyperosmolality-gated calcium-permeable channel encoded by *reduced hyperosmolality-induced* $[Ca^{2+}]_i$ *increase1* (*OSCA1*) was identified as an osmotic stress sensor in *Arabidopsis* [33], but its role in stress sensing in rice needs to be investigated. Salt-stress induced reduction in cell turgor pressure can be perceived by mechanosensitive sensors, such as mechanosensitive channel-like (MSL), Mid1-complementing activity (MCA), and two-pore potassium channel (TPK) family proteins [34].

2.2. ROS scavenging and signalling

The major ROS in plants include hydrogen peroxide (H_2O_2), superoxide anion (O_2^-), singlet oxygen ($^1O_2$), and hydroxyl radical ($OH^·$), which are also produced in chloroplasts, mitochondria, peroxisomes, and by several apoplastic sources. Reduced rate of photosynthesis induced by high salinity accelerates the formation of ROS in chloroplasts [35].

ROS function as important signalling molecules in response to external stimuli. The plant NADPH oxidases designated as respiratory burst oxidase homologs (RBOHs) are key signalling nodes in the ROS signalling pathways. The possession of two Ca^{2+}-binding EF-hand motifs and phosphorylation target sites in the N-terminal extension of plant RBOHs provides the ability to integrate calcium signalling with ROS production [36]. In *Arabidopsis* NADPH oxidase RBOHF can be activated by direct Ca^{2+} binding to its EF-hands and Ca^{2+}-dependent phosphorylation by CBL1/9–CIPK11/26 complexes and OST1 kinase at the plasma membrane [37]. The *Arabidopsis* RBOHD regulates long-distance signalling via a dynamic autopropagating wave of ROS traveling at a rate of up to 8.4 cm min^{-1} across the entire plant in response to diverse environmental stimuli [38]. Rice *rbohA*, which was the first *rboh* gene isolated from a plant, mediates ROS level under abiotic stresses including salinity [39]. Recently, Liu et al. [40] found that melatonin upregulates the expression of genes involved in Ca^{2+} associated CBL/CIPK and CDPK pathways as well as genes encoding respiratory burst NADPH oxidases (*OsRBOHA* and *OsRBOHF*) under salt stress in rice. Further study suggested that melatonin-induced *OsRBOHF*-dependent ROS signalling is required to increase the expression of K^+ uptake transporters

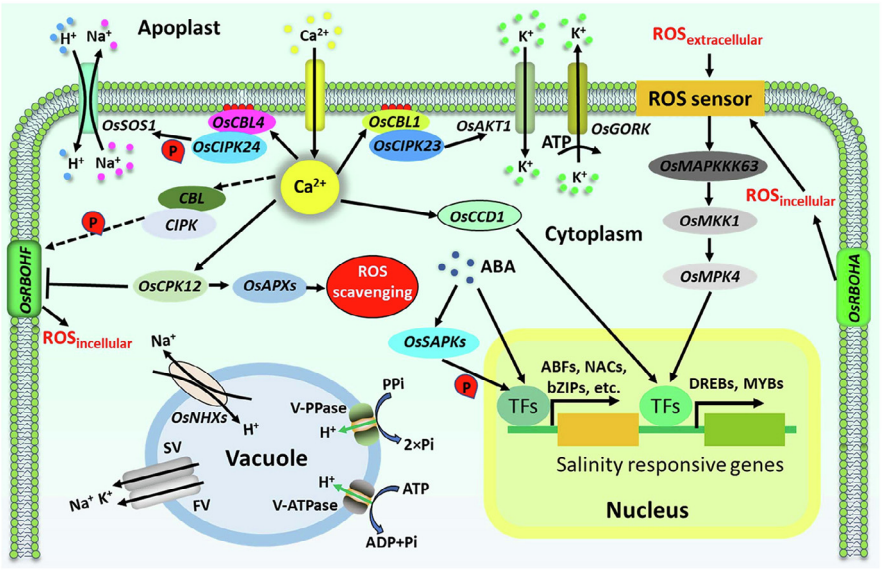

Fig. 1. Salt stress signaling pathways of rice. The CBL-CIPK calcium signaling network plays a critical role in sensing salt-induced Ca^{2+} signals and in the regulation of Na^+/K^+ ion homeostasis. Salt-induced elevation in cytosolic Ca^{2+} activates the CBL/CIPK protein kinase complexes which modulates the activity of Na^+/H^+ antiporter *OsSOS1* and K^+ transporter *OsAKT1*. OsCCD1 can bind cellular Ca^{2+} and enhance transcription levels of transcription factors under high salinity. The *OsGORK* governed by ATP is a K^+ efflux channel under salinity stress. *OsRBOHA/F* are involved in the production of ROS at plasma membrane, and accumulated ROS is scavenged by *OsAPXs* which is regulated by *OsCPK12*. MAP kinase cascades, consisting of *OsMAPKKK63*, *OsMKK1*, and *OsMPK4* are involved in the ROS signal transduction pathways triggered by salinity stress. Activated *OsMPK4* transduce signals to downstream transcription factors. *OsSAPKs* can be activated by ABA signal and directly phosphorylate downstream transcription factors. In the vacuole, *OsNHXs* energized by either V-ATPase or V-PPase H^+ pumps, slow-vacuolar (SV) ion channels and fast-vacuolar (FV) ion channels are involved in the regulation of ion homeostasis under high salinity. The dashed lines indicate uncertain pathways that remain to be identified. Solid arrows indicate established direct regulation.

(*OsAKT1*, *OsHAK1* and *OsHAK5*) in rice root tips [40]. While ROS are important signalling molecules, their homeostasis should be strictly controlled to prevent possible damage. Excessive accumulation of ROS causes oxidative stress leading to DNA damage, protein oxidation and lipid peroxidation [41].

Stress-induced accumulation of ROS disturbs ionic homeostasis in the cells by activating many different types of ROS-sensitive ion channels causing damages to the key cellular structures. To cope with stress, plants have evolved both enzymic and non-enzymatic mechanisms for ROS-scavenging [42]. The ascorbate–glutathione (AsA-GSH) recycling pathway also referred to as Halliwell-Asada Pathway is the heart of the redox homeostasis and has a key role in H_2O_2 scavenging in plants [43]. Ascorbate peroxidase (APX), which belongs to the heme-peroxidase (class I) [44], plays an important role in scavenging ROS via catalysing the conversion of H_2O_2 to H_2O and O_2. A total of 8 *APX* genes have been identified in rice [45]. *OsAPX2* might control the H_2O_2 concentration in the cytosol under stress [46] and overexpression of *OsAPX2* improved salt tolerance in rice [47]. NaCl-induced expression of *OsAPX8* in rice roots is associated more with Na^+ than Cl^- or osmotic components [48] and is mediated through an accumulation of ABA instead of H_2O_2 [49].

Reduced glutathione (GSH) is another antioxidant conferring stress alleviation. Exogenous GSH increases endogenous GSH contents and activates superoxide dismutase (SOD), APX and glutathione reductase (GR), resulting in enhanced salt tolerance [50]. GR, which catalyzes the reduction of oxidized glutathione (GSSG) to GSH with the accompanying oxidation of nicotinamide adenine dinucleotide phosphate (NADPH), plays an important role in AsA-GSH cycle [51]. *RGRC2* encodes GR in rice and is strongly induced by ABA-related, abiotic stresses including salinity [52]. One cytosolic GR (*OsGR2*) and two chloroplastic GRs (*OsGR1* and *OsGR3*) have been identified in rice [53,54]. *OsGR3* was dual-localized in the chloroplasts and mitochondria, conferring salt tolerance through regulating GSH redox state [55]. Reduced glutathione also acts as a substrate for glutathione peroxidases (GPX) and glutathione S-transferase (GST) which are involved in ROS scavenging associated with salt stress in rice. Rice GPX gene family comprises of five members where the mitochondrial *OsGPX3* being essential for H_2O_2 homeostasis and salt tolerance [56]. Several other rice genes related to AsA–GSH pathway have been reported to contribute to salt tolerance. The *dehydroascorbate reductase 1* (*OsDHAR1*) confers enhanced tolerance to salinity stress by maintaining the AsA pool, ion homeostasis and redox homeostasis [57]. The rice GMPase gene *OsVTC1-1* is involved in response to salt stress in rice through AsA scavenging of excess ROS at both vegetative and reproductive stages [58].

The mitogen-activated protein (MAP) kinase cascades also play a pivotal role in ROS signal transduction pathways. In rice, overexpression of *OsMAPK44* leads to less damage and a higher K^+/Na^+ ratio under high salt conditions [59]. In contrast, *OsMAPK33* overexpressing transgenic lines show greater reduction in biomass accumulation and a lower K^+/Na^+ ratio [60]. *OsMKK1* is found to phosphorylate *OsMPK4* in a signalling pathway that regulates the expression of transcription factors and salt tolerance in rice [61]. *OsMKK6* (or *OsMEK1*) is also involved in salt stress signalling [62]. *OsMAPKKK63* is induced by several abiotic stresses and interacts with both *OsMKK1* and *OsMKK6* in dealing with stresses, implying that *OsMAPKKK63* may be involved in the high salinity response [63]. A lectin receptor-like kinase *SIT1* was reported to activate MPK3 and MPK6 in the presence of salt and a SIT1-MPK3/6 cascade was demonstrated to mediate salt sensitivity by affecting ROS and ethylene homeostasis and signalling in rice [64].

Several other genes, such as *dehydration-stress inducible protein 1* (*OsDhn1*) [65], *glutaredoxin 20* (*OsGRX20*) [66], *vitamin E deficient 1* (*OsVTE1*) [67], *cyclophilin 2* (*OsCYP2*) [68], and *domains of unknown function 810.7* (*OsDUF810.7*) [69] were found to act as regulators of ROS homeostasis and confer salt tolerance in rice.

2.3. Transcription factors and microRNAs

Transcriptional regulation is a crucial part of plant response to abiotic stresses in plants. To date, many TFs that regulate expression of downstream target genes under stress conditions have been identified and functionally characterized [70]. In rice, major TF families regulating salt tolerance have been well addressed. These include the dehydration-responsive element (DRE) binding protein (DREB), ABA-responsive element (ABRE) binding protein/factor (AREB/ABF) and NAC (NAM, ATAF1/2, CUC2).

Transcription factors DREBs were reported to bind to the DRE (dehydration-responsive element)/CRT (C-Repeat) element which was identified as a *cis*-acting element regulating gene expression in response to salt, drought, and cold stresses in *Arabidopsis* [71]. Several DREBs have been identified in the rice genome based on genome-wide conserved sequences analysis and some are responsive to salinity stress. However, the regulatory mechanism of stress-responsive gene expression via DREB in rice is still unclear. Dubouzet et al. [72] isolated five DREB homologs in rice: *OsDREB1A*, *OsDREB1B*, *OsDREB1C*, *OsDREB1D*, and *OsDREB2A*. *OsDREB1* (*OsDREB1A, OsDREB1B, OsDREB1F* and *OsDREB1G*) and *OsDREB2A (OsDREB2A* and *OsDREB2B)* show similar functions to *AtDREB1* (*AtDREB1A, AtDREB1B* and *AtDREB1C*) in response to salt stress, indicating the functional conservation of DREB1 [72]. Further studies suggested that *OsDREB1F* might also be involved in the ABA-dependent pathway [73]. In addition to *DREB1s* and *DREB2s*, *OsDREB4-1* from the *DREB4* subgroup was found to be induced by high salt and was assumed to be a *trans*-acting factor in the DRE/DREB regulated stress-responsive pathway [74]. *OsDREB6*, an A-6 type of DREB, was hypothesized to participate in stress responses in both ABA-dependent and ABA-independent signal transduction pathways [75]. *SERF1*, belonging to group IIc ERFs of DREB subfamily, was reported to be a positive regulator of short- and long-term salt stress tolerance in rice [76] and could amplify the ROS-activated MAPK cascade signal in roots upon salt stress, which plays a dominant role in salt stress-induced root-to-shoot communication rather than ABA [76].

ABA, acting as a pivotal signal molecule in biotic and abiotic stress responses of plants, is required for full activation of AREB/ABF TFs [77]. AREB/ABF is a bZIP (basic leucine zipper) -type transcription factor, which can bind to the *cis*-acting elements responding to ABA [78]. Many *AREB*/*ABF*-homologous genes have been reported to be regulated by salt stress. Both *OsABF1* and *OsABF2* were positive regulators for abiotic stress responses and ABA-dependent signalling transduction pathways in rice [79,80]. Several other bZIP TFs, such as *OsbZIP23* [81], *OsbZIP46* [82], *OsbZIP72* [83], can bind to ABRE and are also suggested to be involved in ABA signal transduction and abiotic stress responses. AREB/ABF-SnRK2 (sucrose non-fermenting-1 related protein kinase 2) pathway plays a crucial role in ABRE-mediated transcription in response to osmotic stress in plants [84]. Three members of the rice subclass III SnRK2 protein kinase family, *OsSAPK8*, *OsSAPK9* and *OsSAPK10,* can be activated by ABA signal and hyperosmotic stress and directly phosphorylate a rice AREB/ABF, *OsTRAB1*, in response to ABA and hyperosmotic stress [85]. *OsSAPK9* positively regulates salt-stress tolerance and bacterial blight resistance by interacting with *OsSGT1* [86]. Two SnRK2 genes, *OsSAPK4* and *OSRK1*, improve salt tolerance in rice by regulating salt-responsive genes and functioning as the upstream regulators of stress signalling in rice [87,88]. A b-ZIP TF OsGATA8 has been shown to contribute towards multiple stress tolerance and seed development in *Arabidopsis* and rice [89].

The NAC gene family encodes plant-specific transcriptional regulators, which constitute one of the largest transcription factor families in plants [90]. Considerable efforts have been directed toward identifying NAC genes in rice, resulting in more than 150 NAC genes being confirmed [91]. *OsNAC* genes might play a crucial role in the crosstalk of different types of stress signalling genes via up-regulating stress responsive genes and thus enhancing salt tolerance [92]. *ONAC106* [93] and *ONAC022* [94] increase salt tolerance via activating stress-related TFs and genes such as *OsDREB2A*, *OsbZIP23*, and *OsLEA3*. In addition, many other rice *NAC* genes like *OsNAC5* [95], *ONAC045* [96] and *OsNAC2* [97,98] are also involved in salt stress response by transcriptionally activating the expression of stress-inducible rice genes like *OsLEA3* and/or *OsSAPK1*. To date, dozens of additional TFs involved in salinity tolerance have been identified in rice (Table 1) [99–120]. These genes triggered by salt stress conditions play crucial roles in signal transduction and regulating the expression of downstream functional genes that are involved in stomatal movement, ROS scavenging, compatible solutes synthesis, and ion transportation.

MicroRNA (miRNA), a kind of small non-coding RNA, regulates gene expression at post-transcriptional levels [121]. The verified targets of miRNAs encode a diverse range of regulatory proteins with approximately 66% of these targets are TFs [122]. The *miR164b* was found to target a rice TF *OsNAC2* [123]. Rice plants overexpressing the *miR164b*-resistant form of *OsNAC2* showed enhanced salinity tolerance [98]. Overexpression of *osa-MIR396c* [124] and *osa-MIR393* [125] in rice and *Arabidopsis* plants increased sensitivity to salinity stress via negatively mediating target growth-regulating factors and other regulatory proteins. Further studies revealed that the downregulation of two auxin-receptor genes *transport inhibitor response 1* (*OsTIR1*) and *auxin signalling f-box 2* (*OsAFB2*) contributed to reduced salinity tolerance in *OsmiR393*-overexpressing rice plants [126]. In addition, the expression of rice-specific *Osa-miR820* targeting *domain rearranged methyltransferase 2* (*OsDRM2*) was regulated by salinity stress [127]. Several other salinity-responsive miRNAs have been identified and characterized in rice [128]. Undoubtedly, further identification and validation of more salinity-responsive miRNAs will bring more alternatives for crop improvement.

3. Molecular mechanisms for salt tolerance in rice: functional adaptation

3.1. Stomatal regulation

High salinity causes low soil–water potential and reduces the ability of plants to take up water, resulting in a marked decrease in stomatal conductance to minimize water loss [129]. Stomatal aperture in response to salt stress is mainly mediated by ABA and H_2O_2, which function as signalling molecules [130]. ABA-independent *DST*-mediated pathway is also reported in rice. Loss-of-function mutation of *DST* in rice plants enhances drought and salt tolerance by reducing stomatal opening and stomatal density. *DST* can bind specifically to a novel *cis*-element (TGCTANNATTG) named DST-binding sequence (DBS). A series of ROS scavenging genes which contain two or three DBSs in promoter region such as *peroxidase 24 precursor* (*Prx 24*) can be directly regulated by *DST* under salt and drought treatment [131]. *DCA1* was subsequently characterized to be a *DST* co-activator in controlling stomatal aperture and regulation of downstream genes [132]. The DCA1-DST-Prx24 pathway contributing to stomatal movement via regulating ROS homeostasis under stress conditions was proposed (Fig. 2). In this model, DST and DCA1 form a heterologous tetramer which appears to regulate the expression of *Prx 24* in guard cells, thereby regulating H_2O_2 homeostasis and stomatal aperture and ultimately affecting abiotic stress response [132]. In addition to *Prx 24*, a leucine-rich repeat (LRR)-RLK gene named *Leaf Panicle 2* (*LP2*), which is also involved in regulating H_2O_2-induced stomatal closure, is transcriptionally regulated by DST [133]. More-

Table 1
Major families of transcript factors regulating salinity tolerance in rice.

Gene name	Method of validation	Phenomena in transgenic plants and function roles	References
Zinc finger TFs			
ZFP252	Overexpression	Enhanced salt tolerance, accumulation of free proline and soluble sugars, regulation of stress-responsive genes	Xu et al. [99]
ZFP177	Overexpression	Increased salt sensitivity, inhibited expression of stress-related genes	Huang et al. [100]
ZFP182	Overexpression	Enhanced salt tolerance, accumulation of free proline and soluble sugars, regulation of stress-responsive genes, interaction with ribosomal proteins	Huang et al. [101]
ZFP185	Overexpression	Increased salt sensitivity, decreased GA and ABA biosynthesis	Zhang et al. [102]
ZFP179	Overexpression	Enhanced salt tolerance, accumulation of free proline and soluble sugars, regulation of stress-responsive genes, increased ROS-scavenging ability	Sun et al. [103]
OsCOIN	Overexpression	Enhanced salt tolerance and proline level	Liu et al. [104]
OsTZF1	Overexpression	Enhanced salt tolerance, delayed leaf senescence	Jan et al. [105]
MYB-type TFs			
OsMYB91	Overexpression	Enhanced salt tolerance, increased ROS-scavenging ability, increased proline levels	Zhu et al. [106]
OsJAMyb	Overexpression	Enhanced salt tolerance, regulation of genes involved in osmotic adjustment, ROS removal, and ion homeostasis	Yokotani et al. [107]
OsMYBc	Knockout	Increased salt sensitivity, reduction in NaCl-induced expression of *OsHKT1;1*	Wang et al. [108]
OsMYB6	Overexpression	Enhanced salt tolerance, higher proline content, higher CAT and SOD activities	Tang et al. [109]
OsMYB3R-2	Overexpression	Enhanced salt tolerance, regulation of stress-responsive genes	Dai et al. [110]
WRKY-type TFs			
OsWRKY13	Overexpression	Increased salt sensitivity, suppression of *SNAC1* and *ERD1*	Qiu et al. [111]
OsWRKY42	Overexpression	Enhanced salt tolerance, regulation several genes involved in JA biosynthesis	Pillai et al. [112]
OsWRKY45-2	Overexpression	Reduced salt tolerance, regulation of ABA signalling	Tao et al. [113]
OsWRKY72	Overexpression	Increased salt sensitivity, interacted with ABA signal and auxin transport pathway	Song et al. [114]
MADS-box type TFs			
OsMADS25	Overexpression	Enhanced salt tolerance, higher free proline content, lower MDA accumulation	Xu et al. [115]
OsMADS27	Overexpression	Enhanced salt tolerance, promoted $NO3^-$ accumulation, regulation of ABA sensitivity	Chen et al. [116]
bHLH TFs			
OsbHLH001	Overexpression	Enhanced salt tolerance, increased expression of *OsAKT1* to regulate the Na^+/K^+ ratio	Chen et al. [117]
OrbHLH2	Overexpression	Enhanced salt tolerance, upregulation of stress-responsive genes	Zhou et al. [118]
OsbHLH035	RT-PCR, Mutation	Enhanced recovery after salt stress, regulation of ABA metabolic genes and *OsHKT1* genes	Chen et al. [119]
OsbHLH068	Overexpression	Enhanced salt tolerance, lower level of MDA and ROS	Chen et al. [120]

over, a rice SIMILAR TO RCD ONE (SRO) protein, *OsSRO1c*, was reported to promote stomatal closure and H_2O_2 accumulation under drought and oxidative stresses through a novel pathway involving the *DST* regulator [134]. Although *abscisic acid-, stress and ripening-induced protein 5* (*OsASR5*) was characterized to modulate stomatal closure via controlling the H_2O_2 accumulation through the ABA-dependent pathway, suppression of *DST* and its downstream gene *Prx* 24 was found in *OsASR5* overexpressing plants [135]. The RING Finger Ubiquitin E3 Ligase *heat tolerance at seedling stage* (*OsHTAS*) was found to be strongly induced by exogenous ABA and be responsive to multiple abiotic stresses including salinity stress by involving in both ABA-dependent and DST-mediated stomatal closure [136].

There are some other genes that have been identified to be involved in stomatal movement in rice under salt stress. The *salt and drought inducible ring-finger 1* (*OsSDIR1*) was up-regulated under drought and high salinity [137]. Overexpression of *OsSDIR1* result in enhanced tolerance to water deficit in plants by decreasing water loss as mediated via stomatal closure response to water deficit. Further analysis indicated that the *SDIR1* is both conserved and function-diverse in monocotyledons and dicotyledons [137]. *OsGPX3*-RNAi silenced rice plants are hypersensitive to salt stress with decreased stomatal conductance, indicating that *glutathione peroxidase 3* (*GPX3*) may mediate salt stress tolerance via an independent ROS-scavenger mechanism in rice [56].

Stomatal conductance and overall water use efficiency (WUE) under hyperosmotic conditions could be controlled not only by the changes in the stomata aperture per se but also via developmental control of stomata density. Overexpressing the rice epidermal patterning factor *OsEPF1* resulted in plants with substantially reduced stomatal density and correspondingly low stomatal conductance that were more WUE and tolerant to drought [138]. Also, the loss of DST function not only increased stomatal closure but also reduced stomatal density, consequently resulting in enhanced drought and salt tolerance in rice [131]. Thus, it appears that reducing stomata density comes with the same beneficial role for salinity tolerance not only in halophytes [129] and salt-tolerant glycophytes such as barley [139] but also in salt-sensitive glycophytic rice.

3.2. Osmotic adjustment

High salinity causes severe osmotic stress in plants, leading to inhibition of water and nutrient uptake, cell elongation, and leaf development [140]. Three major mechanisms, including maintaining water uptake, preventing water loss, and osmotic adjustment in exposed tissues, can be activated to alleviate osmotic stress.

Plant aquaporins are ubiquitous water channel proteins that play a distinct role in water transportation across cell membranes [141]. Over 30 rice aquaporin genes composed of 12 plasma membrane intrinsic proteins (PIPs), 10 tonoplast intrinsic proteins (TIPs), 10 nodulin26-like intrinsic proteins (NIPs) and two small basic intrinsic proteins (SIPs) have been identified in the rice genome [142] and facilitate water flux and maintenance of the water potential in different tissues and cells [143]. However, only a few of them respond to salt response. For instance, rice TIPs were significantly up-regulated by high salinity in both shoots and roots [144]. The expression of *OsPIP 1–3* was induced by salt treatment in leaves and roots of two-month-old rice seedlings [145]. Moderate expression of *OsPIP1;1* elevated rice salt tolerance and water conductance [146].

The synthesis and accumulation of compatible solutes (proline, glycine betaine, trehalose, polyols, etc.) is essential for balancing the osmotic pressure induced by high salinity [147]. The biosynthesis of these compatible solutes is often associated with salinity tolerance in rice [148]. Both the exogenous application of these compatible solutes or overexpression of appropriate genes

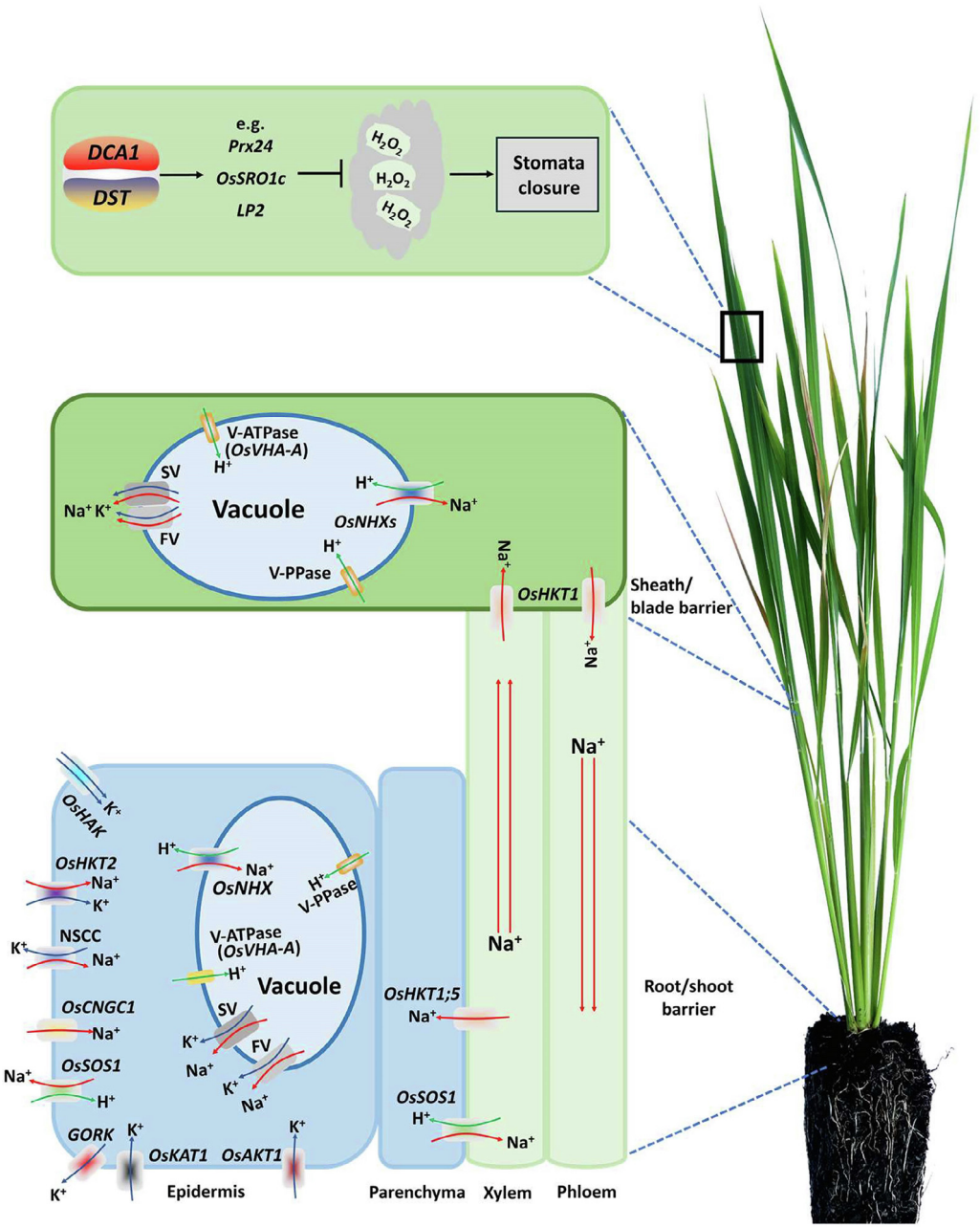

Fig. 2. The gene networks regulating stomata closure and ion transportation under salinity stress of rice. In leaves, DCA1 and DST complex binds to genes regulating H_2O_2 homeostasis such as *Prx24*, *OsSR01c*, and *LP2*, thereby influencing stomatal closure under salinity stress. Na^+ uptake in the root epidermis is regulated by nonselective cation channels including cyclic nucleotide-gated channels. *OsHKT2;1* also plays an important role in Na^+ uptake. The outward-rectifying K^+ efflux GORK channels are central to salinity stress-induced K^+ loss. The cellular Na^+/K^+ homeostasis is regulated by active Na^+ efflux channels via SOS1 Na^+/H^+ exchangers and K^+ influx channels controlled by *OsHAKs*, *OsKAT1*, and *OsAKT1*. Na^+ loading into the xylem is mediated by *OsSOS1* while Na^+ withdrawal from the xylem is achieved by high-affinity K^+ transporter OsHKT1;5. *OsHKT1* genes control both Na^+ unloading from the xylem and Na^+ loading into the phloem in leaves for Na^+ recirculation. Vacuolar Na^+ sequestration is conferred by *OsNHXs* fueled by either V-ATPase or V-PPase H^+ pumps. Slow-vacuolar (SV) ion channels and fast-vacuolar (FV) ion channels allow Na^+ and K^+ to leak back to the cytosol from vacuole.

involved in osmolyte biosynthesis could improve salt tolerance in rice [149]. In plants, trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP) are involved in catalysing the biosynthesis of trehalose. Overexpression of *OsTPS1* enhanced salt tolerance of rice seedling by increasing trehalose and proline concentrations and up-regulating stress-associated genes [67]. Another rice TPS gene *OsTPS8* was characterized to control salinity stress tolerance as well as several key agronomic traits in rice [150]. *OsTPS8* influences salinity tolerance via controlling the amount of soluble sugars and regulating the expression levels of genes involved in ABA signalling via the regulation of SAPK9 – a sucrose non-fermenting 1-related kinase 2. Overexpression of *OsTPP1* increased the tolerance of rice to salinity by activating stress response genes, including *OsTPS1*, rather than by regulating trehalose content [151]. Increase in trehalose in rice has also been found to enhance tolerance in a high yielding rice IR64 towards drought, salinity and sodic conditions [152]. Use of ABA-inducible promoter in marker free constructs have been found useful in the case to drive the expression of trehalose biosynthesis genes to avoid energy drain under non-stress condition in plants and to minimize the number of foreign genes. Some other genes such as *betaine aldehyde dehydrogenase 1* (*OsBADH1*) [153] and *cho-*

line monooxygenase (*OsCMO*) [154] are reported to function in increasing glycine betaine accumulation to enhance salt tolerance.

While the role of organic osmolytes in plant osmotic adjustment has been well established, their *de novo* synthesis comes with a high energy cost [155]. Hence, halophytes and salt-tolerant glycophyte species use organic osmolytes for osmotic adjustment in the cytosol only, while the bulk of osmotic adjustment in the vacuole is achieved by means of inorganic osmolytes [156,157]. Given the lack of any major progress in developing salt-tolerant rice cultivars, targeting this trait and breeding rice for halophytism may represent a previously unexplored avenue. It anticipated that use of stress inducible promoters and marker-free constructs could be a step forward towards commercialization of products as proposed [152].

It is also important to mention that the role of these compatible solutes is not limited to a merely osmotic adjustment. In this context, enhanced *OsP5CS1* gene expression that results in increased proline accumulation is involved in both calmodulin and ABA signalling cascades [158]. Some compatible solutes may also operate as highly potent ion channel regulators. Choline was found to function as a potent slow-activated vacuolar (SV) channels blocker, thus enabling efficient Na^+ sequestration and osmotic adjustment in vacuole under salinity stress [159]. Moreover, compatible solutes have been suggested to be essential for alleviation or prevention of oxidative stress [160]. Salinity-induced accumulation of organic osmolytes in barley and wheat leaves correlated with increased oxidative stress tolerance [161]. Overexpression of a myo-inositol oxygenase (*OsMIOX*) in rice increased free proline contents and ROS-scavenging ability under drought stress, thus improving rice drought tolerance [162].

3.3. Ion homeostasis

Salinity stress is usually associated with an excessive amount of NaCl. Traditionally, the second constraint imposed by salinity is called "ion toxicity" or "ionic stress" [163]. Recently, Zhao et al. [34] proposed that the term "ionic imbalance" is more appropriate as excessive Na^+ and Cl^- accumulation interferes with the influx or metabolism of other essential ions like K^+ rather than causing nutrient toxicity *per se*. Not surprisingly, more than half of studies concerning salt stress focused on revealing the mechanisms of ion (mainly Na^+ and K^+) transport in plants. In the past few decades, many reviews have been published on the mechanisms of how plants regulate ion homeostasis under salt stress and their significance [164–167]. Several key mechanisms such as Na^+ efflux from uptake, vacuolar Na^+ sequestration, xylem Na^+ loading and retrieval from the shoot, and K^+ retention in the cytosol confer plant ionic homeostasis under saline conditions (Fig. 2). Here, we focus on key transporters regulating the above processes in rice.

Two major mechanisms for Na^+ entering the root are via nonselective cation channels (NSCCs) and high-affinity K^+ transporters (HKT) [168]. Two families, cyclic nucleotide-gated channels (CNGCs) and glutamate-like receptors (GLRs), have been suggested to be the candidates for non-selective cation channels. In rice, most of the *CNGCs* were reported to be induced by multiple stimuli including biotic and abiotic stresses [169]. However, the operational modes and the roles of specific rice *CNGC* and *GLR* channels remain elusive. Rice *HKT* family consists of nine genes which can be divided into two subfamilies based on amino acid sequence similarity and differences in Na^+ and K^+ transport capacity [170]. *OsHKT2;1* was reported to mediate the nutritional Na^+ influx in K^+-starved rice roots [171]. *OsHKT2;1* plays an important role in Na^+ uptake and is a key sodium transporter affecting K^+ use efficiency [172]. However, under sufficient K^+ supply, *OsHKT2;1* enhances the accumulation of Na^+ only in roots, suggesting that other Na^+ transporters might be involved in transporting Na^+ from roots to shoots [173]. The *HKT* Subfamily 2 member, *OsHKT2;2*, which shows close homologous to *OsHKT2;1* is present in an *indica* landrace Pokkali but absent in a *japonica* cultivar Nipponbare [170], functions as a Na^+-K^+ cotransporter, showing K^+-stimulated Na^+ influx and Na^+-stimulated K^+ influx [174,175].

In general, plants should exclude 98% of the salt back into the soil solution to maintain growth thus salt exclusion is the most important adaptive feature mediating the internal salt load of plants [156]. The plant plasma membrane Na^+/H^+ antiporter gene, *SOS1*, preferentially expressed in the root tip epidermis cells and xylem parenchyma cells, is the unique Na^+ efflux transporter that has been characterized to date in *Arabidopsis* [176]. In rice, the *OsSOS1* was recently reported to mediate both net root Na^+ uptake and Na^+ redistribution between roots and shoots at the xylem-parenchyma boundary [177] and partially regulate Na^+ efflux [178]. However, it is also suggested that the wild alleles of SOS1 have been lost during domestication in tomato making them salinity sensitive [179]. Such studies for other key genes for ion sequestration in rice plants will be very useful towards rewilding them for salinity tolerance.

The vacuolar Na^+ sequestration also reduces cytosolic Na^+ load and is mediated by the tonoplast NHX. In rice, *OsNHX1* plays a crucial role in this process [180]. *OsNHX2*, *OsNHX3*, and *OsNHX5* were subsequently identified based on sequence search and characterized for function in Na^+ compartmentation [181]. In plants, the tonoplast- and the plasma membrane-based Na^+/H^+ antiporters are energized by two H^+-pumps, vacuolar H^+-inorganic pyrophosphatase (V-PPase) and vacuolar H^+-ATPase (V-ATPase) [182]. Transgenic rice plants expressing a vacuolar H^+-ATPase subunit c1 gene (*SaVHAc1*) from the halophyte grass *Spartina alterniflora* showed enhanced salt tolerance and up-regulated *OsNHX1* activity in roots [183]. *OsPLDα1* regulated salt tolerance via activating tonoplast H^+-ATPase *OsVHA-A*, the plasma membrane H^+-ATPase *OSA2*, and *OsNHX1* [184].

Apart from *OsSOS1*, several other transporters have been characterized to function in the xylem Na^+ loading, its retrieving and recirculation in the phloem. The *OsHKT1;5*/*SKC1* was hypothesized to regulate K^+/Na^+ homeostasis under salt stress through unloading Na^+ from the xylem in rice [185] although direct measurements of Na^+ transport in root stele have questioned this hypothesis [186]. *OsHKT1;5* also plays an important role in Na^+ exclusion from leaves via mediating Na^+ unloading via the phloem [187]. *OsHKT1;1*, which is regulated by *OsMYBc*, controls both Na^+ unloading from the xylem and Na^+ loading into the phloem in leaves for Na^+ recirculation [108]. *OsHKT1;4* mediates xylem Na^+ unloading in both leaf sheaths and stems, particularly at reproductive stage in rice [188].

Potassium, an essential ion for plant growth, plays a key role in salt tolerance regulation as the cytosolic K^+/Na^+ ratio appears to determine plant salt tolerance [164,189]. To alleviate the constraints of salt-induced Na^+ accumulation in the cytosol and K^+ efflux from root, plants need to active high-affinity K^+-uptake systems. To date, several genes encoding root K^+ uptake channels have been identified in rice. Among them, *OsAKT1* [190] and *OsKAT1* [191] are involved in salinity response via maintaining a low Na^+/K^+ ratio due to the increase of K^+ uptake. Other high-affinity K^+ transporters (*HAKs*), such as *OsHAK1* [192], *OsHAK5* [193], and *OsHAK21* [194], also play important roles in maintaining high K^+/Na^+ ratios under salt stress by activating K^+ uptake.

4. Breeding for improved salinity tolerance in rice

4.1. Mining of salt-tolerance in rice germplasm resources

Rice possesses a very broad, natural genetic diversity within both the species and genus. More than 130,000 rice accessions

including cultivated species, wild relatives and related genera species are being preserved at the International Rice Genebank at the International Rice Research Institute (IRRI) (https://www.irri.org/international-rice-genebank), providing a rich source of natural diversity. So far, thousands of rice genotypes have been screened for salt tolerance using various parameters with a bias towards seedling stage [195]. Different indicators have been used to evaluate salinity stress tolerance. These include germination rate (GR) and germination index (GI) [196], plant survival, salt injury score and plant biomass at whole-plant level [197]. Various whole-plant physiological indicators such as chlorophyll content, Na^+ and K^+ concentration in shoots and roots [198], relative growth rate (RGR), transpiration rate (TR) and WUE were also applied to plants at the vegetative growth stage [199]. Also, multiple yield-related parameters including spikelet number per panicle, spikelet fertility, tiller number per plant and yield per plant were employed as indices of salt tolerance [200]. These studies revealed a broad range of genetic variability in salinity tolerance amongst accessions of *O. sativa* and *O. glaberrima* [201]. Some Indian wild rice accessions comprising *O. rufipogon* and *O. nivara* also had moderate tolerance to salinity [202]. However, most of the treatments are conducted under varying salt levels and at seedling-stage with a relatively short period of (10–14 days) salinity treatments, when the osmotic component of the salt stress dominates [163], and specific ion toxicity is not readily apparent. At the same time, appropriate isotonic controls are also missing from most of these reports. Most recently, two seawater adapted rice landraces, Changmaogu [203] and Sea Rice 86 [204], discovered from coastal areas in China, have drawn wide attention. Changmaogu showed stronger tolerance to salinity than Pokkali at the germination stage with a germination rate of 18.7% in 140 mmol L^{-1} (~0.8%) NaCl treatment [203]. Sea Rice 86 showed 98% germination inhibition at 0.8% NaCl salinity, and no germination at concentrations higher than that [204]. Salinity stress tolerance was present in wild rice relatives but has been lost during domestication [205]. Recent research from an extreme halophyte species *Oryza coarctata* with the KKLL genome appears to be more promising [206]. Understanding the molecular and physiological mechanisms of its superior tolerance to salt may open the potential to introduce some key traits into breeding programs [207]. For instance, some allele mining studies have shown that a single base addition resulting in the frame shift for 37 amino acids in the L-myo-inositol 1-phosphate synthase (MIPS) protein is capable of increasing salinity tolerance in rice, a unique example of molecular adaptations contributing to salinity tolerance [208].

In addition to natural variation, several mutants have been identified for salinity tolerance in rice. The *dst* mutant was isolated after screening >270,000 ethyl methanesulfonate (EMS)-mutagenized M2 rice seedlings of Zhonghua 11 at 140 mmol L^{-1} NaCl. The key gene *Drought and Salt Tolerance* (*DST*), encoding a zinc finger transcription factor that controls stomatal aperture via direct modulation of genes related to H_2O_2 homeostasis in guard cells, was found to be a negative regulator of drought and salt tolerance in rice [131]. A salt-tolerant mutant *hitomebore salt tolerant 1* (*hst1*) was selected from 6000 EMS mutant lines of a local elite cultivar 'Hitomebore'. The loss-of-function of *OsRR22*, which acts in cytokinin signalling, was found to be responsible for the salinity-tolerance phenotype of *hst1* [209].

4.2. Mapping of QTL/genes for salt tolerance in rice

Over the past two decades, a large number of quantitative trait loci (QTL) linked to salinity tolerance have been identified in rice. Yet, only a few QTL showing significant effects have been successfully isolated or fine-mapped. Two major QTL, *qSNTQ-7* for shoot Na^+ concentration (SNC) and *qSKC-1* for shoot K^+ concentration (SKC), were identified from a cross between salt-tolerant Nona Bokra and salt-susceptible Koshihikari [210]. The *qSKC-1* on chromosome 1 explained 40.1% of total phenotypic variation and was further fine mapped and isolated. The original functional analysis revealed that the *SKC1* gene encodes an HKT-type transporter (*OsHKT1;5*), which is preferentially expressed in the parenchyma cells surrounding the xylem vessels in rice and regulates K^+/Na^+ homeostasis under salt stress [185]. However, more recent electrophysiological data showed that Na^+ reabsorption occurred in wild type but not in NIL(SKC1) plants, thus questioning the functional role of *Os*HKT1;5 as a transporter operating in the direct Na^+ removal from the xylem [186]. Instead, changes in the expression level of *OsHKT1;5* altered the activity of membrane transporters involved in K^+ and Ca^{2+} acquisition and homeostasis in the rice epidermis and stele, implying a complex feedback regulation of activities of other transporters involved in the maintenance of plant ionic homeostasis and signalling under stress conditions. Another notable QTL *Saltol* associated with the shoot Na^+/K^+ ratio at the seedling stage was identified from a salt-tolerant landrace Pokkali [211]. The *SKC1* gene (*OsHKT1*;5) was suggested to be the functional gene underlying the *Saltol* segment [212]. Transcript abundance analysis on corresponding genes within this QTL using contrasting rice genotypes revealed that the levels of transcripts for the genes encoding the transcription factors (TFs) and signalling related genes were constitutively higher in the landrace than a salt-sensitive high yielding rice cultivar IR64. The salinity tolerant landrace was able to induce expression of these genes even during late phases of salinity treatment while the sensitive IR64 showed a decline in transcript abundance after a few hours of stress [213,214]. In rice, *histone-gene binding protein* (*OsHBP1b*) and zinc-finger transcription factor (*OsGATA8*), both located in the *Saltol* QTL region, also play an important role in seedling salt tolerance by regulating the expression of several genes related to chlorophyll biosynthesis, ion homeostasis, reactive oxygen species (ROS) scavenging and stress tolerance [89,215]. Considering its importance and role in seedling level salinity tolerance, attempts have been made to introgress *Saltol* to a high yielding but salinity sensitive rice Pusa Basmati 1121 [216]. The study showed enhanced tolerance towards salinity in the recipient, raising hopes for the successful breeding of salinity tolerant, high-yielding rice using marker assisted selection. The QTL *qST1.1* for seedling salinity tolerance identified from Sea Rice 86 was located within the *Saltol* region with the amino acid sequence of *SKC1* (*OsHKT1;5*) of Sea Rice 86 being the same as that in Nona Bokra [217]. The *qSE3* QTL isolated from a Chinese landrace Jiucaiqing was found to function as a high-affinity K^+ uptake transporter (*OsHAK21*), facilitating seed germination and seedling establishment under salinity stress [218]. Increasing both K^+ and Na^+ uptake and abscisic acid (ABA) levels and reducing ROS levels were suggested to be the main physiological mechanisms of *qSE3*. Through genome-wide meta-analyses of QTL for various traits associated with rice salt tolerance [219,220] and integrative meta-analysis for rice salinity tolerance [221] revealed more than 20 candidate genes in *Saltol* and nearly 20 meta-QTL regions.

Compared to the seedling stage, there are limited reports on QTL mapping for salt tolerance during the reproductive stage. A QTL for Na^+ uptake and Na^+/K^+ ratio in the shoot at reproductive stage was found to be located on chromosome 1 at a different position to *Saltol* [222]. Three QTL on chromosome 1 at positions 32.3, 35.0, and 39.5 Mb were identified for grain yield per plant under salinity stress from a salinity-tolerant *indica* rice variety CSR11

[223]. Two QTL, *qDEG-S-2-2* for spikelet degeneration and *qSSI-STE-2-1* for spikelet sterility, were mapped on chromosome 2, accounting for 34.4% and 38.8% phenotypic variances, respectively, with tolerance alleles from Pokkali [224].

The genome-wide association study (GWAS) approach could offer a powerful strategy for dissecting the genetic architecture of various complex traits and identifying allelic variations of candidate genes in rice [225] and other cereal crops. GWAS has also been implemented in trait-associated loci for salt tolerance. The *Saltol* QTL region (affecting Na^+/K^+ ratio at rice seedling stage) was also responsible for balancing Na^+/K^+ ratio at reproductive stage [226]. Another major QTL, *RNC4*, which controls root Na^+/K^+ ratio and root Na^+ content under moderate salinity stress, was identified in a ~575 kb region on chromosome 4 [227]. The sodium transporter gene *OsHKT1;1* is located in this region mediating root Na^+ content and underlaying the divergence between *indica* and *japonica* rice subspecies. A set of specific genes involved in the ubiquitination pathway have been proposed to play an important role in salt tolerance [228]. From a large collection of 478 rice accessions, two auxin-biosynthesis genes were identified as candidate genes for salinity tolerance [229]. More recently, 15 promising candidate genes including transcription factors and cation transporters were found to be associated with grain yield and its related traits under saline stress conditions [200]. QTL for salt tolerance on chromosome 1 (surrounding 40 Mb) were detected underlying several salt-related traits in diverse rice species including cultivated varieties, landraces and wild rice [223,230–233]. Several candidate genes, such as a high-affinity K^+ transporter gene *OsHAK6* and two small ubiquitin-like protein modifier (SUMO) genes (*OsSUMO1* and *OsSUMO2*) located at this region, were speculated to be involved in salinity tolerance [232,233].

4.3. Allele/haplotype mining

Genes/QTL for salt tolerance show allelic variations among different genotypes. Identifying favorable or effective alleles for different genes/QTL is the pre-condition for unlocking the full potential of salt-tolerant genes/QTL in breeding programs. Useful alleles of genes encoding CaM, late embryogenesis abundant protein (*LEA3*), and salt-inducible rice gene (*Sal* T) were identified from different rice genotypes including cultivated and wild species [234]. Allelic variants in coding sequence (CDS) for five key salt-associated genes, *calcium-dependent protein kinase 17* (*OsCPK17*), *root meander curling* (*OsRMC*), *Na^+/H^+ antiporter 1* (*OsNHX1*), *OsHKT1;5* and *Sal* T in 392 *O. sativa* accessions were also reported [235]. Six ecotypic variants of *OsHKT2;1* were identified with the new HKT isoform, No-*OsHKT2;2/1* in Nona Bokra, contributed to salinity tolerance [175]. Ten alleles for the *OsHKT1;5* gene exist in *O. sativa* species with the *Aromatic* allele showing the lowest leaf Na^+ concentration [201]. Yang et al. [236] revealed that the haplotypes of *$HKT1;5^{NB}$* (*OsHKT1;5* from Nona Bokra) representing the "His" amino acid at the 184th position showed the lowest Na^+ concentration in straws. These two alleles of *OsHKT1;5* provide conducive information in breeding programs when choosing the best donor. Re-sequencing of the eight *HKT* type genes from 103 rice accessions including 95 Indian wild species revealed novel salt-tolerant alleles of *HKT1;5* and *HKT2;3* [202]. Recent advantages in high-throughput genotyping strategies have enhanced the power of allele mining. In 2014, the "3000 rice genomes project (3K RGP)" [237] was set up to sequence 3000 cultivated rice accessions representing global genetic and functional diversity. In the past few years, this set of germplasm has been widely applied in QTL mapping and allele mining for diverse traits including salt tolerance in rice [200,227]. The database named RFGB v2.0 (http://www.rmbreeding.cn/Index/) was newly constructed for online allele-mining analysis in rice [238]. The identification of favorable alleles of different genes/QTL for salt tolerance will help exploit more useful information for breeding salt tolerance varieties.

4.4. Approaches for breeding salinity tolerance rice

Developing rice varieties with salinity tolerance is the most direct and efficient way of solving the problem of yield losses. However, so far all attempts to improve the salinity tolerance of rice have received limited success, with rice remaining the most salt-sensitive species amongst cereals. Many rice varieties have been developed for saline and alkaline areas worldwide by conventional methods [239], yet their threshold of salinity tolerance remains relatively low. In the last few decades, rice breeders preferred the strategy of obtaining better Na^+ exclusion or lower tissue Na^+/K^+ ratio as a proxy for salinity tolerance, losing sight of other important tolerant mechanisms discussed above [205]. These new varieties do not possess similar levels of salinity tolerance to their donor parents [240]. Also, salinity tolerance of most of these varieties are specific only for a particular region or environment due to the complex nature of climatic and soil conditions [241].

QTL based marker assisted selection (MAS) and marker assisted backcrossing (MABC) have been proven to be successful in crop molecular breeding. The *Saltol* QTL derived from Pokkali, which is responsible for shoot Na^+/K^+ homeostasis, has been successfully introgressed into commercial varieties via MAS and MABC [239]. Similarly the introgression of the *OsRR22* gene identified from the salinity-tolerant mutant *hst1* to the elite cultivar Hitomebore [209] and a high-yielding cultivar Yukinko-mai [242] has improved salinity tolerance at both seedling and reproductive stages. However, most of the QTL/genes were trait specific and growth stage specific, pyramiding multiple genes would be practical in improving salinity tolerance at different growth stages for various environments. Based on trait-specific introgression lines (ILs) in target backgrounds developed via MABC, designed QTL pyramiding has been successfully practiced for improving rice salinity tolerance at IRRI and in China [243,244]. This unique strategy could integrate specific traits/QTL from diverse salinity-tolerant donors into single target background or cultivar.

Although MAS and MABC have been routinely used in rice salinity-tolerance breeding, the limitation known as 'linkage drag' still exist. Transgenic approach is another potential way of achieving salinity tolerance in rice. Almost all the mechanisms discussed above have been brought into genetic modification programs to improve salinity tolerance in rice. However, transgenic approaches have mostly been performed on single genes and for one of the tolerance mechanisms. This limits success in significantly improved salinity tolerance, in particular, the tolerance during the reproductive stage. The emerging CRISPR/Cas9-based genome editing technology, which includes knockout, base editing, allele exchange, is an alternative approach for accelerating crop breeding. Knock out of *OsRR22* or *OsSPL10* gene using the CRISPR/Cas9 editing system enhanced salinity tolerance in rice [245,246]. This technology also provides an effective tool for the identification and use of miRNAs regulating stress tolerance. Knock out of *OsmiR535* via CRISPR/Cas9 knockout system in rice enhanced the tolerance to salinity, ABA, and dehydration stresses [247]. A further critical advantage of genome editing technology is the possibility to modify several sites simultaneously. For example, three grain weight-related genes (*GW2*, *GW5*, and *TGW6*) were simultaneously mutated in rice via the CRISPR/Cas9-mediated multiplex genome editing system,

demonstrating that trait/gene pyramiding could be rapidly generated [248]. Similar to genetically modified organisms (GMO), genome-edited plants may also have limitation in commercial use due to various classifications and regulation procedures [249].

5. Conclusions and perspective

To date, large numbers of genes involved in various salt-tolerant mechanisms in rice have been identified (Table S1). Understanding their function and crosstalk at molecular level could provide valuable information for improving salt tolerance in rice. In this review, we present the current understanding of the gene networks responsive to salinity stress in rice. Several gene families and interaction networks of salt responsive signaling components, functional genes and TFs have been uncovered. For instance, the SOS signalling pathway controls Na^+ efflux; the DCA1-DST-Prx24 pathway mediates stomatal movement; the AsA-GSH recycling pathway confers ROS scavenging; *OsNHX* and *OsHKT* families' function in ion homeostasis; TFs families regulate downstream salt-induced genes. Modifying salinity tolerance by targeting this signaling networks may be promising but challenging, as this might have pleiotropic effects on various developmental and adaptive tolerance mechanisms. We are still far from having a clear picture of the crosstalk between different genes and pathways regulating salt tolerance in rice as most of these insights are acquired from studies on *Arabidopsis* using reverse genetic approaches. Even though Na^+ transport processes like SOS pathway, *NHX* genes, and *HKT* genes identified in *Arabidopsis* do operate similarly in rice, the results regarding Na^+ tolerance in *Arabidopsis* should be extrapolated to rice with care [250]. Development and use of the tremendous, existing genetic resources and their variations within rice species (especially wild rice relatives) must complement the work in *Arabidopsis*. Moreover, a majority of the functional analyses are based on whole-plant level with only a few reports focused on tissue- and/or cell-specific expression in rice [178,186–188,251]. More details of salt-responsive channel and transporter activities at tissue- and cell-specific level still need to be revealed before such understanding can meaningfully guide breeding programs.

In the past few decades, limited progress has been made in developing real salt-tolerance rice varieties duo to lack of both genetic resources with high salinity tolerance and reliable salinity-tolerance genes/QTL with large effects. Most of the research efforts on salinity have also been biased towards seedling-stage tolerance instead of reproductive-stage tolerance which ultimately determines grain yield [128]. Breeding strategies would benefit from more targeted efforts of integrating mechanisms resulting in adult plant salinity tolerance. Although a number of transgenic rice lines with enhanced salt tolerance have been obtained, none of them have been successfully released or commercialized. The precise genome editing technology has shown a high potential in developing salinity tolerant rice cultivars. Approaches using target editing of miRNAs and genes involved in stress signalling cascades and transcriptional networks are promising strategies in rice salinity tolerance breeding. Future studies should also focus on diversity of available genetic resources and, in particular, wild rice relatives, to re-incorporate salinity tolerance traits lost during domestication. Moreover, mining favorable alleles/haplotypes associated with salinity tolerance and combining them seems to be a more effective approach to germplasm improvement. Similarly, breeders should target the multi-stress responsive genes via stress inducible promoter and marker free constructs. An important next step would be to test the genetically engineered plants under field conditions to evaluate their stress tolerance [7] and then model their responses in order to obtain a global assessment of the likely impact of such improved varieties.

CRediT authorship contribution statement

Tianxiao Chen: Writing - original draft, Visualization. **Sergey Shabala:** Conceptualization, Writing - review & editing, Conceptualization. **Yanan Niu:** Visualization. **Zhong-Hua Chen:** Writing - review & editing. **Lana Shabala:** Writing - review & editing. **Holger Meinke:** Writing - review & editing. **Gayatri Venkataraman:** Writing - review & editing. **Ashwani Pareek:** Writing - review & editing. **Jianlong Xu:** Conceptualization, Funding acquisition, Project administration, Writing - review & editing. **Meixue Zhou:** Conceptualization, Funding acquisition, Project administration, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data for this article can be found online at https://doi.org/10.1016/j.cj.2021.03.005.

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