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ROS Regulation During Abiotic Stress Responses in Crop Plants

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Abiotic stresses such as drought, cold, salt and heat cause reduction of plant growth and loss of crop yield worldwide. Reactive oxygen species (ROS) including hydrogen peroxide (H_2O_2), superoxide anions ($O_2^{\bullet-}$), hydroxyl radical ($OH\bullet$) and singlet oxygen ($^1O_2$) are by-products of physiological metabolisms, and are precisely controlled by enzymatic and non-enzymatic antioxidant defense systems. ROS are significantly accumulated under abiotic stress conditions, which cause oxidative damage and eventually resulting in cell death. Recently, ROS have been also recognized as key players in the complex signaling network of plants stress responses. The involvement of ROS in signal transduction implies that there must be coordinated function of regulation networks to maintain ROS at non-toxic levels in a delicate balancing act between ROS production, involving ROS generating enzymes and the unavoidable production of ROS during basic cellular metabolism, and ROS-scavenging pathways. Increasing evidence showed that ROS play crucial roles in abiotic stress responses of crop plants for the activation of stress-response and defense pathways. More importantly, manipulating ROS levels provides an opportunity to enhance stress tolerances of crop plants under a variety of unfavorable environmental conditions. This review presents an overview of current knowledge about homeostasis regulation of ROS in crop plants. In particular, we summarize the essential proteins that are involved in abiotic stress tolerance of crop plants through ROS regulation. Finally, the challenges toward the improvement of abiotic stress tolerance through ROS regulation in crops are discussed.

Keywords: crop plants, transcription factors, reactive oxygen species, abiotic stress, antioxidative enzymes, gene regulation

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INTRODUCTION

Abiotic stress conditions such as drought, heat, or salinity affect plant growth and reduce agricultural production worldwide. These reductions result from climate change and the freshwater-supply shortage as well as the simultaneous occurrence of different abiotic stresses (Mittler and Blumwald, 2010; Hu and Xiong, 2014). To meet the demands of food security in the face of an increasing world population and environmental challenge, scientists envisage a crucial need for a "second green revolution" to enhance crop

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Abbreviations: ABA, abscisic acid; AOX, alternative oxidases; APX, ascorbate peroxidase; AsA, ascorbic acid; ASR, ABA-, stress-, and ripening-induced; BR, brassinosteroid; CCaMK, calcium/calmodulin-dependent protein kinase; CDPK, calcium-dependent protein kinase; CIPK, calcineurin B-like protein-interacting protein kinase; DHAR, dehydroascorbate reductase; GPX, glutathione peroxidase; GR, glutathione reductase; GRX, glutaredoxin; GSH, reduced glutathione; GST, glutathione S-transferase; MAPK, mitogen-activated protein kinase; MAPKKK, MAPK kinase kinase; MDHAR, monodehydroascorbate reductase; MT, metallothionein; PAs, polyamines; POD, peroxidase; PRX, peroxiredoxin; RBOH, respiratory burst oxidase homolog; RCD, radical-induced cell death; ROS, reactive oxygen species; SOD, superoxide dismutase; SRO, similar to RCD one; TRX, thioredoxin.

yield and yield stability under non-optimal and adverse growing conditions by a combination of approaches based on the recent advances in genomic research (Zhang, 2007; Eckardt et al., 2009).

To cope with adverse conditions, plants have evolved a range of physiological and metabolic responses by activation of a great many of stress-responsive genes and synthesis of diverse functional proteins through a complex signal transduction network, so as to confer tolerance to the environmental stresses (Hirayama and Shinozaki, 2010). Reactive oxygen species (ROS), including hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet -}$), hydroxyl radical (OH•) and singlet oxygen ($^1O_2$) etc., resulting from excitation or incomplete reduction of molecular oxygen, are harmful by-products of basic cellular metabolism in aerobic organisms (Apel and Hirt, 2004; Miller et al., 2010). Besides the toxicity of ROS, ROS are also considered to be signaling molecules that regulate plant development, biotic and abiotic stress responses (Apel and Hirt, 2004; Mittler et al., 2004). Many excellent reviews have focused on ROS metabolism (Apel and Hirt, 2004; Noctor et al., 2014), ROS sensory and signaling networks (Miller et al., 2010; Suzuki et al., 2012; Baxter et al., 2014), as well as the cross-talk with other signaling molecules function in developmental and stress response processes (Suzuki et al., 2012; Noctor et al., 2014). However, most of these reviews provided an overall retrospective for model plant *Arabidopsis*. Gill and Tuteja (2010) reviewed enzymatic and non-enzymatic antioxidants and their roles in abiotic stress tolerance of crop plants. However, the regulation mechanism of the antioxidant system and the key components involved in ROS regulation and abiotic stress tolerance have not yet been summarized in crop plants. In this review, we provide an overview of current knowledge about ROS homeostasis regulation in crop plants. In particular, the genes that have been characterized in ROS homeostasis regulation affecting abiotic stress resistance in crop plants were summarized.

ROS HOMEOSTASIS IN PLANT

The evolution of aerobic metabolic processes such as respiration and photosynthesis unavoidably led to the production of ROS in mitochondria, chloroplast, and peroxisome (Apel and Hirt, 2004; Gill and Tuteja, 2010). Under optimal growth conditions, intracellular ROS are mainly produced at a low level in organelles. However, ROS are dramatically acclimated during stress. Under abiotic stress condition, limitation of CO_2 uptake, caused by stress-induced stomatal closure, favors photorespiratory production of H_2O_2 in the peroxisome and production of superoxide and H_2O_2 or singlet oxygen by the overreduced photosynthetic electron transport chain (Apel and Hirt, 2004; Noctor et al., 2014). In addition to organelles, plasma membrane together with apoplast is the main site for ROS generation in response to endogenous signals and exogenous environmental stimuli. Several types of enzymes, such as NADPH oxidases, amine oxidases, polyamine oxidases, oxalate oxidases, and a large family of class III peroxidases, that localized at the cell surface or apoplast are contributed to production of apoplast ROS (Apel and Hirt, 2004; Cosio and Dunand, 2009; Gill and Tuteja, 2010).

Overproduction of ROS caused by stress conditions in plant cells is highly reactive and toxic to proteins, lipids, and nucleic acid which ultimately results in cellular damage and death (Gill and Tuteja, 2010). On the other hand, the increased production of ROS during stresses also thought to act as signals for the activation of stress response pathways (Baxter et al., 2014). Plants have evolved an efficient enzymatic and non-enzymatic antioxidative system to protect themselves against oxidative damage and fine modulation of low levels of ROS for signal transduction.

ROS-scavenging enzymes of plants include superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione *S*-transferase (GST), and peroxiredoxin (PRX). These antioxidant enzymes are located in different sites of plant cells and work together to detoxify ROS. SOD acts as the first line of defense converting $O_2^{\bullet -}$ into H_2O_2. CAT, APX, and GPX then detoxify H_2O_2. In contrast to CAT, APX requires an ascorbic acid (AsA) and/or a glutathione (GSH) regenerating cycle involved MDHAR, DHAR, and GR. GPX, GST, and PRX reduce H_2O_2 and organic hydroperoxides through ascorbate-independent thiol-mediated pathways using GSH, thioredoxin (TRX) or glutaredoxin (GRX) as nucleophile (Dietz et al., 2006; Meyer et al., 2012; Noctor et al., 2014). Non-enzymatic antioxidants include GSH, AsA, carotenoids, tocopherols, and flavonoids are also crucial for ROS homeostasis in plant (Gill and Tuteja, 2010). Besides traditional enzymatic and non-enzymatic antioxidants, increasing evidences indicated that soluble sugars, including disaccharides, raffinose family oligosaccharides and fructans, have a dual role with respect to ROS (Couee et al., 2006; Keunen et al., 2013). Soluble sugars were directly linked with the production rates of ROS by regulation ROS producing metabolic pathways, such as mitochondrial respiration or photosynthesis. Conversely, they also feed NADPH-producing metabolism to participate in antioxidative processes (Couee et al., 2006).

In addition to the antioxidative system, avoiding ROS production by alleviating the effects of stresses on plant metabolism may also be important for keeping ROS homeostasis. Alternative oxidases (AOX) can prevent the excess generation of ROS in the electron transport chains of mitochondria (Maxwell et al., 1999). By diverting electrons flowing through electron-transport chains, AOX can decrease the possibility of electron leaking to O_2 to generate $O_2^{\bullet -}$. Other mechanisms, such as leaf movement and curling, photosynthetic apparatus rearranging, may also represent an attempt to avoid the over-reduction of ROS by balancing the amount of energy absorbed by the plant with the availability of CO_2 (Mittler, 2002).

REGULATION OF NADPH OXIDASES IN CROP PLANTS

Plant NADPH oxidases, also known as respiratory burst oxidase homologs (RBOHs), are the most studied enzymatic source of ROS. Plant RBOHs have cytosolic FAD- and NADPH-binding domains in the C-terminal region, and transmembrane domains that correspond to those in mammalian NADPH oxidases (Suzuki et al., 2011). In addition, plant RBOHs have a cytosolic N-terminal extension contains regulatory regions such as calcium-binding EF-hands and phosphorylation target sites that are important for the function and regulation of the plant NADPH oxidases (Oda et al., 2010; Suzuki et al., 2011). Increasing evidence demonstrated NADPH oxidases as key signaling nodes in the ROS regulation network of plants integrating numerous signal transduction pathways with ROS signaling and mediating multiple important biological processes, including cell growth and plant development, abiotic stress response and adaptation, plant–microbe pathogenic and symbiotic interactions (Torres and Dangl, 2005; Suzuki et al., 2011; Marino et al., 2012). Numerous studies have uncovered several regulatory mechanisms of plant NADPH oxidases in *Arabidopsis*, which involved various signaling components including protein phosphorylation, Ca^{2+}, CDPKs, and phospholipase Dα1 (PLDα1) (Baxter et al., 2014). Ca^{2+} regulates NADPH oxidase-dependent ROS production by binding directly to the EF-hand motif in the N terminus of RBOH protein and/or regulating Ca^{2+}-dependent phosphorylation medicated by CDPK (Ogasawara et al., 2008; Dubiella et al., 2013). RBOHs were also found to be phosphorylated by SnRK2 protein kinase OPEN STOMATA 1 (OST1) during ABA-dependent stomatal closure (Sirichandra et al., 2009).

Functions and regulatory mechanisms of several RBOH proteins were investigated in crops. The activity of NADPH oxidase was increased by drought, and exhibited high-temperature stability and an alkaline-philic feature, suggesting its important role in response to drought stress (Duan et al., 2009). Treatment with ABA and Ca^{2+} also considerably induced the activity of NADPH oxidase in leaves of maize seedlings (Jiang and Zhang, 2002a, 2003). Nine NADPH oxidase (RBOH) genes (*OsRBOHA*–*OsRBOHI*) were identified in the rice genome (Wong et al., 2007). Rice *RBOH* genes exhibited unique patterns of expression changes in response to various environmental stresses (Wang et al., 2013). A small GTPase Rac in rice (OsRac1) was identified as a positive regulator of OsRBOHB involved in pathogen defense (Wong et al., 2007). A direct interaction between OsRac1 and the N-terminal extension of OsRBOHB may be required for NADPH oxidase activity modulated by the cytosolic Ca^{2+} concentration in plants (Wong et al., 2007). Further mutation analyses of the regulatory domains of OsRBOHB indicated that not only the EF-hand motif but also the upstream N-terminal region was essential to Ca^{2+}-dependent but not phosphorylation-dependent activation (Takahashi et al., 2012). In addition, Liu et al. (2012) found that phosphatidylinositol 3-kinase (PI3K) regulated NADPH oxidase activity by modulating the recruitment of Rac1 to plasma membrane. Rice histidine kinase OsHK3 showed to regulate the expression of NADPH oxidase genes and the production of H_2O_2 in ABA signaling (Wen et al., 2015). In potato, two CDPKs, StCDPK4 and StCDPK5, were found to induce the phosphorylation of StRBOHB and regulated the oxidative burst during pathogen defense (Kobayashi et al., 2007). In tobacco, NbRBOHA and NbRBOHB are in charge of the generation of ROS during the defense response (Yoshioka et al., 2003). Further study indicated that mitogen-activated protein kinase (MAPK) cascades MEK2-SIPK/NTF4 and MEK1-NTF6 were involved in the NbRBOHB-dependent oxidative burst in response to pathogen signals (Asai et al., 2008). Two tomato RBOH genes, *SlRBOHB* (*SlWfi1*) and *SlRBOHG* (*SlRBOH1*), have turned out to participate in wounding response and development (Sagi et al., 2004). Other studies revealed that SlRBOHG (SlRBOH1) is vital for brassinosteroid (BR)-induced H_2O_2 production, ABA accumulation, stomatal closure/opening and oxidative stress tolerance (Xia et al., 2014; Zhou et al., 2014a), while SlRBOHB was found to positively regulate the defense response against *B. cinerea*, the flg22-induced immune response and drought stress response (Li et al., 2015). Lin et al. (2009) observed that the activity of NADPH oxidase is regulated by H_2O_2 and ZmMPK5 in maize. Zhu et al. (2013b) identified a BR induced microtubule-associated protein, ZmMAP65-1a, interacts with a MAPK and functions in H_2O_2 self-propagation by regulating the expression of NADPH oxidase genes in BR signaling in maize.

REGULATION OF ANTIOXIDATIVE SYSTEM IN CROP PLANTS

Plant antioxidative system consists of numerous enzymatic and non-enzymatic antioxidative components that work together with ROS-generating pathway to maintain ROS homeostasis. Several studies showed important roles of antioxidative components in ROS homeostasis in crop plants. The rice (*japonica*) genome has eight genes that encode putative SODs, including two cytosolic copper-zinc SODs (*cCuZn-SOD1* and *cCuZn-SOD2*), one putative CuZn-SOD-like *(CuZn-SOD-L*), one plastidic SOD (*pCuZn-SOD*), two iron SODs (*Fe-SOD2* and *Fe-SOD3*), and one manganese SOD (*Mn-SOD1*) (Nath et al., 2014). Transgenic rice plants overexpressing *Mn-SOD1* showed less mitochondrial $O_2^{\bullet-}$ under stress and reduced the stress induction of *OsAOX1a/b* specifically (Li et al., 2013). There are eight APX genes in rice, including two cytosolic APXs (*OsAPX1* and *OsAPX2*), two peroxisomal APXs (*OsAPX3* and *OsAPX4*), two mitochondrial APXs (*OsAPX5* and *OsAPX6*) and two chloroplastic APXs (*OsAPX7* and *OsAPX*8) (Teixeira et al., 2004, 2006). Two cytosolic APXs, OsAPX1 and OsAPX2, have crucial roles in abiotic stress resistance in rice (Sato et al., 2011; Zhang et al., 2013). Interestingly, rice mutants double silenced for cytosolic APXs (APX1/2s) exhibit significant changes in the redox status indicated by higher H_2O_2 levels and increased glutathione and ascorbate redox states, triggering alterations in the ROS signaling networks and making the mutants able to cope with abiotic stress similar to non-transformed plants (Bonifacio et al., 2011). Some of the ROS-scavenging enzymes, such as GST (Dixon and Edwards, 2010), TRX, and GRX (Meyer et al., 2012), have evolved into large multigene families with varied functions that cope with a variety of adverse environmental conditions. Recent mutational and transgenetic plants analyses revealed special member of multigene enzyme family as a key player in ROS homeostasis regulation in crop plants. *OsTRXh1*, encodes h-type TRX in rice, regulates the redox state of the apoplast and participates in plant development and stress responses (Zhang et al., 2011). OsTRXh1 protein possesses reduction activity and secreted into the extracellular space. Overexpression of *OsTRXh1* produce less H_2O_2 under salt stress, reduce the expression of the salt-responsive genes, lead to a salt-sensitive phenotype in rice. In another study, Perez-Ruiz et al. (2006) reported that rice NADPH thioredoxin reductase (NTRC) utilizes NADPH to reduce the chloroplast 2-Cys PRX BAS1, thus protects chloroplast against oxidative damage by reducing H_2O_2.

The involvement of ROS in signal transduction implies that there must be coordinated function of regulation networks to maintain ROS at non-toxic levels in a delicate balancing act between ROS production and ROS-scavenging pathways, and to regulate ROS responses and subsequent downstream processes (Mittler et al., 2004). Numerous studies from different plant species observed that the generation of ROS and activity of various antioxidant enzymes increased during abiotic stresses (Damanik et al., 2010; Selote and Khanna-Chopra, 2010; Tang et al., 2010; Turan and Ekmekci, 2011). There is an increasing body of literature concerning the mechanisms by which regulation of antioxidative system response to abiotic stresses in crops. Intrinsic to this regulation is ROS production and signaling that integrated with the action of hormone and small molecules.

The plant hormone ABA is the key regulator of abiotic stress resistance in plants, and regulates large number of stress-responsive genes by a complex regulatory network so as to confer tolerance to the environmental stresses (Cutler et al., 2010; Raghavendra et al., 2010). ABA-induced stress tolerance is partly linked with the activation of antioxidant defense systems, including enzymatic and non-enzymatic constituents, which protects plant cells against oxidative damage (Huang et al., 2012; Zhang et al., 2012a, 2014). Water stress-induced ABA accumulation and exogenous ABA treatment triggers the increased generation of ROS, then leads to the activation of the antioxidant system in crops (Jiang and Zhang, 2002a,b; Ye et al., 2011). Small molecules, such as Ca^{2+}, calmodulin (CaM), NO and ROS have been demonstrated to play vital roles in ABA-induced antioxidant defense (Jiang and Zhang, 2003; Hu et al., 2007). In rice, a Ca^{2+}/CaM-dependent protein kinase (CCaMK), OsDMI3, is necessary for ABA-induced increases in the expression and the activities of SOD and CAT. ABA-induced H_2O_2 production activates OsDMI3, and the activation of OsDMI3 also enhances H_2O_2 production by increasing the expression of NADPH oxidase genes (Shi et al., 2012). Further study indicated that OsDMI3 functions upstream of OsMPK1, to regulate the activities of antioxidant enzymes and the production of H_2O_2 in rice (Shi et al., 2014). Recent study provides evidence to show that rice histidine kinase OsHK3 functions upstream of OsDMI3 and OsMPK1, and is necessary for ABA-induced antioxidant defense (Wen et al., 2015). Zhang et al. (2012a) reported that C2H2-type ZFP, ZFP182, is involved in ABA-induced antioxidant defense. Another C2H2-type ZFP, ZFP36, is also necessary for ABA-induced antioxidant defense (Zhang et al., 2014). Moreover, ABA-induced H_2O_2 production and ABA-induced activation of OsMPKs promote the expression of *ZFP36*, and *ZFP36* also up-regulates the expression of NADPH oxidase and MAPK genes and the production of H_2O_2 in ABA signaling (Zhang et al., 2014). In maize, ABA and H_2O_2 increased the expression and the activity of ZmMPK5, which is required for ABA-induced antioxidant defense. The activation of ZmMPK5 also enhances the H_2O_2 production by increasing the expression and the activity of NADPH oxidase, thus there is a positive feedback loop involving NADPH oxidase, H_2O_2, and ZmMPK5 in ABA signaling (Zhang et al., 2006; Hu et al., 2007; Ding et al., 2009; Lin et al., 2009). Subsequent experiments confirmed that ABA-induced H_2O_2 production mediates NO generation in maize leaves, which, in turn, activates MAPK and increases the expression and the activities of antioxidant enzymes in ABA signaling (Zhang et al., 2007). Moreover, a maize CDPK gene, *ZmCPK11*, acts upstream of ZmMPK5, is essential for ABA-induced up-regulation of the expression and activities of SOD and APX, and the production of H_2O_2 in maize leaves (Ding et al., 2013). Hu et al. (2007) found that Ca^{2+}-CaM is required for ABA-induced antioxidant defense and functions both upstream and downstream of H_2O_2 production in leaves of maize plants. Afterward, Ca^{2+}/CaM-dependent protein kinase, ZmCCaMK, was reported to be essential for ABA-induced antioxidant defense, and H_2O_2-induced NO production is involved in the activation of ZmCCaMK in ABA signaling (Ma et al., 2012).

Brassinosteroids are a group of steroid hormones and important for a broad spectrum of plant growth and development processes, as well as responses to biotic and abiotic stresses (Bajguz and Hayat, 2009; Divi and Krishna, 2009; Yang et al., 2011; Zhu et al., 2013a). Numerous studies have shown that BR can activate antioxidant defense systems to improve stress tolerance in crops (Özdemir et al., 2004; Xia et al., 2009). Zhang et al. (2010) reported that ZmMPK5 is required for NADPH oxidase-dependent self-propagation of ROS in BR-induced antioxidant defense systems in maize. Further study founded that a 65 kDa microtubule-associated protein (MAP65), ZmMAP65-1a, directly phosphorylated by ZmMPK5, is required for BR-induced antioxidant defense (Zhu et al., 2013b). Recently, Ca^{2+} and maize CCaMK gene, *ZmCCaMK*, was demonstrated to be required for BR-induced antioxidant defense (Yan et al., 2015).

GENES INVOLVED IN ROS REGULATION AND ABIOTIC STRESS TOLERANCE IN CROPS

To cope with abiotic stress, plants have evolved multiple and interconnected signaling pathways to regulate different sets of stress-responsive genes for producing various classes of proteins, such as protein kinases, transcriptional factors, enzymes, molecular chaperones, and other functional proteins, resulting in diverse physiological and metabolic response so as to confer tolerance to the environmental stresses. Hundreds or even

1000s of genes that regulate stress responses have been identified in crop plants by diverse functional genomics approaches (Hu and Xiong, 2014). In parallel to this, the functions of numerous stress-responsive genes involved in ROS homeostasis regulation and abiotic stress resistance have been characterized in transgenic plants (**Figure 1**; **Table 1**).

Protein Kinases and Phosphatases

Mitogen-activated protein kinase cascades are involved in diverse processes from plant growth and development to stress responses. MAPK cascades also play crucial roles in ROS signaling, and several studies in *Arabidopsis* have shown that ROS are not only the trigger, but also the consequence of activation of MAPK signaling (Kovtun et al., 2000; Pitzschke and Hirt, 2006; Pitzschke et al., 2009). However, few MAPK cascades components have been functionally characterized in crops. Two MAPK kinases (MAPKKs), GhMKK1 and GhMKK5 have been characterized to be involved in stress resistance and ROS homeostasis in cotton (Zhang et al., 2012b; Lu et al., 2013). Overexpression of *GhMKK1* in tobacco improved its tolerance to salt and drought stresses, exhibited an enhanced ROS scavenging capability and significantly elevated activities of antioxidant enzymes (Lu et al., 2013). Whereas, overexpression of another cotton MAPKK gene, *GhMKK5*, in tobacco reduced their tolerance to salt and drought stresses. *GhMKK5*-overexpressing plants showed significantly up-regulated expression of ROS-related and cell death marker genes, and resulted in excessive accumulation of H_2O_2 and hypersensitive response (HR)-like cell death (Zhang et al., 2012b). In another study, a drought-hypersensitive mutant (drought-hypersensitive mutant1 [*dsm1*]) of a putative MAPK kinase kinase gene has been identified in rice (Ning et al., 2010). The *dsm1* mutant was sensitive to oxidative stress with down-regulated expression of two peroxidase (POD) genes and reduced POD activity.

Calcium-dependent protein kinase proteins regulate the downstream components in calcium signaling pathways. A rice CDPK gene, *OsCPK12*, enhances tolerance to salt stress by reducing the accumulation of ROS (Asano et al., 2012). Expression of genes encoding ROS-scavenging enzymes (*OsAPx2* and *OsAPx8*) were up-regulated, whereas the NADPH oxidase gene (*OsRBOHI*) was down-regulated in *OsCPK12*-overexpressing plants compared with wild type plants. Conversely, the *oscpk12* mutant and RNAi plants were more sensitive to high salinity and accumulated more H_2O_2 than wild type plants (Asano et al., 2012). Overexpression of another CDPK gene, *OsCPK4*, results in increased tolerance to salt and drought stresses in rice plants. Transgenic plants exhibited higher expression of numerous genes involved in lipid metabolism and

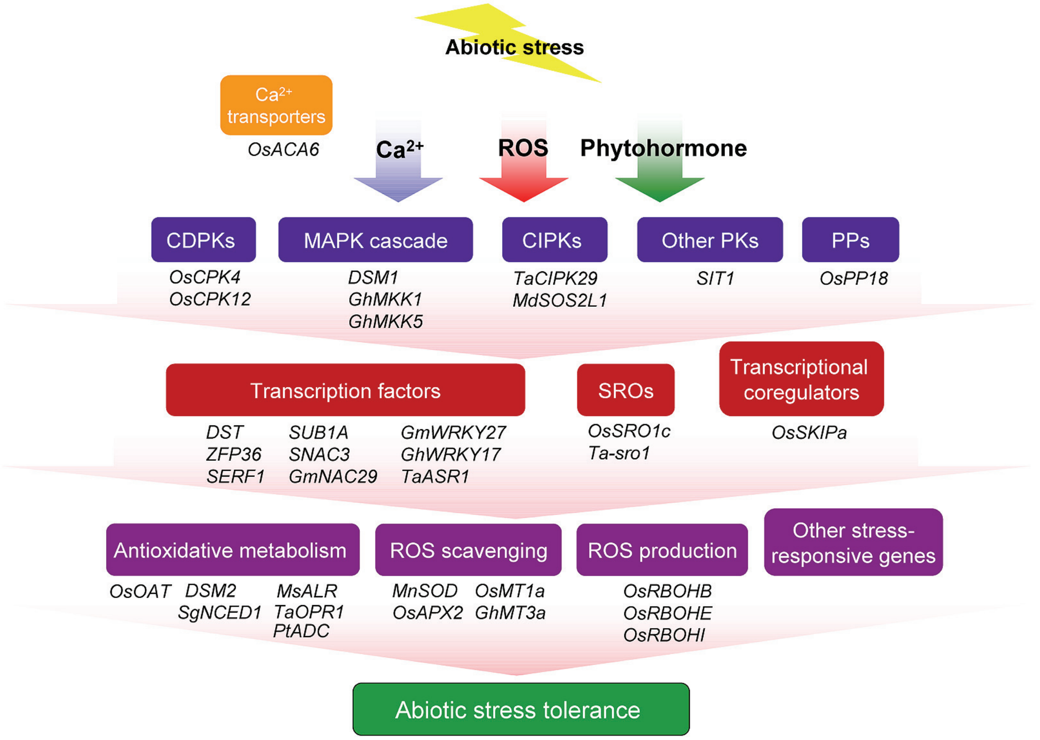

FIGURE 1 | Overview of major genes that involved in abiotic stress resistance through ROS regulation in crop plants. Plant cells perceive abiotic stress signals and transduce them through various signaling pathways including secondary signaling molecules, plant hormones, and transcriptional regulators. The regulation of gene expression by different transcription regulators results in the induction of various defense pathways, such as, reactive oxygen species (ROS) scavenging and antioxidative metabolism. Transcription regulators also mediate ROS producing systems and activate the expression of stress-responsive gene so as to confer tolerance to the environmental stresses. CDPK, calcium-dependent protein kinase; CIPK, calcineurin B-like protein-interacting protein kinase; MAPK, mitogen-activated protein kinase; PK, protein kinase; PP, protein phosphatase; SRO, similar to RCD one.

TABLE 1 | Representative genes that involved in abiotic stress resistance in major crops through ROS regulation.

Functional category	Genes	Protein function	Origin	Transformation receptor	ROS regulation	Abiotic stress resistance	Reference
Protein kinase							
MAPKs	*GhMKK1*	MAPKK	*G. hirsutum*	*N. benthamiana*	ROS scavenging	Drought and salt stress	Lu et al., 2013
	DSM1	MAPKKK	*O. sativa*	*O. sativa*	ROS scavenging	Drought stress	Ning et al., 2010
CDPK	*OsCPK4*	calcium-dependent protein kinase	*O. sativa*	*O. sativa*	ROS scavenging	Drought and salt stress	Campo et al., 2014
	OsCPK12	calcium-dependent protein kinase	*O. sativa*	*O. sativa*	ROS production and scavenging	Salt stress	Asano et al., 2012
CIPK	*TaCIPK29*	CBL-interacting protein kinase	*T. aestivum*	*N. benthamiana*	ROS scavenging	salt stress	Deng et al., 2013
	MdSOS2L1	CBL-interacting protein kinase	*Malus x domestica*	*Malus x domestica*; *S. lycopersicum*	ROS scavenging; antioxidative metabolism	Salt stress	Hu et al., 2015
Other kinase	*SIT1*	Lectin receptor-like kinase	*O. sativa*	*O. sativa*	ROS production	Salt stress	Li et al., 2014
Protein phosphatase	*OsPP18*	Protein phosphatase 2C	*O. sativa*	*O. sativa*	ROS scavenging	Drought and oxidative stress	You et al., 2014
Transcription factors							
Zinc finger	*DST*	C2H2 zinc finger	*O. sativa*	*O. sativa*	ROS scavenging	Drought and salt stress	Huang et al., 2009
	ZFP36	C2H2 zinc finger	*O. sativa*	*O. sativa*	ABA-induced antioxidant defense	Drought and oxidative stress	Zhang et al., 2014
	OsTZF1	CCCH zinc finger	*O. sativa*	*O. sativa*	ROS scavenging	Drought, salt and oxidative stress	Jan et al., 2013
AP2/ERF	*SERF1*	ERF	*O. sativa*	*O. sativa*	ROS signaling	Salt stress	Schmidt et al., 2013
	SUB1A	ERF	*O. sativa*	*O. sativa*	ROS scavenging	Drought, submerge and oxidative stress	Fukao et al., 2011
	JERF3	ERF	*S. lycopersicum*	*N. benthamiana*	ROS scavenging	Drought, salt and freezing stress	Wu et al., 2008
WRKY	*GmWRKY27*	WRKY	*G. max*	*G. max*	ROS production	Drought and salt stress	Wang et al., 2015
	GhWRKY17	WRKY	*G. hirsutum*	*N. benthamiana*	ROS scavenging	Drought and salt stress	Yan et al., 2014
NAC	*GmNAC29*	NAC	*G. max*	*G. max*	ROS production	Drought and salt stress	Wang et al., 2015
	SNAC3	NAC	*O. sativa*	*O. sativa*	ROS scavenging	Drought, heat and oxidative stress	Fang et al., 2015
Other TF	*TaASR1*	ASR	*T. aestivum*	*N. benthamiana*	ROS scavenging	Drought and oxidative stress	Hu et al., 2013
Other nuclear proteins							
SRO protein	*OsSRO1c*	SRO	*O. sativa*	*O. sativa*	ROS scavenging	Drought and oxidative stress	You et al., 2013
	Ta-sro1	SRO	*T. aestivum*	*T. aestivum*; *A. thaliana*	ROS production and scavenging	Osmotic, salt and oxidative stress	Liu et al., 2014
Other	*OsSKIPa*	Ski-interaction protein	*O. sativa*	*O. sativa*	ROS scavenging	Drought stress	Hou et al., 2009
ABA metabolism	*DSM2*	Carotene hydroxylase	*O. sativa*	*O. sativa*	antioxidative metabolism	Drought and oxidative stress	Du et al., 2010
	SgNCED1	9-*cis*-epoxycarotenoid	*S. guianensis*	*N. benthamiana*	ABA-induced antioxidant defense	Drought and salt stress	Zhang et al., 2009
ROS scavenging	*MnSOD*	MnSOD	*N. plumbaginifolia*	*M. sativa*	ROS scavenging	Drought stress	McKersie et al., 1996
	OsAPX2	APX	*O. sativa*	*O. sativa*	ROS scavenging	Drought, salt and cold stresses	Zhang et al., 2013

(Continued)

TABLE 1 | Continued

Functional category	Genes	Protein function	Origin	Transformation receptor	ROS regulation	Abiotic stress resistance	Reference
Detoxification proteins	*MsALR*	NADPH-dependent aldose/aldehyde reductase	*M. sativa*	*N. benthamiana*	antioxidative metabolism	Drought and oxidative stress	Oberschall et al., 2000
	OsMT1a	type 1 metallothionein	*O. sativa*	*O. sativa*	ROS scavenging	Drought stress	Yang et al., 2009
	GhMT3a	Type 3 metallothionein	*G. hirsutum*	*N. benthamiana*	ROS scavenging	Drought, salt and cold stresses	Xue et al., 2009
Calcium transporters	*OsACA6*	type IIB Ca^{2+}ATPase	*O. sativa*	*N. benthamiana*	ROS scavenging	Drought and salt stress	Huda et al., 2013
Polyamines metabolism	*PtADC*	Arginine decarboxylase	*P. trifoliata*	*N. benthamiana*; *L. esculentum*	ROS scavenging	Drought stress	Wang et al., 2011
Amino acid metabolism	*OsOAT*	Ornithine δ-aminotransferase	*O. sativa*	*O. sativa*	antioxidative metabolism; ROS scavenging	Drought and oxidative stress	You et al., 2012
Helicase	*OsSUV3*	NTP-dependent RNA/DNA helicase	*O. sativa*	*O. sativa*	ROS scavenging	Drought and salt stress	Tuteja et al., 2013
Unknown function	*TaOPR1*	12-oxo-phytodienoic acid reductases	*T. aestivum*	*T. aestivum*; *A. thaliana*	ABA-induced antioxidant defense	Salt and oxidative stress	Dong et al., 2013

protection against oxidative stress, therefore, reduced levels of membrane lipid peroxidation under stress conditions (Campo et al., 2014).

Calcium-dependent protein kinase proteins also have been found to be responsive to abiotic stress via ROS regulation. Overexpression of wheat CIPK gene *TaCIPK29* in tobacco resulted in increased salt tolerance. Transgenic tobacco seedlings maintained high K^+/Na^+ ratios and Ca^{2+} content by up-regulating the expression of some transporter genes, and also reduced ROS accumulations by increasing the expression and activities of ROS-scavenging enzymes under salt stress (Deng et al., 2013). Overexpression of *MdSOS2L1,* a CIPK gene from apple, also conferred salt tolerance in apple and tomato (Hu et al., 2015). Molecular analysis and functional characterization of MdSOS2L1 exhibited that it increases the ROS scavenging-enzymes and antioxidant metabolites such as procyanidin and malate, leading to enhanced salt tolerance in apple and tomato (Hu et al., 2015). A rice lectin receptor-like kinase, salt intolerance 1 (SIT1) was demonstrated mediates salt sensitivity by regulating ROS and ethylene homeostasis and signaling (Li et al., 2014). SIT1 phosphorylates MPK3 and 6, and their activation by salt requires SIT1. SIT1 promotes accumulation of ROS, leading to plant death under salt stress, which occurred in an MPK3/6- and ethylene signaling-dependent manner (Li et al., 2014).

The dephosphorylation mediated by protein phosphatase is an important event in the signal transduction process that regulates various cellular activities. A rice protein phosphatase 2C (PP2C) gene, *OsPP18*, was identified as a SNAC1-regulated downstream gene (You et al., 2014). The *ospp18* mutant exhibited sensitive to drought and oxidative stress with reduced activities of ROS-scavenging enzymes. The ABA-induced expression of ABA-responsive genes has not been disrupted in *ospp18* mutant, indicating *OsPP18* mediates drought stress resistance by regulating ROS homeostasis through ABA-independent pathways (You et al., 2014).

Transcriptional factors

Transcriptional factors (TFs) are one of the important regulatory proteins involved in abiotic stress responses. They play essential roles downstream of stress signaling cascades, which could alter the expression of a subset of stress-responsive genes simultaneously and enhance tolerance to environmental stress in plants. Members of AP2/ERF (APETALA2/ethylene response factor), zinc finger, WRKY, bZIP (basic leucine zipper), and NAC (NAM, ATAF, and CUC) families have been characterized with roles in the regulation of plant abiotic stress responses (Yamaguchi-Shinozaki and Shinozaki, 2006; Ariel et al., 2007; Ciftci-Yilmaz and Mittler, 2008; Fang et al., 2008), and some of them have been demonstrated to be involved in ROS homeostasis regulation and abiotic stress resistance in crops.

Proteins containing zinc finger domain(s) were widely reported to be key players in the regulation of ROS-related defense genes in *Arabidopsis* and other species. For example, the expression of some zinc finger genes in *Arabidopsis*, *ZAT7*, *ZAT10* and *ZAT12*, is intensely up-regulated by oxidative stress in AtAPX1 knockout plants (Miller et al., 2008). Subsequent experiments showed that these zinc finger proteins were involved in ROS regulation and multiple abiotic stresses tolerance (Davletova et al., 2005; Mittler et al., 2006; Ciftci-Yilmaz et al., 2007). The zinc finger proteins are divided into several types, such as C2H2, C2C2, C2HC, CCCH and C3HC4, based on the number and the location of characteristic residues (Ciftci-Yilmaz and Mittler, 2008). The signaling pathways participating in stomatal movement were well studied in the model plant *Arabidopsis*, but were largely unknown in crops. Huang et al. (2009) identified a drought and salt tolerance (*dst*) mutant, and the DST was cloned by the map-based cloning. DST encoded a C2H2-type zinc finger transcription factor that negatively regulated stomatal closure by direct regulation of genes related to H_2O_2 homeostasis, which identified a novel signaling pathway of DST-mediated H_2O_2-induced stomatal closure (Huang et al., 2009). Loss of DST function increased the accumulation of H_2O_2 in guard cell, accordingly, resulted in increased stomatal closure and enhanced drought and salt tolerance in rice. Other two C2H2-type zinc finger proteins, ZFP36 and ZFP179, also play circle role in ROS homeostasis regulation and abiotic stress resistance in rice. *ZFP179* encodes a salt-responsive zinc finger protein with two C2H2-type zinc finger motifs (Sun et al., 2010). The *ZFP179* transgenic rice plants increased ROS-scavenging ability and expression levels of stress-related genes, and exhibited significantly enhanced tolerance to salt and oxidative stress (Sun et al., 2010). *ZFP36* is an ABA and H_2O_2-responsive C2H2-type zinc finger protein gene, and plays a important role in ABA-induced antioxidant defense and the tolerance of rice to drought and oxidative stresses (Zhang et al., 2014). Moreover, ZFP36 is a major player in the regulation of the cross-talk involving NADPH oxidase, H_2O_2, and MAPK in ABA signaling (Zhang et al., 2014). OsTZF1, a CCCH-tandem zinc finger protein, was identified as a negative regulator of leaf senescence in rice under stress conditions (Jan et al., 2013). Meanwhile, OsTZF1 confers tolerance to oxidative stress in rice by enhancing the expression of redox homeostasis genes and ROS-scavenging enzymes (Jan et al., 2013). A cotton CCCH-type tandem zinc finger gene, *GhTZF1*, also serves as a key player in modulating drought stress resistance and subsequent leaf senescence by mediating ROS homeostasis (Zhou et al., 2014b).

Members of AP2/ERF (APETALA2/ethylene response factor) transcription factor family, including DREB/CBF transcription factors, are especially important as they regulate genes involved in multiple abiotic stress responses (Mizoi et al., 2012). During the initial phase of abiotic stresses, elevated ROS levels might act as a vital acclimation signal. But the key regulatory components of ROS-mediated abiotic stress response signaling are largely unknown. Rice salt- and H_2O_2-responsive ERF transcription factor, SERF1, has a critical role in regulating H_2O_2-mediated molecular signaling cascade during the initial response to salinity in rice (Schmidt et al., 2013). SERF1 regulates the expression of H_2O_2-responsive genes involved in salt stress responses in roots. SERF1 is also a phosphorylation target of a salt-responsive MAPK (MAPK5), and activation the expression of salt-responsive MAPK cascade genes (*MAPK5* and *MAPKKK6*), well established salt-responsive TF genes (*ZFP179* and *DREB2A*), and itself through direct interaction with the corresponding promoters in plants (Schmidt et al., 2013). The authors proposed that SERF1 is essential for the propagation of the initial ROS signal to mediate salt tolerance. SUB1A, an ERF transcription factor found in limited rice accessions, limits ethylene production and gibberellin responsiveness during submergence, economizing carbohydrate reserves and significantly prolonging endurance (Fukao and Xiong, 2013). After floodwaters subside, submerged plants encounter re-exposure to atmospheric oxygen, leading to postanoxic injury and severe leaf desiccation (Setter et al., 2010; Fukao and Xiong, 2013). SUB1A also positively affects postsubmergence responses by restrained accumulation of ROS in aerial tissue during desubmergence (Fukao et al., 2011). Consistently, SUB1A promptes the expression of ROS scavenging enzyme genes, resulting in enhanced tolerance to oxidative stress. On the other hand, SUB1A improves survival of rapid dehydration following desubmergence and water deficit during drought by increasing ABA responses, and activating stress-inducible gene expression (Fukao et al., 2011). A jasmonate and ethylene-responsive ERF gene, JERF3, was isolated from tomato and involved in a ROS-mediated regulatory module in transcriptional networks that govern plant response to stress (Wu et al., 2008). JERF3 modulates the expression of genes involved in osmotic and oxidative stresses responses by binding to the osmotic- and oxidative-responsive related *cis* elements. The expression of these genes leads to reduce accumulation of ROS, resulting in enhanced abiotic stress tolerance in tobacco (Wu et al., 2008).

The WRKY family proteins have one or two conserved WRKY domains comprising a highly conserved WRKYGQK heptapeptide at the N-terminus and a zinc-finger-like motif at the C-terminus (Eulgem et al., 2000). The conserved WRKY domain plays important roles in various physiological processes by binding to the W-box in the promoter regions of target genes (Ulker and Somssich, 2004; Rushton et al., 2010). Wang et al. (2015) reported a multiple stress-responsive WRKY gene, *GmWRKY27*, reduces ROS level and enhances salt and drought tolerance in transgenic soybean hairy roots. GmWRKY27 interacts with GmMYB174, which, in turn, acts in concert to reduce promoter activity and gene expression of *GmNAC29* (Wang et al., 2015). Further experiments showed that GmNAC29 is a negative factor of stress tolerance for enhancing the ROS production under abiotic stress by directly activating the expression of the gene encoding ROS production enzyme. In another study, overexpression of cotton WRKY gene, *GhWRKY17*, reduced transgenic tobacco plants tolerance to drought and salt stress. Subsequent experiments showed that GhWRKY17 involved in stress responses by regulating ABA signaling and cellular levels of ROS (Yan et al., 2014). Sun et al. (2015) isolated a WRKY gene, *BdWRKY36*, from *B. distachyon*, and found it functions as a positive regulator of drought stress response by controlling ROS homeostasis and regulating transcription of stress-related genes.

Members of other TF families also functioned in abiotic stress response through ROS regulation. ASR proteins are plant-specific TFs and considered to be important regulators of plant response to various stresses. Wheat ASR gene, *TaASR1*, a positive regulator of plant tolerance to drought/osmotic stress, is involved in the modulation of ROS homeostasis by activating antioxidant system and transcription of stress-responsive genes (Hu et al., 2013). Soybean NAC TF, GmNAC2, was identified as a negative regulator during abiotic stress, and participates in ROS signaling pathways through modulation of the expression of genes related to ROS-scavenging (Jin et al., 2013). Ramegowda et al. (2012) isolated a stress-responsive NAC gene, *EcNAC1*, from finger millet (*E. coracana*). Transgenic tobacco plants expressing *EcNAC1* increased ROS scavenging activity, up-regulated many stress-responsive genes, and exhibited tolerance to various abiotic stresses and MV-induced oxidative stress (Ramegowda et al., 2012). Recently, a NAC transcription factor gene, *SNAC3*, functions as a positive regulator under high temperature and drought stress, was identified in rice (Fang et al., 2015). SNAC3 enhances the abiotic stresses tolerance by modulating H_2O_2 homeostasis state through controlling the expression of ROS-associated enzyme genes (Fang et al., 2015).

In addition to TFs, transcriptional coregulator as well as spliceosome component, OsSKIPa, a rice homolog of human Ski-interacting protein (SKIP), has been studied for effects on drought resistance (Hou et al., 2009). *OsSKIPa*-overexpressing rice exhibited significantly enhanced drought stress tolerance at both the seedling and reproductive stages by increased ROS-scavenging ability and transcript levels of many stress-related genes (Hou et al., 2009).

SRO PROTEINS

The SRO (SIMILAR TO RCD ONE) protein family was recently identified as a group of plant-specific proteins, and they are characterized by the plant-specific domain architecture which contains a poly (ADP-ribose) polymerase catalytic (PARP) and a C-terminal RCD1-SRO-TAF4 (RST) domain (Jaspers et al., 2010). In addition to these two domains, some SRO proteins have an N-terminal WWE domain. Our limited knowledge of SRO proteins is mainly from the study in *Arabidopsis* mutant *rcd1* (*radical-induced cell death 1*). *rcd1* exhibits pleiotropic phenotypes related to a wide range of exogenous stimulus responses and developmental processes, including sensitivity to apoplastic ROS and salt stress, resistance to chloroplastic ROS caused by methyl viologen (MV) and UV-B irradiation (Ahlfors et al., 2004; Fujibe et al., 2004; Katiyar-Agarwal et al., 2006). RCD1 interacts with SOS1 and a large number of transcription factors which have been identified or predicted to be involved in both development and stress-related processes (Katiyar-Agarwal et al., 2006; Jaspers et al., 2009). Recent study demonstrated that RCD1 is possibly involved in signaling networks that regulate quantitative changes in gene expression in response to ROS (Brosche et al., 2014).

In rice, an SRO protein, OsSRO1c, was characterized as a direct target of the drought stress-related transcription factor SNAC1 (You et al., 2013). *OsSRO1c* was induced in guard cells by drought stress. Overexpression of *OsSRO1c* resulted in accumulated H_2O_2 in guard cells, which, in turn, decreased stomatal aperture and reduced water loss. Further experiments indicated that OsSRO1c has dual roles in drought and oxidative stress tolerance of rice by promoting stomatal closure and H_2O_2 accumulation through a novel pathway involving the SNAC1 and DST regulators (You et al., 2013). Recently, an SRO gene was also identified to be crucial for salinity stress resistance by modulating redox homeostasis in wheat (Liu et al., 2014). Ta-*sro1*, the allele of the salinity-tolerant bread wheat cultivar Shanrong No. 3, is derived from the wheat parent allele via point mutation. Unlike *Arabidopsis* SRO proteins, Ta-sro1 has PARP activity. Both the overexpression of *Ta-sro1* in wheat and *Arabidopsis* promotes the accumulation of ROS by regulating ROS-associated enzyme. Ta-sro1 also enhances the activity of AsA-GSH cycle enzymes and GPX cycle enzymes, which regulate ROS content and cellular redox homeostasis (Liu et al., 2014).

ROS-scavenging or Detoxification Proteins

Reactive oxygen species-scavenging enzymes such as SOD, APX, CAT were properly described its role in ROS-scavenging pathway. The presence of antioxidant enzymes and compounds in almost all cellular compartments suggests the importance of ROS detoxification for protection against various stresses (Mittler et al., 2004). The effect of these ROS-scavenging enzymes in abiotic stress resistance was also investigated in crop plants. Transgenic alfalfa expressing MnSOD cDNA from *Nicotiana plumbaginifolia* improved survival and vigor after exposure to water deficit. Most importantly, transgenic alfalfa showed increased yield and survival rate over three winters in natural field environments (McKersie et al., 1996). A cDNA encoding a cytosolic copper-zinc SOD from the mangrove plant *Avicennia marina* was transformed into rice. The transgenic plants exhibited more tolerant to drought, salinity and oxidative stresses compared with the untransformed control plants (Prashanth et al., 2008). Overexpression of *OsAPX2* increased APX activity and reduced H_2O_2 and malondialdehyde (MDA) levels in transgenic plants under stress treatments (Zhang et al., 2013). More importantly, *OsAPX2*-overexpressing plants were more tolerant to drought stress than wild-type plants at the booting stage as indicated a significantly increase in spikelet fertility under abiotic stresses (Zhang et al., 2013). Transgenic rice plants that overexpressing another APX gene, *OsAPX1*, also exhibited increased spikelet fertility under cold stress (Sato et al., 2011).

Accumulation of toxic products from ROS with lipids and proteins significantly contributes to the damage of crop plants under biotic and abiotic stresses. A novel plant NADPH-dependent aldose/aldehyde reductase, which has the reduction activity toward toxic products of lipid peroxidation, was isolated from alfalfa. Tobacco plants overproducing the alfalfa aldose/aldehyde reductase showed lower concentrations of reactive aldehydes (products of lipid peroxidation) and tolerance to oxidative and drought stress (Oberschall et al., 2000).

Metallothioneins (MTs) are a group of low molecular weight proteins with the characteristics of high cysteine (Cys) residue content and metal-binding ability. The presence of several Cys residues in MTs suggests their involvement in the detoxification of ROS or in the maintenance of redox levels. *OsMT1a*, encoding a type 1 MT in rice, was induced by dehydration and Zn^{2+} treatment (Yang et al., 2009). Transgenic rice plants overexpressing *OsMT1a* enhanced antioxidant enzyme activities of CAT, POD and APX, and enhanced tolerance to drought. OsMT1a also regulates the expression of several zinc finger transcription factors by the modulation of Zn^{2+} homeostasis, which leads to enhanced plant stress tolerance (Yang et al., 2009). *GhMT3a* encodes a type 3 plant MT in cotton. Recombinant GhMT3a protein showed an ability to bind metal ions and scavenge ROS *in vitro*. Transgenic tobaccos showed more tolerance to multiple abiotic stresses, and lower H_2O_2 levels when compared with wild-type plants (Xue et al., 2009). The *SbMT-2* gene from a halophyte was also involved in maintaining cellular homeostasis by regulating ROS scavenging during stresses and thus improved tolerance to salt and osmotic stress in transgenic tobacco (Chaturvedi et al., 2014).

ABA Metabolic-related Proteins

Abscisic acid is a key phytohormone that medicates the adaptive responses to abiotic stresses of plants. ABA-induced antioxidant defense has been well documented in plants. ABA biosynthesis and catabolism also involved in antioxidant defense and abiotic stresses. Du et al. (2010) isolated a rice drought-sensitive mutant *dsm2*, impaired in the gene encoding a putative β-carotene hydroxylase. β-carotene hydroxylase is predicted for the biosynthesis of zeaxanthin, a carotenoid precursor of ABA. Under drought stress, *dsm2* mutants had reduced zeaxanthin and ABA, lower Fv/Fm and non-photochemical quenching (NPQ) capacity than the wild type. Overexpression of *DSM2* in rice increases the xanthophylls and NPQ capacity, stress-related ABA-responsive genes expression, and resulted in enhancing resistance to drought and oxidative stresses (Du et al., 2010). *OsABA8ox3*, encoding ABA 8′-hydroxylase involved in ABA catabolism, is also a key gene regulating ABA accumulation and anti-oxidative stress capability under drought stress (Nguyen et al., 2015). *OsABA8ox3* RNAi plants exhibited significant improvement in drought stress tolerance. Consistent with this, *OsABA8ox3* RNAi plants showed increased SOD and CAT activities and reduced MDA levels during dehydration treatment. In another study, overexpression of the 9-*cis*-epoxycarotenoid dioxygenase gene from *Stylosanthes guianensis* (*SgNCED1*) in the transgenic tobacco increased ABA content and tolerance to drought and salt stresses (Zhang et al., 2009). Moreover, enhanced abiotic stresses tolerance in transgenic plants is associated with ABA-induced production of H_2O_2 and NO, which, in turn, activate the expression and activities of ROS-scavenging enzymes (Zhang et al., 2009).

Calcium Transporters and Calcium-binding Proteins

Calcium (Ca^{2+}) regulates numerous signaling pathways involved in growth, development and stress tolerance. The influx of Ca^{2+} into the cytosol is countered by pumping Ca^{2+} out from the cytosol to restore the basal cytosolic level, and this may be achieved either by P-type Ca^{2+}ATPases or antiporters. Huda et al. (2013) report the isolation and characterization of *OsACA6*, which encodes a member of the type IIB Ca^{2+}ATPase family from rice. Overexpression of *OsACA6* confers tolerance to salinity and drought stresses in tobacco, which was correlated with reduced accumulation of ROS and enhanced the expression of stress-responsive genes in plants (Huda et al., 2013). In addition, overexpression of *OsACA6* confers Cd^{2+} stress tolerance in transgenic lines by maintaining cellular ion homeostasis and modulating ROS-scavenging pathway (Shukla et al., 2014). Annexins are calcium-dependent, phospholipid-binding proteins with suggested functions in response to environmental stresses and signaling during plant growth and development. OsANN1, a member of the annexin protein family in rice, has ATPase activity, the ability to bind Ca^{2+}, and the ability to bind phospholipids in a Ca^{2+}-dependent manner. OsANN1 confers abiotic stress tolerance by modulating antioxidant accumulation and interacting with OsCDPK24 (Qiao et al., 2015).

Other Functional Proteins

Polyamines are low molecular weight aliphatic amines found in all living cells. Because of their cationic nature at physiological pH, PAs have strong binding capacity to negatively charged molecules (DNA, RNA, and protein), thus stabilizing their structure (Alcazar et al., 2010). The PAs biosynthetic pathway has been thoroughly investigated in many organisms, and arginine decarboxylase (ADC) plays a predominant role in the accumulation of PAs under stresses (Capell et al., 2004; Alcazar et al., 2010). Wang et al. (2011) isolated an arginine decarboxylase gene (*PtADC*) from *Poncirus trifoliata*. The transgenic tobacco and tomato plants elevated endogenous PAs level, accumulated less ROS and showed an improvement in drought tolerance. Jang et al. (2012) identified a highly oxidative stress-resistant T-DNA mutant line carried an insertion in *OsLDC-like 1* in rice. The mutant produced much higher levels of PAs compared to the wild type plants. Based on their results, the authors suggested that PAs mediate tolerance to abiotic stresses through their ability to decrease ROS generation and enhance ROS degradation.

The 12-oxo-phytodienoic acid reductases (OPRs) are classified into two subgroups, OPRI and OPRII. OPRII proteins are involved in jasmonic acid synthesis, while the function of OPRI is as yet unclear. Dong et al. (2013) characterizated the functions of the wheat OPRI gene *TaOPR1*. Overexpression of *TaOPR1* in wheat and *Arabidopsis* enhanced tolerance to salt stress by regulating of ROS and ABA signaling pathways (Dong et al., 2013).

Helicases are ubiquitous enzymes that catalyze the unwinding of energetically stable duplex DNA or RNA secondary structures, and thereby play an important role in almost all DNA and/or RNA metabolic processes. OsSUV3, an NTP-dependent RNA/DNA helicase in rice, exhibits ATPase, RNA and DNA helicase activities (Tuteja et al., 2013). *OsSUV3* sense transgenic rice plants showed lesser lipid peroxidation and H_2O_2 production, along with higher activities of antioxidant enzymes, consequently resulting in increased tolerance to high salinity (Tuteja et al., 2013).

Ornithine δ-aminotransferase (δ-OAT) is considered to be an enzyme involved in proline and arginine metabolism. *OsOAT*-overexpressing rice plants exhibited significantly increased δ-OAT activity and proline levels under normal growth conditions, and enhanced drought, osmotic, and oxidative stress tolerance (You et al., 2012).

CONCLUSION AND PERSPECTIVES

The discovery of the enzymatic activity of SOD 45 years ago (McCord and Fridovich, 1969) ushered in the field of ROS biology. During the last two decades, the major sources and sites of ROS production, and the key antioxidant molecules and enzymes that scavenge ROS have been chartered in plant. However, our current knowledge about ROS homeostasis and signaling remains fragmental. Apoplastic ROS are rapidly produced in plants as a defense response to pathogen attack and abiotic stress. Whereas, in addition to NADPH oxidase, the function and regulation of other apoplastic ROS-associated enzymes, such as class III peroxidases, in stress responses signaling are largely unknown. On the other hand, 100s of genes that encode for ROS-metabolizing enzymes and regulators compose ROS gene network in plants. Thus, more than one enzymatic activity that produces or scavenges ROS exits in certain cellular compartment. How these different enzymes are coordinated within each compartment and between different compartments to adjust a particular ROS at an appropriate level during stresses is an important question needs to be addressed. There is increasing evidence suggesting the vital role of ROS signaling pathway in plant development and stress responses. However, regulatory mechanisms at the biochemical level, the mechanisms of extracellular ROS perception, transduction of ROS-derived signals, and especially the communication and interaction between different subcellular compartments in ROS signaling are still poorly understood. To build comprehensive regulation networks in ROS signaling and responses requires a combination of transcriptomics, proteomics and metabolomics approaches with analysis of mutant as well as protein–protein interactions.

Plants need diverse responses and adjustment of multiple adaptation mechanisms to cope with the multiple stresses exist in nature. Comparison of transcription profiles of rice in response to multiple stresses suggested the central role of ROS homeostasis in different abiotic stresses (Mittal et al., 2012). Therefore, manipulating endogenous ROS levels provides us with an opportunity to improve common defense mechanisms against different stresses to ensure crop plants growth and survival under adverse growing condition. The functions of numerous stress-responsive genes involved in ROS homeostasis regulation and abiotic stress resistance have been characterized in transgenic plants (**Table 1**). As expected, transgenic crop plants harbored these genes enhanced tolerance to multiple abiotic stresses (Wu et al., 2008; Fukao et al., 2011; Lu et al., 2013; Campo et al., 2014). However, few studies have reported the abiotic stress tolerance of transgenic plant at the reproductive or flowering stage based on yield and/or setting rate, and very few of these tests were conducted under field conditions. Additionally, most of the reported ROS-associated genes that involved in abiotic stress just have been demonstrated its role in regulation of expression and/or activity of ROS-scavenging enzymes. Thus, network involving in function of these genes in ROS homeostasis to medicate abiotic stress resistance needs to be fully investigated, and the new components need to be integrated into the signaling pathway. With a long-term goal to improve the abiotic stress resistance of crop plants by the utilizing of ROS regulation pathways, more and more key regulators need to be identified. It is also very important to clarify the mechanisms regulating ROS signaling pathways and their interplay during abiotic stresses. This can finally help to incorporate multiple necessary ROS-associated genes into the genetic backgrounds of elite cultivars or hybrids to enhance their abiotic stress resistance under real agricultural field conditions.

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