



Review Article

Role of Reactive Oxygen Species and Contribution of New Players in Defense Mechanism under Drought Stress in Rice

Muhammad Kamran Qureshi¹, Sana Munir¹, Ahmad Naeem Shahzad², Sumaira Rasul³, Wasif Nouman⁴ and Kashif Aslam^{3*}

¹Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences & Technology, Bahauddin Zakariya University, Multan, Pakistan

²Department of Agronomy, Faculty of Agricultural Sciences & Technology, Bahauddin Zakariya University, Multan, Pakistan

³Institute of Molecular Biology & Biotechnology, Bahauddin Zakariya University, Multan, Pakistan

⁴Department of Forestry, Faculty of Agricultural Sciences & Technology, Bahauddin Zakariya University, Multan, Pakistan

*For correspondence: dr.kaslam@gmail.com

Abstract

Rice (*Oryza sativa*) falls among the staple food crops in different parts of the globe. In current scenario of climate change, drought stress leads to significant decrease in crop production. It has negative effect on rice growth and development by affecting cellular, physiological and molecular processes. Photo-respiration increases under drought stress leads to overproduction of reactive oxygen species (ROS) in different organelles of the cell like chloroplasts, mitochondria and peroxisomes etc., which induce severe oxidative stress in rice. Over production of ROS can cause damage to proteins, lipids and DNA leading to lipid peroxidation, proteins oxidation, mutation, DNA damage that can lead to cell death. Under drought stress, ROS turn over in various organelles overload antioxidant quenching mechanism leading to oxidative damage. Oxidative stress can be overcome by the scavenging system, which consists of enzymatic and non-enzymatic antioxidants. Moreover, ROS also acts as signaling molecule and triggers defense mechanism through specific signal transduction network under stress. Under stress condition, activation of molecular cascades is initiated through the perception of stress that leads to the activation of signal transduction pathway including expression of transcription factors and stress related genes. Understanding of this regulatory mechanism of plant development and growth in drought-ROS stress can be promising in the development of improved transgenic rice under this stress. This review will provide an overview of ROS synthesis and signaling pathway under drought condition in rice. © 2018 Friends Science Publishers

Keywords: Antioxidant; *Oryza sativa*; Oxidative stress; Photorespiration; Signal transduction; Transcription factors

Introduction

Oryza sativa (Rice) serves as a staple food in different countries of the world (Bishwajit *et al.*, 2013; Chutipaijit, 2016) and ranks second among cultivated cereals (Madabula *et al.*, 2016). Asia is on the top in terms of production and consumption of rice. According to FAO report (2016–2017), average production of rice is estimated as 499.1 million tonnes, which is lower as compared to wheat with 760.1 million tonnes in the same year (FAOSTAT, 2017). It is grown in temperate, tropical, subtropical and semi-arid regions. Climate change is becoming major threat and has a negative impact on agriculture especially in the developing countries. Global climate changes manipulate the frequency and extent of hydrological fluctuations, causing floods and drought (Turrall *et al.*, 2011).

Rice yield is adversely affected by about forty-two stresses including both biotic and abiotic (Sarkar *et al.*, 2006). Abiotic stresses include salinity, severe temperatures,

drought, heavy metals, ozone and ultra-violet radiations. Drought is one of the important limiting factors among these stresses in terms of growth and production of rice. Rice is particularly susceptible to drought stress as it is a paddy field crop (Tao *et al.*, 2006; Yang *et al.*, 2008).

Based on ecosystem, rice is classified into two categories: low land (Asiatic zone) and upland rice (Latin America and African zone). Lowland rice needs standing water in their paddies and drought can rapidly occur at any stage of the crop under water shortage period affecting the crop and ultimately leads to yield losses. While upland rice rarely experienced standing water and stress ranges from mild to severe under the condition with high evapotranspiration or low rainfall (Kamoshita *et al.*, 2008). In comparison to irrigated production system, rice is more subjected to drought in rainfed areas of the world. Drought can rapidly occur at any stage affecting crop and ultimately leading to yield reduction (Bashir *et al.*, 2016). Under drought stress, rice plant undergo leaf rolling and wilting

resulted from osmotic variations, decrease in photosynthesis and during reproductive stage there is a reduction in fertility and ultimately yield losses (Kamoshita *et al.*, 2008; Pandey and Shukla, 2015).

In plants, drought can reduce different biological processes e.g., ion uptake, photosynthesis, growth, respiration metabolism and in severe condition ultimately results in plant death (Jaleel *et al.*, 2009). Drought affects overall development and growth of rice by affecting its morphology, physiology, biochemistry and anatomy (Lima *et al.*, 2015). It may suffer from drought stress either at vegetative stage or at reproductive stage. During vegetative growth, reduction in plant height, number of tillers and biomass are affected and rolling of leaves occurs in rice (Ji *et al.*, 2012). Under drought stress, plant releases hormones like ethylene that inhibit leaf and root growth on primary phase (Basu *et al.*, 2016) and stress occurring before flowering reduces yield. At reproductive stage, drought severely disturbs grain development and spikelet infertility resulting in unfilled grains (Kamoshita *et al.*, 2004; Botwright *et al.*, 2008). During grain filling, drought causes early senescence in plant which shortens its filling period (Plaut *et al.*, 2004) resulting in overall yield reduction.

In plant cells, ROS are produced under normal conditions because of partial reduction of the atmospheric oxygen (O_2). It is generated in plants as a byproduct during normal cellular metabolic processes and can damage cellular components. Different forms of ROS, includes singlet oxygen (1O_2), superoxide (O_2^-), hydroxyl (OH) radicals and hydrogen peroxide (H_2O_2) produced in organelles such as chloroplasts, peroxisomes and mitochondria having high rate of electron flow or oxidizing activity. These different forms have oxidizing nature (Mittler, 2002) and can damage lipids, proteins (Gill and Tuteja, 2010), or even cause cell death (Nouman *et al.*, 2014). ROS mainly 1O_2 and OH ions are highly reactive (Mittler *et al.*, 2004). Different forms of ROS, their sources of generation, type of action, extent of reactivity and other features are given in Table 1.

Under normal state, plant cells have a well-regulated antioxidant defense mechanism with the ability to maintain balance between ROS synthesis and scavenging and protects plant cells from oxidative damage (Foyer and Noctor, 2005; Navrot *et al.*, 2007). The antioxidant system consists of enzymatic and non-enzymatic components. These antioxidant systems are localized in various cell organelles like mitochondria, chloroplast, vacuoles, peroxisome etc. similar to enzymatic antioxidants and detoxify different forms of ROS (Das and Roychoudhury, 2014).

The enzymatic antioxidants include catalase (CAT), guaiacol peroxidase (GPX), superoxide dismutase (SOD), enzymes of ascorbate-glutathione (AsA-GSH) cycle such as ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR) and glutathione reductase (GR) (Roy *et al.*, 2009; Gill and

Tuteja, 2010). Plant NADPH oxidases catalyze the reduction of dioxygen to O_2^- from the oxidation of NADPH. O_2^- undergoes a dismutation catalyzed by apoplasmic superoxide dismutase (SOD), and produce H_2O_2 . SOD act as a primary defense against ROS in plant cell (Nouman *et al.*, 2016). SOD converts O_2^- to O_2 and H_2O_2 while CAT catalyzes H_2O_2 (Roy *et al.*, 2009). Peroxidases oxidize variety of substrates by utilizing H_2O_2 . Other enzymes also interact with various ROS molecules and detoxify them. The non-enzymatic antioxidants are lipid- or water-soluble and membrane associated. These consist of glutathione, carotenoids, flavonoids and tocopherols.

Under stress conditions, the balance between ROS production and its scavenging is disturbed inside the cell (Apel and Hirt, 2004; Vellosillo *et al.*, 2010). Thus, exposure of plants to various environmental stresses can result in the overproduction of ROS (Mittler *et al.*, 2004). Drought stress induces intracellular ROS elevation in plants (Van Breusegem and Dat, 2006). This excessive amount of ROS is generated due to electron leakage to oxygen during respiration and photosynthesis in water deficit plants (Kao, 2017). The overproduction of ROS further results in oxidative stress, which is one of the main damaging factors when plants are exposed to abiotic stresses such as drought (Sharma and Dubey, 2005).

Drought is also a limiting factor in rice production, which can leads to the overproduction of ROS. At lower level of ROS production, the housekeeping antioxidant mechanism acts as a restorer redox homeostasis. Interestingly, apart from acting as toxic molecule, ROS also acts as regulators in plant development and signaling molecule (Chan *et al.*, 2016) as in the induction of tolerance against stresses (Gechev *et al.*, 2006). Therefore, the efficient pathway in improving tolerance against drought induced oxidative damage is either reducing the production of ROS and/or increasing the efficiency of antioxidant activity in rice (Duan *et al.*, 2012; Yin *et al.*, 2015).

Highlighting new players (genes) linked with drought stress signaling pathway is purpose of this review. By controlling ROS scavenging mechanism, rice performance and overall yield can be increased. Role of ROS signaling and cross talk under drought is the important emerging issue to explore the drought-dependent redox signaling. In this cross talk, many key players are involved including gene, proteins and transcription factor. Main focus will be on ROS-(in) dependent transcription factors that are involved in drought stress signaling in rice.

ROS Production under Drought Stress

Drought can also cause imbalance between ROS production and its quenching in rice. Electron leakage is the one of major source of ROS generation. The leakage occur due to electron transport (ET) from activities of different cellular compartments like plasma membrane, mitochondria, chloroplasts or through different metabolic activities like

beta-oxidation that leads to ROS production (Table 2; Blokhina and Fagerstedt, 2010; Heyno *et al.*, 2011; Gilroy *et al.*, 2016; Kerchev *et al.*, 2016; Kao, 2017).

Different cellular responses are generated to cope different environmental stresses. Stability of cell membrane is the main criteria of cellular response under stress. Cell membrane is the foremost cell organelle affected by drought. Production of radical ions under drought stress not only induces lipid peroxidation but also causes injury to membrane. Decrease in cell membrane stability in susceptible genotypes under drought is reported in contrast to tolerant genotypes (Chutipajit, 2016).

Plant response to stress occurs in a systematic way. Signal transduction is a cascade of reactions by which environmental signals are perceived and transduced into chemical form that in turn activate cell to respond in a specific way. Many signaling molecule are present, which can activate signal transduction processes. These molecules can be classified as primary and secondary messengers. Common second messengers may have an interaction with one another and create a network known as "cross talk". Plant hormones [auxins (IAA), gibberellins (GA), abscisic acid (ABA), cytokinins (CK), salicylic acid (SA), ethylene (ET), jasmonates (JA) and brassinosteroids (BR)] are molecules essential for the regulation of biological processes such as growth, development, reproduction, survival and plant defense mechanisms (Denance *et al.*, 2013). In nucleus, the biotic and abiotic stress signal is amplified to activate number of genes or the synthesis of regulatory molecules like ABA, SA, JA and ET, which can activate the second step of signaling network etc. Abscisic acid (ABA) is an important signal molecule in rice involved in several physiological processes like germination, seed dormancy, drought stress response (Ye *et al.*, 2011) and cause oxidative stress (Jiang and Zhang, 2001). It was reported that under stress conditions ABA is induced commonly because of activation of genes, which encodes ABA biosynthesis. Along with stress signals, ABA made apoplast a major site for H₂O₂ production (Hu *et al.*, 2006a). ABA plays a vital role in cell signaling in response to drought stress in rice and regulates the osmotic balance and enhances drought tolerance (Yin *et al.*, 2017). ABA also induced expression for genes coding for antioxidants such as SOD and CAT (Guan *et al.*, 2000) and thus increases the antioxidants activity such as CAT, SOD and of APX (Jiang and Zhang, 2001).

Jiang and Zhang (2002) reported that inhibition of ABA synthesis reduced the activity of plasma membrane-NADPH oxidase and generation of O₂⁻ in leaves and reciprocal effects were obtained by exogenous application of ABA. It showed that NADPH oxidase is involved in ABA induced-ROS production, which ultimately results in the induction of antioxidants defense system under drought and enhance drought tolerance in rice (Varshikar and Tan, 2016).

At high level of oxidative stress, ROS can damage

plant cellular components and biological molecules. For example, under drought stress excessive electron leakage to O₂ occurs during photosynthesis, generating ROS by Mehler reaction. Additionally, during Calvin cycle, the limited CO₂ fixation will reduce the NADP⁺ regeneration triggering the over-reduction of electron transport chain (Gechev *et al.*, 2006; Halliwell, 2006). Drought stress also affects photo-respiratory pathway, which produces excessive amount of H₂O₂ (de Carvalho, 2008; Miller *et al.*, 2010; Kao, 2017).

In rice leaves, H₂O₂ and O₂⁻ production increased under drought stress. H₂O₂ and O₂⁻ act as intracellular second messengers that regulate the induction of resistance, control different biological processes such as cell cycle, growth, cell death, hormone signaling development and drought stress responses in rice (Duan *et al.*, 2009).

Chloroplast is a robust cellular organelle in terms of having antioxidant enzymes and other metabolites for ROS quenching. Nevertheless, in drought stress, excessive quantity of OH⁻ radical is produced in thylakoids of chloroplast. Though OH⁻ radical has a short half-life, yet it has strong oxidizing nature and the ability to react with all biological molecules. Additionally, antioxidant defense system is unable to eliminate this extremely reactive radical. Thus, the accumulation of OH⁻ radical is deleterious for thylakoid membrane and the overall photosynthetic machinery (Asada, 2006; de Carvalho, 2008). Major limiting factor in rice production is oxidative stress caused by overproduction of ROS in rice organs under drought. Therefore, the efficient way to enhance drought tolerance in rice is to reduce ROS overproduction or enhance antioxidants activity in rice organs (Meng *et al.*, 2012).

Drought Signal Perception and ROS

Drought unlike most stresses triggers signaling cascade in plants. ROS also plays a significant role in this signal transduction under drought (Gilroy *et al.*, 2016). The signaling pathway is highly conserved and initiated by mitogen-activated protein kinases (MAPKs). In rice, under drought stress, transduction signaling pathway is also investigated (Singh and Jwa, 2013). H₂O₂ induces MAPKs, which are involved in downstream signal transduction cascades, MAPKs then triggers the activation of antioxidant system and ultimately which adjust expression of stress related genes (Kovtun *et al.*, 2000; Samuel *et al.*, 2000). For example, drought hypersensitive mutant 1 (DSM1; a MAPKKK) gene enhances drought tolerance in rice by regulating expression of two peroxidase genes (POX22.3 and POX8.1) expression, and ROS quenching (Ning *et al.*, 2010). The DSM2 mutant also exhibited enhanced tolerance in rice to oxidative and drought stress by controlling xanthophylls and abscisic acid (ABA) cycle (Du *et al.*, 2010). Similarly, overexpressed OsCPK4 gene (member of calcium-dependent protein kinases gene family in rice) showed drought tolerance by avoiding lipid peroxidation,

Table 1: Forms and production of ROS in plant cell and their features

Forms of ROS	Half life	Extent of reactivity	Type of action	Source of generation in cells	References
1O_2	3 ms	Highly reactive	Oxidize lipids, nucleic acid, proteins	ET reactions of photosystem II and Photo inhibition in chloroplasts.	(Zulfugarov <i>et al.</i> , 2014)
H_2O_2	1 ms	Moderately reactive	Oxidize thiol group of enzymes	Urate oxidase, Photorespiration and MnSOD and β -oxidation of fatty acid present in peroxisomes. ETCs of endoplasmic reticulum, chloroplasts, plasma membrane and mitochondria.	(Kao, 2014)
OH $^\cdot$	1 ns	Very highly reactive	React with lipids, proteins and DNA	O_3 decomposition occurs in apoplastic zone. Fenton reaction and Haber-Weiss reaction.	(Foyer <i>et al.</i> , 1997; Gill and Tuteja, 2010)
$O_2^{\cdot-}$	2-4 μ s	Moderately reactive	React with iron-sulfur compounds	Mehler reaction, mitochondrial ETCs reactions, photooxidation reactions, peroxisomes, glyoxisomal photorespiration and plasma membrane. NADPH oxidase in membranes. OH $^\cdot$ and O_3 reactions in apoplastic zone. Polypeptides and Xanthine oxidase in peroxisomes.	(Karuppanapandian <i>et al.</i> , 2011; Zulfugarov <i>et al.</i> , 2014)

1O_2 = Singlet oxygen; H_2O_2 = Hydrogen peroxides; OH $^\cdot$ = Hydroxyl ion; $O_2^{\cdot-}$ = Superoxide ion, MnSOD = Manganese-superoxide dismutase, ETC = electron transport chain, O_3 = Ozone, NADPH = Nicotinamide adeninedinucleotide phosphate

Table 2: ROS production in different sites of cellular organelles

Sites	Majorly produce	Biochemical processes responsible for ROS production	References
Peroxisomes	O_2 , H_2O_2	Flavin oxidases reactions, disproportionation of $O_2^{\cdot-}$ radicals and beta-oxidation of fatty acids and oxidation of glycolate. $O_2^{\cdot-}$ generated by xanthine oxidase (XOD) in peroxisomes and then converted by SOD to O_2 and H_2O_2 .	(del Rio <i>et al.</i> , 2006)
Mitochondria	H_2O_2 , $O_2^{\cdot-}$, OH $^\cdot$	Over reduction of ETC, Over-reduction of the ubiquinone (UQ). Major sites complex I (NADH dehydrogenase) and complex III (ubisemiquinone) produces $O_2^{\cdot-}$.	(Davidson and Schiest, 2001; Rhoads <i>et al.</i> , 2006; Quan <i>et al.</i> , 2008; Miller <i>et al.</i> , 2010)
Chloroplasts	1O_2 , H_2O_2 , $O_2^{\cdot-}$	Over reduction of ETC in photosystems I and in photosystem II (PSII) electrons leakage from QA and QB leads to ROS production	(Cleland and Grace, 1999; Miller <i>et al.</i> , 2010)
Endoplasmic reticulum	$O_2^{\cdot-}$	Cytochrome P_{450} reacts with an organic substrate which leads to the production of superoxide	(Mittler, 2002)
Apoplast	H_2O_2	Apoplastic ROS are produced by the enzymes oxidases and peroxidases and polyamine oxidases, oxalate oxidase	(Mittler, 2002; Moschou <i>et al.</i> , 2008; Voothuluru <i>et al.</i> , 2013)
Cell wall	H_2O_2 , OH $^\cdot$	Cell wall malate dehydrogenase and diamine oxidases are responsible for ROS production.	(Kao, 2017)
Plasma membrane	H_2O_2 , $O_2^{\cdot-}$	Production of superoxide is regulated by the NADPH in the plasma membrane	(Kao, 2014)

1O_2 = Singlet oxygen; H_2O_2 = Hydrogen peroxides, OH $^\cdot$ = Hydroxyl ion; $O_2^{\cdot-}$ = Superoxide ion, SOD = Superoxide dismutase, ETC = Electron transport chain, NADH = nicotinamide adenine dinucleotide hydrogen, QA = Primary acceptor quinone, QB = Secondary acceptor quinone, NADPH = Nicotinamide adenine dinucleotide phosphate

which is a symptom of oxidative stress (Campo *et al.*, 2014). Receptor-like kinases also play central role in rice development and in abiotic stresses. The *O. sativa* Stress-Induced protein Kinase gene 1 (OsSIK1) plays significant role under both salt and drought stress. Overexpressed OsSIK1 rice plants showed tolerance to oxidative, drought and salt stress by inducing antioxidant system. It was observed that the activity of antioxidants enzymes like catalase, super-oxide dismutase and peroxidases was higher in overexpressed rice plants with subsequent lower level of H_2O_2 (Ouyang *et al.*, 2010).

Rice plant roots detect drought stress and transmit the signals produced by hormones to leaves through xylem tissues where these signals trigger the closure of stomata (Miao *et al.*, 2006; Rivero *et al.*, 2007; Boursiac *et al.*, 2008) caused by ABA (Chen *et al.*, 2006; Nahar *et al.*, 2016). The stomatal closure reduces the amount of water loss through transpiration and limits the entry of CO_2 in the leaf tissues for photosynthesis in rice (Hung and Kao, 2004; Ji *et al.*, 2012; You *et al.*, 2013). Cross talk also exists between ROS and ABA under drought stress. Under drought, ABA accumulates in plants, which triggers the

activation of ABA-dependent downstream response in plant cell. In rice guard cells, ABA is responsible for the synthesis of H_2O_2 by NADPH oxidase (Hung and Kao, 2004). H_2O_2 further helps in stomatal closure (Kwak *et al.*, 2003) that leads in the reduction of water loss during transpiration in rice (You *et al.*, 2013).

Additionally, ROS signals originate from organelles during stress are also responsible for transcriptional reprogramming that can either protect plant cell or induce programmed cell death (Foyer and Noctor, 2005; Gechev *et al.*, 2006; Rhoads *et al.*, 2006). This type of reprogramming 0061so exists in rice, which involves organelle retrograde signaling in mediating ROS in synchronization with stress response. H_2O_2 production rate is faster in peroxisomes and chloroplasts (Foyer and Noctor, 2003), whereas, mitochondria are the more susceptible to such type of oxidative damage induced by H_2O_2 (Bartoli *et al.*, 2004). Downstream events altered by H_2O_2 in rice are protein phosphorylation, calcium mobilization, and gene expression (Steffens and Sauter, 2009).

The cytosolic Ca^{++} increases through the activation of Ca^{++} permeable channels. ROS has been shown to induce

the activation of these channels. In addition, H₂O₂ also induces MAPKs, which further triggers signaling cascade and modulation of gene expression. It also promotes the accumulation of antioxidants and induces the expression of respective genes like the up-regulation of AOX nuclear genes, increasing the synthesis of mitochondrial AOX enzyme thus regulating the redox status of the plant cell (de Carvalho, 2008).

Effect of Drought on Rice Plant

Drought stress is one of the limiting components in rice production as it causes cellular dehydration. Rice displays a variety of morphological, biochemical and physiological responses against water stress. These responses include stomatal closure, leaf rolling, osmotic adjustment and high relative water contents (Lima *et al.*, 2015; Nahar *et al.*, 2016). In rice, water stress at vegetative stage results in reducing photosynthesis efficiency, reduction in the rate of leaf expansion, leaf rolling, stunted growth, leaf senescence, reducing number of tillers and yield losses. Growth retardation starts because of poor root growth and reduction in leaf traits such as cuticular wax, colour, pubescence etc. (Nahar *et al.*, 2016). This disturbs the radiation absorption by leaf canopy inhibiting the energy reserves and affecting normal maturity (Blum, 2011). Drought stress also causes early leaf senescence that starts from the leaf tips and extended through the whole rice plant parts and eventually to all tillers (Bunnag and Pongthai, 2013). Drought influence various physiological processes and induces respective responses in rice like transpiration rate, net photosynthesis, stomatal conductance, intercellular CO₂, relative water contents, water use efficiency and photosystem activity (Liu *et al.*, 2006; Chaves *et al.*, 2009; Zlatev, 2009; Yang *et al.*, 2014).

Rice plant cells losses turgidity that is due to reduced water availability resulting in the reduction in cell division and expansion, severely affecting cell growth. Drought influences both cell expansion and elongation thus decreasing number of tillers and plant height of rice (Bunnag and Pongthai, 2013). Thus, it significantly reduces fresh/dry weight of plants affecting biomass production. The decreased shoot and root weight and their length ultimately lowers the rate of water uptake and photosynthesis. Both cell growth and photosynthesis are the vital processes affected by drought. It can directly affect the availability of CO₂ diffusing through the mesophyll and the stomata (Flexas *et al.*, 2007). It decreases leaf photosynthetic machinery (Ort, 2001). These effects can vary with time and intensity of stress along with plant species and leaf age. Mature leaves are more affected by the drought as compared to younger leaves (Munns, 2002; Flexas *et al.*, 2004).

Stomatal closure results due to the poor atmospheric vapor pressure and leaf turgor (Chaves *et al.*, 2009) leading to lower photosynthesis rate under drought (Flexas *et al.*,

2004; Chaves *et al.*, 2009). Drought stress decreases the ability of mesophyll cells to use the existing CO₂ (Karaba *et al.*, 2007). Consequently, quantity of active chlorophyll also decreases (Sarwar *et al.*, 2013). So, reduced photosynthetic activity results in insufficient photosynthetic products required for normal activities in plant cells leading to poor growth of rice plant (Bunnag and Pongthai, 2013). Drought adversely influences functionality of photosystem I and II (PSI, PSII) (Liu *et al.*, 2006; Zlatev, 2009). PSII activity is crucial in reduction reaction and ATP synthesis. Under unfavorable condition, the over-production of electrons in electron transport chain leads to ROS over-production. A balance must be maintained between the photo-assimilates requirement and photochemical activity. Drought disturbs this balance in rice plant especially in the flag leaf. It also causes damage to oxygen evolving center (OEC) located in PSII (Kawakami *et al.*, 2009) and degradation of D1 polypeptide (subunit of the PS II reaction center) leading to the inactivation of PSII reaction complex (Liu *et al.*, 2006; Zlatev, 2009). Such inactivation leads again to the production of ROS, which further leads to photo-inhibition and oxidative damage (Ashraf, 2009; Gill and Tuteja, 2010).

Osmoregulation is the major process in plant (Thapa *et al.*, 2011). Accumulation of various osmolytes such as proline, soluble sugar, phenolic contents and total free amino acids increases under drought stress and plays role in drought tolerance in plants by ROS scavenging (Anjum *et al.*, 2017). In plants, free proline and soluble sugar accumulation is involved in drought tolerance (Ito *et al.*, 2006). Glycine betaine (GlyBet) also protects photosynthetic machinery by stabilizing the Ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) structure and acts as oxygen ion scavenger under drought stress (Chen and Murata, 2008; Rezaei *et al.*, 2012). Exogenous application of GlyBet enhances the growth and yield in rice (Farooq *et al.*, 2009).

As yield is the ultimate objective of any crop plant. Drought has a negative effect on rice especially at reproductive stage and is responsible for low crop productivity (Pantuwan *et al.*, 2002). Time, duration and intensity of drought stress are linked with the delayed flowering. Particularly drought occurring at the end of vegetative stage results in delayed panicle development (Jonaliza *et al.*, 2004). The yield decline may be due to impairment of photosynthesis causing disturbance in source-sink ratio, phloem loading and translocation of assimilates. This may be attributed to reduction in CO₂ level, stomatal conductance, leaf area, chlorophyll pigments, water use efficiency and starch and sucrose synthesizing enzymes. All these attributes contribute to the reduction in rice plant growth and development resulting of overall losses in grain yield (Farooq *et al.*, 2009; Anjum *et al.*, 2011). Fig. 1 illustrates drought stress affecting possible mechanisms, which ultimately leads to retarded growth and yield reduction in rice.

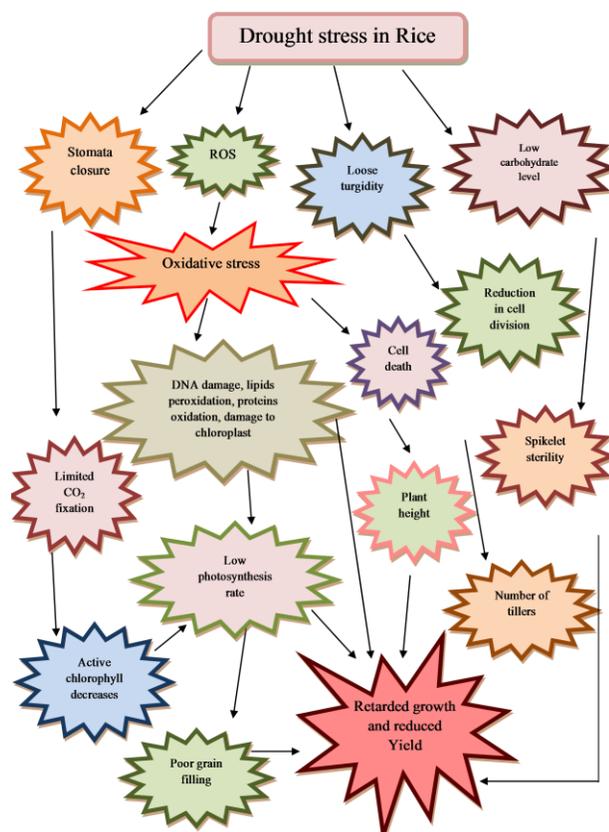


Fig. 1: Drought stress affecting possible mechanisms which ultimately lead to retarded growth and reduced yield in rice plant

In rice, drought induces spikelet sterility, which is responsible in reduction of rice yield (Jongdee *et al.*, 2002). Fluctuation in carbohydrates level and activities of enzymes linked with the blockage of starch accumulation in pollens are main causes of sterility in spikelet (Sheoran and Saini, 1996). Additionally, drought enhances the formation of ROS resulting in peroxidation of lipids, denaturation of proteins and nucleic acid damage affecting the whole metabolism (Hansen *et al.*, 2006; Gill and Tuteja, 2010) resulting in the reduction in grain yield. ROS acts both as stress and as signaling molecule, therefore understanding the production and quenching of ROS and its signaling role against (a) biotic stresses especially under drought stress and is very important in enhancing defense mechanism within plant cells.

Antioxidant Defense System and ROS

Plant possesses antioxidant defense system as a protection against oxidative damage (Gill and Tuteja, 2010). Antioxidants consist of enzymatic components such as MDHAR, CAT, GR, APX, SOD, GPX and enzymes involved in ascorbate-glutathione cycle (Mittler *et al.*, 2004; Karuppanapandian *et al.*, 2011; Kao, 2017). The detail of

cellular location, features and role of enzymatic antioxidants in ROS scavenging is described in Table 3. Phenolic compounds, tocopherol, carotenoid, flavonoids and glutathione are the components of non-enzymatic antioxidant defense system (Ji *et al.*, 2012). These compounds not only affect plant growth and development but also affecting the phenomena from cell enlargement and mitosis to senescence and even cell death (de Pinto and Gara, 2004). Location and role of non-enzymatic antioxidants with their features are given in Table 4.

The improvement in the expression of this system can improve tolerance in rice against drought stress (Wang *et al.*, 2005b). Therefore, increasing the efficiency of antioxidant system components can be a strategy against oxidative stress and increasing drought tolerance mechanism (Table 5). For example, activities of enzymatic antioxidants like CAT, POD and SOD increases under drought stress effectively decreasing the level of intracellular ROS in rice (Yang *et al.*, 2014). It was observed that the activity of SOD increased in rice under drought stress, exhibiting its role in detoxifying ROS under this type of abiotic stress. The activity of CAT enzyme is heterogeneous under drought stress. The reports indicated that the CAT activity either increases, unchanged or even decrease under drought stress in different plant species. Meng *et al.* (2012) also reported SOD1 mimic significant reduction in ROS production in rice root and leaf while increasing the antioxidants activity comprising on CAT and SOD1. It causes drought tolerance in rice tissues.

APX are the enzymatic antioxidants that convert H_2O_2 into O_2 and H_2O . It is suggested that APX is the major counteracting enzyme for ROS under drought stress. When activity of APX is inhibited due to excessive amount of ROS, CAT plays the role of quenching ROS. Compared to APX, which is present in different cellular organelles, CAT is present only in peroxisomes and removes excessive amount of ROS generated under stress conditions providing a clue of variation in its activity (de Carvalho, 2008). However, CAT activity can be inhibited by herbicides induced by ROS like methyl-viologen/paraquat (PQ) and 3-aminotriazole (AT) (Gechev *et al.*, 2008; Qureshi *et al.*, 2011). The rice APX plays an important role in development especially at seedling and reproductive stage by scavenging H_2O_2 under drought and some of the other abiotic stress (Zhang *et al.*, 2013).

The enzymes SOD, CAT and POD are vital antioxidant enzymes in rice cell (Chutipaijit, 2016). Among enzymatic antioxidants, ROS scavenging mechanism consists of two steps. In first step, SOD convert superoxide radicals into H_2O_2 while in second step H_2O_2 is further catalyzed by the POD and POD into H_2O to guard plant cell from H_2O_2 accumulation. However, H_2O_2 produced in result of SOD enzyme can perform a dual function either playing a role in oxidative stress signaling or act as secondary messenger to defend reactions leading to produced POD and CAT activity in rice plants. Furthermore, it was revealed

Table 3: Enzymatic antioxidants under drought stress their location and features in plants

Enzymatic Antioxidants	Location	Scavenging ROS form	Features and their Role	References
Superoxide dismutase	Cytosol, Chloroplasts, Peroxisomes and Mitochondria	O_2^-	Dismutate O_2^- and reduced to H_2O_2 and oxidized to O_2 . Enhanced drought tolerance.	(Roy <i>et al.</i> , 2009; Gill and Tuteja, 2010)
Guaiacol peroxidase	Chloroplasts, Cytosol, Mitochondria and Endoplasmic reticulum	H_2O_2	Many biosynthetic processes are in association of GPX comprising cell wall's lignification, wound healing, ethylene synthesis, degradation of IAA and resistance against drought.	(Asada, 2000)
Ascorbate peroxidase	Cytosol, Peroxisomes, Chloroplasts, and Mitochondria	H_2O_2	Significant role is played by APX in maintaining the ROS levels in cells. APX reduces H_2O_2 to water.	(Gill and Tuteja, 2010)
Monodehydro-ascorbate reductase	Chloroplasts, Mitochondria, and Cytosol	H_2O_2	MDHAR catalyzes the regeneration of AsA from MDHA. It has ability to use MDA an organic radical as a substrate and to reduce phenoxyl radicals.	(Sharma <i>et al.</i> , 2012)
Dehydroascorbate reductase	Chloroplasts, Mitochondria, and Cytosol	H_2O_2	It catalyzes reduction of DHA by GSH to AsA and shows a vital role in maintenance of AsA (reduced form).	(Boo and Jung, 1999; Sharma and Dubey, 2005)
Glutathione reductase	Cytosol, Chloroplasts, and Mitochondria	H_2O_2	GSSG is reduced to GSH by GR and cellular GSH/GSSG ratio is thus maintained by GR. It contains an essential disulfide group. It also detoxifies H_2O_2 produced in Mehler reaction.	(Boo and Jung, 1999; Sharma <i>et al.</i> , 2012)
Catalase	Peroxisomes, Glyoxisomes, and Mitochondria	H_2O_2	H_2O_2 produced in peroxisomes is mainly scavenged by CAT. Has specificity for H_2O_2 . CAT enhances the tolerance against abiotic stress in transgenic plants	(Roy <i>et al.</i> , 2009)

H_2O_2 = Hydrogen peroxides; O_2^- = Superoxide ion, O_2 = Oxygen, GPX = Guaiacol peroxidase, IAA = Indoleacetic acid, APX = Ascorbate peroxidase, MDHAR = Monodehydroascorbate reductase, AsA = Ascorbic acid, MDHA = Monodehydro ascorbate, MDA = Malondialdehyde, GSH = Glutathione, GSSG = Glutathione disulfide, GR = Glutathione reductase, CAT = Catalase

Table 4: Non-Enzymatic antioxidants their location and features in plants

Non-enzymatic Antioxidants	Location	Detoxify	Features and their Role	References
Ascorbic acid	Cytosol, Chloroplasts, Peroxisomes, Mitochondria, Vacuoles and Apoplast	H_2O_2	Ascorbate has a key role in defense against oxidative stress caused by overproduction of ROS. AsA plays an important role in several physiological processes in plants, including growth, differentiation and metabolism.	(Sharma and Dubey, 2005)
Glutathione	Cytosol, Chloroplasts, Peroxisomes, Mitochondria, Vacuoles and Apoplast	H_2O_2 , OH and O_2^-	It is non-protein thiol that plays an important role in intracellular defense against ROS-induced oxidative damage. GSH plays an important role in diverse biological processes, including cell growth/division, signal transduction, synthesis of proteins and nucleic acids and the expression of the stress responsive genes.	(Sharma and Dubey, 2005)
Flavonoids	Leaves, floral parts, pollens and vacuoles	OH and 1O_2	Flavonoids have many functions like flowers, fruits, and seed pigmentation, protection against UV light; defense against phyto-pathogens, role in plant fertility and germination of pollen. Flavonoids can directly scavenge H_2O_2 and OH.	(Lovdal <i>et al.</i> , 2010; Olsen <i>et al.</i> , 2010)
Tocopherols	Membranes	Lipid peroxides, and quench 1O_2	Tocopherols belong to lipophilic antioxidants group involved in scavenging of oxygen free radicals, lipid peroxy radicals, and 1O_2 . Tocopherols protect lipids and other membrane components by physically quenching and chemically reacting with O_2 in chloroplasts, thus protecting the structure and function of PSII.	(Foyer <i>et al.</i> , 1997; Kiffin <i>et al.</i> , 2006)

1O_2 = Singlet oxygen; H_2O_2 = Hydrogen peroxides; OH = Hydroxyl ion; O_2^- = Superoxide ion, AsA = Ascorbic acid, GSH = Glutathione

that the small increase in POD and CAT activity in drought-susceptible genotypes could decrease efficiency of rice plant cell to scavenge ROS (Chutipaijit, 2016). Drought tolerance in rice can be achieved by scavenging ROS using dehydrin proteins. Transgenic plants with overexpressed dehydrin proteins showed lower level of H_2O_2 production and thus rescue the rice plant from oxidative stress (Kumar *et al.*, 2014).

Other antioxidants, which play role especially in rice under drought stress, are glutathione (GSH), GR and MDHAR (Pandey and Shukla, 2015). Similarly, GPX are diverse antioxidant isozymes that reduce ROS and protect plant cellular component against oxidative stress. GPX are effective scavengers of lipid hydro-peroxides and H_2O_2 and enhance abiotic stress tolerance in rice (Koji *et al.*, 2009). They help in maintaining membrane integrity, redox homeostasis and tolerance to oxidative stress (Islam *et al.*,

2015). In rice, under drought stress, accumulation of proline showed that it is involved in solute regulation and reduction of water loss and thus play an important role in osmosis regulation. Proline also provides energy to growth and thus helps rice to tolerate water stress (Lum *et al.*, 2014). Improving the naturally occurring enzymatic and non-enzymatic antioxidant components can be one of the strategies of either preventing or reducing oxidative stress and thus improving drought tolerance in plants.

Novel Genes Linked with Tolerance and ROS Scavenging Mechanism

In stress perception to stress-responsive signaling transduction network, different transcription factors functions as transcriptional switches for the expression of stress related genes (Jiang *et al.*, 2015).

Table 5: Measurement of antioxidants at sensitive stages of rice prone to drought stress

Sensitive stages of rice	Antioxidants activity	References
Vegetative stages		
Seedling stage	SOD and APX activity increases under low and mild stress while decrease in severe stress while subsequent increase occurred with stress severity in case of GPX.CAT, POD and SOD activity increases under stress in rice. Thus, showing antioxidants activity is correlated with drought tolerance in rice	(Mishra and Panda, 2017; Lum <i>et al.</i> , 2014; Chutipaiji, 2016)
Flag leaf stage	MDA content increases depicting more lipid peroxidation in susceptible rice genotypes under drought stress. SOD converts O ₂ ⁻ radical into H ₂ O ₂ which is further quenched by APX and CAT within cells.	(Refli <i>et al.</i> , 2014)
Jointing stage	Antioxidants activity increases under stress leading to tolerance in rice genotypes SOD, CAT, APX, POD and GR significantly increased under drought and linked with drought tolerance in rice	(Duan <i>et al.</i> , 2009)
Reproductive stages		
Booting stage	DHAR and SOD activity increased under drought stress and provide antioxidant defense against oxidative stress in tolerant rice genotypes	(Ji <i>et al.</i> , 2012)
Panicle initiation	Higher antioxidant activity of SOD, APX, GR and GSH showed an important role in oxidative defense in rice tolerant genotypes by minimizing drought induced spikelet sterility	(Selote and Chopra, 2004)
Heading stage	Less MDA content and high SOD and POD activity was measured in drought tolerant rice genotypes while reciprocal results were obtained in susceptible genotypes	(Li <i>et al.</i> , 2015)
Grain filling stage	SOD activity increase under drought stress in mild stress in comparison to severe drought stress in rice	(Refli <i>et al.</i> , 2014)

SOD = Superoxide dismutase, APX = Ascorbate peroxidase, GPX = Guaiacol peroxidase, CAT= Catalase, POD = Peroxidases, MDA = Malondialdehyde, O₂⁻ = Superoxide ion, H₂O₂ = Hydrogen peroxides, GR = Glutathione reductase, DHAR = Dehydroascorbate reductase, GSH = Glutathione

Drought triggers the expression of huge array of genes inside the cell. The expression of these genes is regulated by complex transcriptional factors (Amorim *et al.*, 2016; Gahlaut *et al.*, 2016). Several key genes in this regulatory network have been identified and characterized. We are highlighting ROS-dependent transcriptional networks under drought stress condition in plants, particularly in rice.

Zinc finger proteins (ZFP) have an important role in cellular processes in eukaryotes (Englbrecht *et al.*, 2004). These proteins are involved in growth and development; stress and subsequent stimulation of the defense response in plants (Huang *et al.*, 2009a; Wang *et al.*, 2005a). Additionally, member of ZFP family play role in plant response to oxidative stress (Qureshi *et al.*, 2013; He *et al.*, 2016). Rice ZFPs have also been found to have a role in drought stress response. *ZFP245* gene transferred to rice showed tolerance for exogenous H₂O₂ indicating the activate role of the gene in antioxidant system. Transgenic rice with overexpressed *ZFP245* exhibited enhanced tolerance to cold, salt and drought stress. It was observed that *ZFP245* triggers the ROS scavenging system by activating antioxidant SOD in rice under drought stress (Huang *et al.*, 2009a). In addition, various members of Cys2/His2 (C2H2) type ZFPs viz., *ZFP179*, *ZFP182*, *ZFP245* and *ZFP252* are involved in responses against drought and oxidative stress in rice. C2H2 type ZFPs have key role in management of ROS signaling. Overexpression of *ZFP179* and *ZFP245* enhances the drought tolerance to oxidative stress by enhancing SOD and peroxidases activities (Huang *et al.*, 2009a; Sun *et al.*, 2010). Similarly, drought and salt tolerance (DST) gene control stomatal closure by regulating the H₂O₂ level in guard cells. Mutation of DST activates the stomata closure due to the H₂O₂ gathering in guard cells. Consequentially, tolerance to drought and salt is achieved in plants (Huang *et al.*, 2009b). Recently, it was found that DST works in close association with DST Co-activator 1 (DCA1) in the control of stomatal aperture and regulation of downstream genes

under both drought and salt stress. In guard cells, this DST-DCA1 complex regulates gene expression involved in the synthesis of peroxidase precursor. Peroxidase is involved in the detoxification of H₂O₂. DCA1 negatively regulates drought stress tolerance as over expression of this gene results in intensified sensitivity to stress (Cui *et al.*, 2015). Higher peroxidase activity was observed with overexpression of *OsAHL1* gene involved in drought tolerance in rice by alleviating plasma membrane (Zhou *et al.*, 2016).

The WRKY belong to a group of large family comprising of 102 and 74 members in *Oryza sativa* and *Arabidopsis thaliana*, respectively. The WRKY name is derivative of the presence of conserved 60 amino acid WRKY domain (Wu *et al.*, 2005). Different members of this family are involved in response to (a) biotic stresses. The increased genetic expression of these WRKY proteins has been associated frequently in response to ROS and ABA in rice under water deficit conditions. For example, *OsWRKY30* play significant role in drought stress as the overexpression of this gene in rice was found to increase drought tolerance. Moreover, the *OsWRKY30* protein also interacts with MAPKs suggesting its downstream interactive role with MAPK cascade (Shen *et al.*, 2012). Another member of this family (*OsWRKY45*) also play an important role against drought stress in *Arabidopsis* and rice (Qiu and Yu, 2008; Tao *et al.*, 2011). The *Arabidopsis* transcriptional factor (*WRKY57*) when transferred to rice confers drought tolerance. These transgenic rice plants exhibited reduced water loss, malondialdehyde (MDA) contents, electrolyte leakage and cell death symptoms, while these plants were also higher in antioxidant enzymes and proline contents. An up-regulation of stress responsive genes was also observed in these transgenic rice plants against drought stress (Jiang *et al.*, 2016).

In plants, NAC (for NAM, ATAF-1,-2 and CUC2) transcription factor family is one of the largest transcription

factor families consisting of over a 100 family members in *Arabidopsis* (Riechmann *et al.*, 2000). Many NAC proteins are involved in hormone related processes such as plant growth and development and in different environmental stresses (Xie *et al.*, 2000; Fujita *et al.*, 2004). In rice, about 151 NAC genes were identified from genome-wide data analysis (Nuruzzaman *et al.*, 2010). Evidences indicate that members of NAC family are involved in drought tolerance or oxidative stress (Chen *et al.*, 2016; Zhu *et al.*, 2016). These transcriptional factors include OsNAC1, OsNAC5, OsNAC6 and OsNAC10 (Hu *et al.*, 2006b; Nakashima *et al.*, 2007; Takasaki *et al.*, 2010). Few of these transcriptional factors are also involved in tolerance to oxidative stress. Such as, OsSRO1c a rice homologue of SRO (a protein family) was characterized with SNAC1 (stress responsive NAC 1). Overexpression of OsSRO1c leads to enhanced drought and oxidative stress tolerance (You *et al.*, 2013). Similarly, overexpression of OsNAC5 (Song *et al.*, 2011) and *ONAC095* transcription factor improves drought and oxidative stress tolerance in rice (Huang *et al.*, 2016).

In plants, drought stress induces ROS generation, which in turn triggers the expression of several ROS scavenging gene families. These include genes expressing APX, SOD, myo-inositol monooxygenase, peroxiredoxin, MDHAR glutathione *S*-transferases and genes for proline synthesis (a non-enzymatic antioxidant). *Manganese-superoxide dismutase (MnSOD)* gene expresses itself in chloroplast of transgenic rice and enhances the tolerance of rice by increasing the antioxidant capacity via higher SOD activity. About 1.5 folds increase in the SOD activity was observed in *MnSOD* transgenic rice. Plants expressing SOD can protect their photosynthetic apparatus and transgenic plant has a higher photosynthetic rate than the wild type plants under drought stress (Wang *et al.*, 2005b). Cytosolic copper/zinc-containing superoxide dismutase (*Cu/Zn SOD*) removes toxic superoxides from plant cells (Pan *et al.*, 2001). *Cu/ZnSOD* gene was transferred from *Avicennia marina* to *Oryza sativa* (Pusa Basmati-1) and thus transgenic plants increased tolerance to drought stress. Transgenic rice with the overexpression of SOD1 (cDNA of cytosolic *Cu/Zn SOD*) showed tolerance for oxidative and drought stress (Prashanth *et al.*, 2008). APX is an antioxidant enzyme that converts H₂O₂ into water. Rice genome contains eight APX genes that translate different isoforms of APX enzyme. Out of these genes, OsAPX2, a member of cytosolic APX genes (Teixeira *et al.*, 2006) and key element of reactive oxygen network in rice genome, plays role in defense against oxidative injury caused by drought stress in rice seedlings (Zhang *et al.*, 2013). It has been reported that APX8 and APX3 genes were responsible for drought tolerance in IR64 and Nagina 22 rice genotype, respectively (Prakash *et al.*, 2016).

GPXs are a group of antioxidant enzymes having peroxidases without haem-thiol group. These enzymes reduce H₂O₂ to water and lipid hydroperoxides to their

respective alcohols by using reduced GSH. It has been shown that *Pennisetum glaucum* GPX (PgGPX) gene plays a significant role against limited water stress in transgenic rice plants. These transgenic plants have lesser amount of MDA and ROS and higher proline contents. This clearly indicates that the PgGPX gene is involved in the repression of ROS production by sustaining a higher level of antioxidant defense activity (Islam *et al.*, 2015). MIOX is a myo-inositol monooxygenase, which has a key role in production of ascorbic acid a major antioxidant which reduces oxidative damage (Shao *et al.*, 2008). Overexpression of OsMIOX (myo-inositol oxygenase gene) enhances drought tolerance and ROS scavenging ability leading to decrease in oxidative damage in rice (Duan *et al.*, 2012). Oornithine δ -aminotransferase (δ -OAT) is an enzyme in plants involved in proline synthesis (Stranska *et al.*, 2008). Proline is a major non-enzymatic antioxidant, which scavenges ROS under abiotic stress (Gill and Tuteja, 2010). Transgenic rice with the overexpression of OsOAT gene showed enhanced tolerance to drought stress. Overexpression of OsOAT in rice also increases the activities of certain enzymes involved in ROS quenching and antioxidants such as GSH content and protect cells from oxidative damage (You *et al.*, 2012). Access to these genes is due to molecular breeding which upgraded many varieties with enhanced tolerance against abiotic stress in rice (Gonzaga *et al.*, 2015).

Conclusion and Future Prospects

It is evident that drought is a major limiting factor of rice production in the world. Drought adversely affects photosynthesis and cell growth and development in rice. Drought stress leads to closure of stomata resulting in lower photosynthesis rate and increases photorespiration, which leads to overproduction of ROS. As a consequent, the balance of ROS and antioxidants is disturbed, leading to excessive production of ROS, which further leads to oxidative stress. ROS acts not only as phytotoxic molecule it also has a signaling role under drought stress. ROS signaling function is under strict control of antioxidant scavenging system and any imbalance between the production and scavenging of antioxidants can effect signal transduction. There is a complex cross-talk between ROS and ABA, calcium and other signaling molecules during drought perception and plant response in addition to other (a) biotic stresses. Plants exhibits drought tolerance through expression of gene cascade that is involved in ROS-dependent pathway. The genes especially transcription factors that are upstream of this pathway are important in regulating the expression of other genes to help reduce ROS toxicity, osmotic stress and maintain plant productivity under drought stress. A large number of gene families are present in rice that have regulatory role yet the data available for drought related gene, especially are linked to ROS, is inadequate as compared to *Arabidopsis*.

Additionally, the information on transcriptional factors and their *cis*-elements is also not available. The information is also lacking for the step-wise activation of ROS dependent and drought associated protein kinase and subsequent cascade. Therefore, further research, for the identification and characterization of drought-ROS responsive genes, is needed to gain a better understanding of cellular mechanism against drought stress. Bioinformatics and expression analyses can be valuable tools for the exploration of transcription factors along with their target genes. Some new genes have been discovered which can help plant to tolerate drought and oxidative stress. Characterization of these key drought tolerant genes can acts as biomarkers of rice stress response. Moreover, drought stress is a complex trait and plant behavior is dependent on the application of drought treatment. For example, there is a difference in plant response to water deficit conditions compared to that of application of chemicals (Polyethylene glycol) that create osmotic pressure and thus reduces water uptake by plants. The plant behavior in the field is also different to that in the controlled environmental conditions. Nevertheless, the technological advancement and progress of expressional data of genes will increase our knowledge of ROS linked drought response in rice. To fulfill the world's requirement for rice, further discoveries are needed to understand the regulatory process of drought induced ROS response and tolerance of plant. Research has to be focused on plants, which can withstand the severe environmental conditions like drought and have the ability to scavenge ROS.

References

- Amorim, L.L.B., J.P.B. Neto, R.F. Santos, J.R.C.F. Neto, E.A. Kido, M. Matos and A.M.B. Iseppon, 2016. Transcription factors involved in plant drought tolerance regulation. In: *Drought Stress Tolerance in Plants: Molecular and Genetic Perspectives*, pp: 315–358. Hossain, M.A., S. Wani, S. Bhattacharjee, D. Burritt and L.S. Tran (eds.). Springer International Publishing, New York, USA
- Anjum, S.A., U. Ashraf, M. Tanveer, I. Khan, S. Hussain, B. Shahzad, A. Zohaib, F. Abbas, M.F. Saleem, I. Ali and L.C. Wang, 2017. Drought induced changes in growth, osmolyte accumulation and antioxidant metabolism of three maize hybrids. *Front. Plant Sci.*, 8: 69
- Anjum, S.A., M. Farooq, L.C. Wang, L.L. Xue, S.G. Wang, L. Wang, S. Zhang and M. Chen, 2011. Gas exchange and chlorophyll synthesis of maize cultivars are enhanced by exogenously-applied glycinebetaine under drought conditions. *Plant Soil Environ.*, 57: 326–331
- Apel, K. and H. Hirt, 2004. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu. Rev. Plant Biol.*, 55: 373–399
- Asada, K., 2006. Production and scavenging of reactive oxygen species in chloroplasts and their functions. *Plant Physiol.*, 141: 391–396
- Asada, K., 2000. The water-water cycle as alternative photon and electron sinks. *Phil. Trans. R. Soc. Lond. B. Biol. Sci.*, 355: 1419–1431
- Ashraf, M., 2009. Biotechnological approach of improving plant salt tolerance using antioxidants as markers. *Biotechnol. Adv.*, 27: 84–93
- Bartoli, C.G., F. Gomez, D.E. Martinez and J.J. Guiamet, 2004. Mitochondria are the main target for oxidative damage in leaves of wheat (*Triticum aestivum* L.). *J. Exp. Bot.*, 55: 1663–1669
- Bashir, N., S. Mahmood, Z. Zafar, S. Rasul, H. Manzoor and H. Athar, 2016. Is drought tolerance in maize (*Zea mays* L.) cultivars at the juvenile stage maintained at the reproductive stage? *Pak. J. Bot.*, 48: 1385–1392
- Basu, S., V. Ramegowda, A. Kumar and A. Pereira, 2016. Plant adaptation to drought stress. *F1000 Res.*, 5: 1554
- Bishwajit, G., S. Sarker, M.A. Kpoghomou, H. Gao, L. Jun, D. Yin and S. Ghosh, 2013. Self-sufficiency in rice and food security: a South Asian perspective. *Agric. Food Secur.*, 2: 10–15
- Blokhina, O. and K.V. Fagerstedt, 2010. Reactive oxygen species and nitric oxide in plant mitochondria: origin and redundant regulatory systems. *Physiol. Plant.*, 138: 447–462
- Blum, A., 2011. Drought tolerance: Is it a complex trait? *Funct. Plant Biol.*, 38: 753–757
- Boo, Y.C. and J. Jung, 1999. Water deficit - Induced oxidative stress and antioxidative defenses in rice plants. *J. Plant Physiol.*, 155: 255–261
- Botwright, A.T.L., H.R. Lafitte and L.J. Wade, 2008. Genotype and environment interactions for grain yield of upland rice backcross lines in diverse hydrological environments. *Field Crops Res.*, 108: 117–125
- Boursiac, Y., J. Boudet, O. Postaire, D.T. Luu, C. Tournaire-Roux and C. Maurel, 2008. Stimulus-induced downregulation of root water transport involves reactive oxygen species-activated cell signalling and plasma membrane intrinsic protein internalization. *Plant J.*, 56: 207–218
- Bunnag, S. and P. Pongthai, 2013. Selection of rice (*Oryza sativa* L.) cultivars tolerant to drought stress at the vegetative stage under field conditions. *Amer. J. Plant Sci.*, 4: 1701–1708
- Campo, S., P. Baldrich, J. Messeguer, E. Lalanne, M. Coca and B. san Segundo, 2014. Overexpression of a calcium-dependent protein kinase confers salt and drought tolerance in rice by preventing membrane lipid peroxidation. *Plant Physiol.*, 165: 688–704
- Chan, K.X., S.Y. Phua, P. Crisp, R. McQuinn and B.J. Pogson, 2016. Learning the languages of the chloroplast: retrograde signalling and beyond. *Ann. Rev. Plant Biol.*, 67: 25–53
- Chaves, M.M., J. Flexas and C. Pinheiro, 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann. Bot.*, 103: 551–560
- Chen, C.W., Y.W. Yang, H.S. Lur, Y.G. Tsai and M.C. Chang, 2006. A novel function of abscisic acid in the regulation of rice (*Oryza sativa* L.) root growth and development. *Plant Cell Physiol.*, 47: 1–13
- Chen, S.P., I.W. Lin, X. Chen, Y.H. Huang, H.C. Chang, H.S. Lo, H.H. Lu and K.W. Yeh, 2016. Sweet potato NAC transcription factor, IbNAC1, upregulates sporamin gene expression by binding the SWRE motif against mechanical wounding and herbivore attack. *Plant J.*, 86: 234–248
- Chen, T.H.H. and N. Murata, 2008. Glycinebetaine: an effective protectant against abiotic stress in plants. *Trends Plant Sci.*, 13: 499–505
- Chutipajit, S., 2016. Changes in physiological and antioxidant activity of indica rice seedlings in response to mannitol-induced osmotic stress. *Chil. J. Agric. Res.*, 76: 455–462
- Cui, L.G., J.X. Shan, M. Shi, J.P. Gao and H.X. Lin, 2015. DCA1 acts as a transcriptional co-activator of DST and contributes to drought and salt tolerance in rice. *PLoS Genet.*, 11: e1005617
- Cleland, R.E. and S.C. Grace, 1999. Voltammetric detection of superoxide production by photosystem II. *FEBS Lett.*, 457: 348–352
- Das, K. and A. Roychoudhury, 2014. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Front. Environ. Sci.*, 2: 53
- Denance, N., A. Sanchez-Vallet, D. Goffner and A. Molina, 2013. Disease resistance or growth: the role of plant hormones in balancing immune responses and fitness costs. *Front. Plant Sci.*, 4: 155
- Davidson, J.F. and R.H. Schiestl, 2001. Mitochondrial respiratory electron carriers are involved in oxidative stress during heat stress in *Saccharomyces cerevisiae*. *Mol. Cell Biol.*, 21: 8483–8489
- de Carvalho, M.H.C., 2008. Drought stress and reactive oxygen species Production, scavenging and signaling. *Plant Signal. Behav.*, 3: 156–165
- de Pinto, M.C. and L.D. Gara, 2004. Changes in the ascorbate metabolism of apoplastic and symplastic spaces are associated with cell differentiation. *J. Exp. Bot.*, 55: 2559–2569
- del Rio, L.A., L.M. Sandalio, F.J. Corpas, J.M. Palma and J.B. Barroso, 2006. Reactive oxygen species and reactive nitrogen species in peroxisomes, production, scavenging, and role in cell signaling. *Plant Physiol.*, 141: 330–335

- Du, H., N. Wang, F. Cui, X. Li, J. Xiao and L. Xiong, 2010. Characterization of the beta-carotene hydroxylase gene DSM2 conferring drought and oxidative stress resistance by increasing xanthophylls and abscisic acid synthesis in rice. *Plant Physiol.*, 154: 1304–1318
- Duan, J., M. Zhanga, H. Zhanga, H. Xionga, P. Liua, J. Ali, J. Li and Z. Li, 2012. OsMIOX, a myo-inositol oxygenase gene, improves drought tolerance through scavenging of reactive oxygen species in rice (*Oryza sativa* L.). *Plant Sci.*, 196: 143–151
- Duan, Z.Q., L. Bai, Z.G. Zhao, G.P. Zhang, F.M. Cheng, L.X. Jiang and K.M. Chen, 2009. Drought-stimulated activity of plasma membrane nicotinamide adenine dinucleotide phosphate oxidase and its catalytic properties in rice. *J. Integr. Plant Biol.*, 51: 1104–1115
- Englbrecht, C.C., H. Schoof and S. Bohm, 2004. Conservation, diversification and expansion of C₂H₂ zinc finger proteins in the *Arabidopsis thaliana* genome. *BMC Genomics*, 5: 39
- FAOSTAT, 2017. *FAO Cereal Supply and Demand Brief*. Available at: <http://www.fao.org/worldfoodsituation/csdb/en/> (Accessed: 7 April 2017)
- Farooq, M., A. Wahid and D.J. Lee, 2009. Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. *Acta Physiol. Plant.*, 31: 937–945
- Flexas, J., A. Diaz-Espejo, J. Galmes, R. Kaldenhoff, H. Medrano and M. Ribas-Carbo, 2007. Rapid variations of mesophyll conductance in response to changes in CO₂ concentration around leaves. *Plant Cell Environ.*, 30: 1284–1298
- Flexas, J., J. Bota, F. Loreto, G. Cornic and T.D. Sharkey, 2004. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biol.*, 6: 269–279
- Foyer, C.H. and G. Noctor, 2005. Oxidant and antioxidant signaling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. *Plant Cell Environ.*, 29: 1056–1107
- Foyer, C.H. and G. Noctor, 2003. Redox sensing and signaling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. *Physiol. Plant.*, 119: 355–364
- Foyer, C.H., H. Lopez-Delgado, J.F. Dat and I.M. Scott, 1997. Hydrogen peroxide and glutathione-associated mechanisms of acclimatory stress tolerance and signaling. *Physiol. Plant.*, 100: 241–254
- Fujita, M., Y. Fujita, K. Maruyama, M. Seki, K. Hiratsu, M. Ohme-Takagi, L.S. Tran, K. Yamaguchi-Shinozaki and K. Shinozaki, 2004. A dehydration-induced NAC protein, RD26, is involved in a novel ABA-dependent stress-signaling pathway. *Plant J.*, 39: 3863–3876
- Gahlaut, V., V. Jaiswal, A. Kumar and P.K. Gupta, 2016. Transcription factors involved in drought tolerance and their possible role in developing drought tolerant cultivars with emphasis on wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.*, 129: 2019–2042
- Gechev, T.S., M.A. Ferwerda, N. Mehterov, C. Laloi, M.K. Qureshi and J. Hille, 2008. *Arabidopsis* AAL-toxin resistant mutant atr1 shows enhanced tolerance to programmed cell death induced by reactive oxygen species. *Biochem. Biophys. Res. Commun.*, 375: 639–644
- Gechev, T.S., F. Van Breusegem, J.M. Stone, I. Denev and C. Laloi, 2006. Reactive oxygen species as signal that modulate plant stress responses and programmed cell death. *BioEssays*, 28: 1091–1101
- Gill, S.S. and N. Tuteja, 2010. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.*, 48: 909–930
- Gilroy, S., M. Bialasek, N. Suzuki, M. Górecka, A.R. Devireddy, S. Karpinski and R. Mittler, 2016. ROS, calcium and electric signals: key mediators of rapid systemic signaling in plants. *Plant Physiol.*, 171: 1606–1615
- Gonzaga, Z.J., K. Aslam, E.M. Septiningsih and B.C.Y. Collard, 2015. Evaluation of SSR and SNP markers for molecular breeding in rice. *Plant Breed. Biotechnol.*, 3: 139–152
- Guan, L., J. Zhao and J.G. Scandalios, 2000. Cis-elements and trans actors that regulate expression of the maize Cat1 antioxidant gene in response to ABA and osmotic stress: H₂O₂ is the likely intermediary signaling molecule for the response. *Plant J.*, 22: 87–95
- Halliwell, B., 2006. Reactive species and antioxidants. redox biology is a fundamental theme of aerobic life. *Plant Physiol.*, 141: 312–322
- Hansen, J.M., Y.M. Go and D.P. Jones, 2006. Nuclear and mitochondrial compartmentation of oxidative stress and redox signaling. *Annu. Rev. Pharmacol. Toxicol.*, 46: 215–234
- He, L., X. Ma, Z. Li, Z. Jiao, Y. Li and D.W. Ow, 2016. Maize OXIDATIVE STRESS2 homologs enhance cadmium tolerance in *Arabidopsis* through activation of a putative SAM-dependent methyltransferase gene. *Plant Physiol.*, 171: 1675–1685
- Heyno, E., V. Mary, P. Schopfer and A. Krieger-Liszskay, 2011. Oxygen activation at the plasma membrane: relation between superoxide and hydroxyl radical production by isolated membranes. *Planta*, 234: 35–45
- Hu, H., M. Dai, J. Yao, B. Xiao, X. Li, Q. Zhang and L. Xiong, 2006b. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance rice. *Proc. Natl. Acad. Sci. USA*, 103: 12987–12992
- Hu, X., A. Zhang, J. Zhang and M. Jiang, 2006a. Abscisic acid is a key inducer of hydrogen peroxide production in leaves of maize plants exposed to water stress. *Plant Cell Physiol.*, 47: 1484–1495
- Huang, J., S.J. Sun, D.Q. Xu, X. Yang, Y.M. Bao, Z.F. Wang, H.J. Tang and H. Zhang, 2009a. Increased tolerance of rice to cold, drought and oxidative stresses mediated by the overexpression of a gene that encodes the zinc finger protein ZFP245. *Biochem. Biophys. Res. Commun.*, 389: 556–561
- Huang, L., Y. Hong, H. Zhang, D. Li and F. Song, 2016. Rice NAC transcription factor ONAC095 plays opposite roles in drought and cold stress tolerance. *BMC Plant Biol.*, 16: 203
- Huang, X.Y., D.Y. Chao, J.P. Gao, M.Z. Zhu, M. Shi and H.X. Lin, 2009b. A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. *Gen. Dev.*, 23: 1805–1817
- Hung, K.T. and C.H. Kao, 2004. Hydrogen peroxide is necessary for abscisic acid-induced senescence of rice leaves. *J. Plant Physiol.*, 161: 1347–1357
- Islam, T., M. Manna and M.K. Reddy, 2015. Glutathione peroxidase of *Pennisetum glaucum* (PgGPx) is a functional Cd²⁺ dependent peroxidoredoxin that enhances tolerance against salinity and drought stress. *PLoS One*, 10: e0143344
- Ito, Y., K. Katsura, K. Maruyama, T. Taji, M. Kobayashi, M. Seki, K. Shinozaki and K. Yamaguchi-Shinozaki, 2006. Functional analysis of rice DREB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice. *Plant Cell Physiol.*, 47: 141–153
- Jaleel, C.A., P. Manivannan, A. Wahid, M. Farooq, H.J. Al-Juburi, R. Somasundaram and R. Panneerselvam, 2009. Drought Stress in Plants: A Review on Morphological Characteristics and Pigments Composition. *Int. J. Agric. Biol.*, 11: 100–105
- Ji, K., Y. Wang, W. Sun, Q. Lou, H. Mei, S. Shen and H. Chen, 2012. Drought-responsive mechanisms in rice genotypes with contrasting drought tolerance during reproductive stage. *J. Plant Physiol.*, 169: 336–344
- Jiang, M. and J. Zhang, 2002. Involvement of plasma-membrane NADPH oxidase in abscisic acid- and water stress-induced antioxidant defense in leaves of maize seedlings. *Planta*, 215: 1022–1030
- Jiang, M. and J. Zhang, 2001. Effect of abscisic acid on active oxygen species, antioxidative defence system and oxidative damage in leaves of maize seedlings. *Plant Cell Physiol.*, 42: 1265–1273
- Jiang, W., J. Wu, Y. Zhang, L. Yin and J. Lu, 2015. Isolation of a WRKY30 gene from *Muscadimia rotundifolia* (Michx) and validation of its function under biotic and abiotic stresses. *Protoplasma*, 252: 1361–1374
- Jiang, Y., Y. Qiu, Y. Hu and D. Yu, 2016. Heterologous expression of AtWRKY57 confers drought tolerance in *Oryza sativa*. *Front. Plant Sci.*, 7: 145
- Jonaliza, C.L., G. Pantuwan, B. Jongdee and T. Toojinda, 2004. Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiol.*, 135: 384–399
- Jongdee, B., S. Fukai and M. Cooper, 2002. Leaf water potential and osmotic adjustment as physiological traits to improve drought tolerance in rice. *Field Crops Res.*, 76: 153–163

- Kamoshita, A., R.C. Babu, N.M. Boopathi and S. Fukai, 2008. Phenotypic and genotypic analysis of drought-resistance traits for development of rice cultivars adapted to rainfed environments. *Field Crops Res.*, 109: 1–23
- Kamoshita, A., R. Rodriguez, A. Yamauchi and L. Wade, 2004. Genotypic variation in response of rainfed lowland to prolonged drought and rewetting. *Plant Prod. Sci.*, 7: 406–420
- Kao, C.H., 2017. Mechanism of salt tolerance in rice plants; cell wall related genes and expansins. *J. Taiwan Agric. Res.*, 66: 87–93
- Kao, C.H., 2014. Role of Hydrogen Peroxide in Rice Plants. *Crop Environ. Biotechnol.*, 11: 1–10
- Karaba, A., S. Dixit, R. Greco, A. Aharoni, K.R. Trijatmiko, N. Marsh-Martinez, A. Krishnan, K.N. Nataraja, M. Udayakumar and A. Pereira, 2007. Improvement of water use efficiency in rice by expression of HARDY, an *Arabidopsis* drought and salt tolerance gene. *Proc. Natl. Acad. Sci. USA*, 104: 15270–15275
- Karuppanapandian, T., J.C. Moon, C. Kim, K. Manoharan and W. Kim, 2011. Reactive oxygen species in plants: their generation, signal transduction, and scavenging mechanisms. *Aust. J. Crop Sci.*, 5: 709–725
- Kumar, M., S.C. Lee, J.Y. Kim, S.J. Kim, S.S. Aye and S.R. Kim, 2014. Over-expression of dehydrin gene, *OsDhn1* improves drought and salt stress tolerance through scavenging of reactive oxygen species in rice (*Oryza sativa* L.). *J. Plant Biol.*, 57: 383–393
- Kwak, J.M., I.C. Mori, Z.M. Pei, N. Leonhardt, M.A. Torres, J.L. Dangl, R.E. Bloom, S. Bodde, J.D.G. Jones and J.I. Schroeder, 2003. NADPH oxidase *AtrbohD* and *AtrbohF* genes function in ROS-dependent ABA signaling in *Arabidopsis*. *EMBO J.*, 22: 2623–2633
- Kawakami, K., Y. Umenab, N. Kamiyab and J. Shen, 2009. Location of chloride and its possible functions in oxygen-evolving photosystem II revealed by X-ray crystallography. *Proc. Natl. Acad. Sci. USA*, 106: 8567–8572
- Kerchev, P., C. Waszczak, A. Lewandowska, P. Willems, A. Shapiguzov, Z. Li, S. Alseekh, P. Mühlentock, F.A. Hoeberichts and F.V. Breusegem, 2016. Lack of GLYCOLATE OXIDASE1, but not GLYCOLATE OXIDASE 2, attenuates the photorespiratory phenotype of CATALASE2- deficient *Arabidopsis*. *Plant Physiol.*, 171: 1704–1719
- Kiffin, R., U. Bandyopadhyay and A.M. Cuervo, 2006. Oxidative stress and autophagy. *Antioxid. Redox Signal.*, 8: 152–162
- Koji, Y., M. Shiro, K. Michio, T. Mitsutaka and M. Hiroshi, 2009. Antioxidant capacity and damages caused by salinity stress in apical and basal regions of rice leaf. *Plant Prod. Sci.*, 12: 319–326
- Kovtun, Y., W.L. Chiu, G. Tena and J. Sheen, 2000. Functional analysis of oxidative stress-activated mitogen-activated protein kinase cascade in plants. *Proc. Natl. Acad. Sci. USA*, 97: 2940–2945
- Li, Y., J. Xiang, Y. Wang, L. Zheng, Y. Fan, Y. Li and F. Zhao, 2015. Analysis of antioxidant characteristics and related gene expression profiles of rice drought-tolerance lines derived from embryo-soaking with *Alternanthera philoxeroides* DNA solution. *RRJBS*, 4: 30–36
- Lima, J.M., M. Nath, P. Dokku, K.V. Raman, K.P. Kulkarni, C. Vishwakarma, S.P. Sahoo, U.B. Mohapatra, S.V.A. Mithra, V. Chinnusamy, S. Robin, N. Sarla, M. Seshashayee, K. Singh, A.K. Singh, N.K. Singh, R.P. Sharma and T. Mohapatra, 2015. Physiological, anatomical and transcriptional alterations in a rice mutant leading to enhanced water stress tolerance. *AoB Plants*, 7: 23
- Liu, N., S. Ko, K.C. Yeh and Y. Chang, 2006. Isolation and characterization of tomato Hsa32 encoding a novel heat-shock protein. *Plant Sci.*, 170: 976–985
- Lovdal, T., K.M. Olsen, R. Slimestad, M. Verheul and C. Lillo, 2010. Synergistic effects of nitrogen depletion, temperature, and light on the content of phenolic compounds and gene expression in leaves of tomato. *Phytochemistry*, 71: 605–613
- Lum, M.S., M.M. Hanafi, Y.M. Rafii and A.S.N. Akmar, 2014. Effect of drought stress on growth, proline and antioxidant enzyme activities of upland rice. *J. Anim. Plant Sci.*, 24: 1487–1493
- Madabula, F.P., R.S. Santos, N. Machado, C. Pegoraro, M.M. Kruger, L.C. Maia, R.O. Sousa and A.C. Oliveira, 2016. Rice genotypes for drought tolerance: morphological and transcriptional evaluation of auxin-related genes. *Bragantia*, 75: 428–434
- Meng, X., M. Wang, N. Jiang, D. Zhang, L. Wang and C. Liu, 2012. Regulation of both the reactive oxygen species level and antioxidant enzyme activity in drought-stressed rice organs by Benzimidazole-Based SOD1 Mimics. *J. Agric. Food Chem.*, 60: 11211–11221
- Miao, Y., D. Lv, P. Wang, X.C. Wang, J. Chen, C. Miao and C.P. Song, 2006. An *Arabidopsis* glutathione peroxidase functions as both a redox transducer and a scavenger in abscisic acid and drought stress responses. *Plant Cell*, 18: 2749–2766
- Miller, G., N. Suzuki, S. Ciftci-Yilmaz and R. Mittler, 2010. Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant Cell Environ.*, 33: 453–467
- Mishra, S.S. and D. Panda, 2017. Leaf traits and antioxidant defense for drought tolerance during early growth stage in some popular traditional rice landraces from Koraput, India. *Rice Sci.*, 24: 207–217
- Mittler, R., 2002. Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.*, 7: 405–410
- Mittler, R., S. Vanderauwera, M. Gollery and F.V. Breusegem, 2004. Reactive oxygen gene network of Plants. *Trends Plant Sci.*, 9: 490–498
- Moschou, P.N., K.A. Paschalidis, I.D. Delis, A.H. Andriopoulou, G.D. Lagiotis, D.I. Yakoumakis and K.A. Roubelakis-Angelakis, 2008. Spermidine exodus and oxidation in the apoplast induced by abiotic stress is responsible for H₂O₂ signatures that direct tolerance responses in tobacco. *Plant Cell*, 20: 1708–1724
- Munns, R., 2002. Comparative physiology of salt and water stress. *Plant Cell Environ.*, 25: 239–250
- Nahar, S., J. Kalita, L. Sahoo and B. Tanti, 2016. Morphophysiological and molecular effects of drought stress in rice. *Ann. Plant Sci.*, 59: 1409–1416
- Nakashima, K., L.S. Tran, D. Van Nguyen, M. Fujita, K. Maruyama, D. Todaka, Y. Ito, N. Hayashi, K. Shinozaki and K. Yamaguchi-Shinozaki, 2007. Functional analysis of a NAC-type transcription factor OsNAC6 involved in abiotic and biotic stress-responsive gene expression in rice. *Plant J.*, 51: 617–630
- Navrot, N., N. Roubier, E. Gelbaye and J.P. Jacquot, 2007. Reactive oxygen species generation and antioxidant systems in plant mitochondria. *Physiol. Plant.*, 129: 185–195
- Ning, J., X. Li, L.M. Hicks and L. Xiong, 2010. A Raf-like MAPKKK gene DSM1 mediates drought resistance through reactive oxygen species scavenging in rice. *Plant Physiol.*, 152: 876–890
- Nouman, W., F. Anwar, T. Gull, A. Newton, E. Rosa and R. Domínguez-Perles, 2016. Profiling of polyphenolics, nutrients and antioxidant potential of germplasm's leaves from seven cultivars of *Moringa oleifera* Lam. *Ind. Crops Prod.*, 83: 166–176
- Nouman, W., S.M.A. Basra, A. Yasmeen, T. Gull, S.B. Hussain, M. Zubair and R. Gul, 2014. Seed priming improves the emergence potential, growth and antioxidant system of *Moringa oleifera* under saline conditions. *Plant Growth Regul.*, 73: 267–278
- Nuruzzaman, M., R. Manimekalai, A.M. Sharoni, K. Satoh, H. Konodoh, H. Ooka and S. Kikuchi, 2010. Genome-wide analysis of NAC transcription factor family in rice. *Gene*, 465: 30–44
- Olsen, K.M., A. Hehn, H. Jugde, R. Slimestad, R. Lørbæk, F. Bourgaud and C. Lillo, 2010. Identification and characterisation of CYP75A31, a new flavonoid 3050- hydroxylase, isolated from *Solanum lycopersicum*. *BMC Plant Biol.*, 10: 21
- Ort, D.R., 2001. When there is too much light. *Plant Physiol.*, 125: 29–32
- Ouyang, S.Q., Y.F. Liu, P. Liu, G. Lei, S.J. He, B. Ma, W.K. Zhang, J.S. Zhang and S.Y. Chen, 2010. Receptor-like kinase OsSIK1 improves drought and salt stress tolerance in rice (*Oryza sativa*) plants. *Plant J.*, 62: 316–329
- Pan, S.M., M.K. Chen, M.H. Chung, K.W. Lee and I.C. Chen, 2001. Expression and characterization of monocot rice cytosolic *Cu/ZnSOD* protein in dicot *Arabidopsis*. *Trans. Res.*, 10: 343–351
- Pandey, V. and A. Shukla, 2015. Acclimation and tolerance strategies of rice under drought stress. *Rice Sci.*, 22: 147–161
- Pantuwan, G., S. Fukai, M. Cooper, S. Rajatasereekul and J.C.O. Toole, 2002. Yield response of rice (*Oryza sativa* L.) genotypes to drought under rainfed lowlands 2. Selection of drought resistant genotypes. *Field Crops Res.*, 73: 169–180

- Plaut, Z., B.J. Butow and C.S. Blumenthal, 2004. Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. *Field Crops Res.*, 86: 185–198
- Prakash, C., S.V. Mithra, P.K. Singh, T. Mohapatra and N.K. Singh, 2016. Unraveling the molecular basis of oxidative stress management in a drought tolerant rice genotype Nagina 22. *BMC Genomics*, 17: 774
- Prashanth, S.R., V. Sadhasivam and A. Parida, 2008. Over expression of cytosolic copper/zinc superoxide dismutase from a mangrove plant *Avicennia marina* in indica Rice varPusa Basmati-1 confers abiotic stress tolerance. *Trans. Res.*, 17: 281–291
- Qiu, Y.P. and D.Q. Yu, 2008. Over-expression of the stress-induced OsWRKY45 enhances disease resistance and drought tolerance in *Arabidopsis*. *Environ. Exp. Bot.*, 65: 35–47
- Quan, L.J., B. Zhang, W.W. Shi and H.Y. Li, 2008. Hydrogen peroxide in plants: a versatile molecule of the reactive oxygen species network. *J. Integr. Plant Biol.*, 50: 2–18
- Qureshi, M.K., N. Sujeth, T.S. Gechev and J. Hille, 2013. The zinc finger protein ZAT11 modulates paraquat induced programmed cell death in *Arabidopsis thaliana*. *Acta Physiol. Plant.*, 35: 1863–1871
- Qureshi, M.K., V. Radeva, T. Genkov, I. Minkov, J. Hille and T.S. Gechev, 2011. Isolation and characterization of *Arabidopsis* mutants with enhanced tolerance to oxidative stress. *Acta Physiol. Plant.*, 33: 375–382
- Refli, R., S. Muljopawiro, K. Dewi and D. Rachmawati, 2014. Expression analysis of antioxidant genes in response to drought stress in the flag leaf of two Indonesian rice cultivars. *Indon. J. Biotechnol.*, 19: 43–55
- Rezaei, M.A., I. Jokar, M. Ghorbanli, B. Kaviani and A. Kharabian-Masouleh, 2012. Morpho physiological improving effects of exogenous glycine betaine on tomato (*Lycopersicon esculentum* Mill.) cv. PS under drought stress conditions. *Plant Omics J.*, 5: 79–86
- Rhoads, D.M., A.L. Umbach, C.C. Subbaiah and J.N. Siedow, 2006. Mitochondrial reactive oxygen species. Contribution to oxidative stress and interorganellar signaling. *Plant Physiol.*, 141: 357–366
- Riechmann, J.L., J. Heard, G. Martin, L. Reuber, C. Jiang, J. Keddie, L. Adam, O. Pineda, O.J. Ratcliffe, R.R. Samaha, R. Creelman, M. Pilgrim, P. Broun, J.Z. Zhang, D. Ghandehari, B.K. Sherman and G. Yu, 2000. *Arabidopsis* transcription factors: genome-wide comparative analysis among eukaryotes. *Science*, 290: 2105–2110
- Roy, R., P.B. Mazumder and G.D. Sharma, 2009. Proline, catalase and root traits as indices of drought resistance in bold grained rice (*Oryza sativa*) genotypes. *Afr. J. Biotechnol.*, 8: 6521–6528
- Rivero, R.M., M. Kojima, A. Gepstein, H. Sakakibara, R. Mittler, S. Gepstein and E. Blumwald, 2007. Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *Proc. Natl. Acad. Sci. USA*, 104: 19631–19636
- Samuel, M.A., G.P. Miles and B.E. Ellis, 2000. Ozone treatment rapidly activates MAP kinase signaling in plants. *Plant J.*, 22: 367–376
- Sarkar, R.K., J.N. Reddy, S.G. Sharma and M.I. Ab-delbagi, 2006. Physiological basis of submergence tolerance in rice and implication for crop improvement. *Curr. Sci.*, 9: 899–906
- Sarwar, N., H. Ali, M. Maqsood, E. Ullah, M. Shahzad, K. Mubeen, A.N. Shahzad, M.A. Shahid and S. Ahmad, 2013. Phenological response of rice plants to different micronutrients application under water saving paddy fields on calcareous soil. *Turk. J. Field Crops*, 18: 52–57
- Selote, D.S. and R.K. Chopra, 2004. Drought-induced spikelet sterility is associated with an inefficient antioxidant defense in rice panicles. *Physiol. Plant.*, 121: 462–471
- Shao, H.B., L.Y. Chu, M.A. Shao, C.A. Jaleel and H.M. Mi, 2008. Higher plant antioxidants and redox signaling under environmental stresses. *Comptes Rendus Biol.*, 331: 433–441
- Sharma, P. and R.S. Dubey, 2005. Drought induces oxidative stress and enhances the activities of antioxidant enzymes in growing rice seedlings. *Plant Growth Regul.*, 46: 209–221
- Sharma, P., A.B. Jha, R.S. Dubey and M. Pessarakli, 2012. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J. Bot.*, 2012: 217037
- Shen, H., C. Liu, Y. Zhang, X. Meng, X. Zhou, C. Chu and X. Wang, 2012. OsWRKY30 is activated by MAP kinases to confer drought tolerance in rice. *Plant Mol. Biol.*, 80: 241–253
- Sheoran, I.S. and H.S. Saini, 1996. Drought-induced male sterility in rice: changes in carbohydrate levels and enzyme activity associated with the inhibition of starch accumulation in pollen. *Sex. Plant Reprod.*, 9: 161–169
- Singh, R. and N.S. Jwa, 2013. The rice MAPKK-MAPK interactome: the biological significance of MAPK components in hormone signal transduction. *Plant Cell Rep.*, 32: 923–931
- Song, S.Y., Y. Chen, J. Chen, X.Y. Dai and W.H. Zhang, 2011. Physiological mechanisms underlying OsNAC5-dependent tolerance of rice plants to abiotic stress. *Planta*, 234: 331–345
- Steffens, B. and M. Sauter, 2009. Epidermal cell death in rice is confined to cells with a distinct molecular identity and is mediated by ethylene and H₂O₂ through an autoamplified signal pathway. *Plant Cell*, 21: 184–196
- Stranska, J., D. Kopečný, M. Tylichova, J. Snegaroff and M. Sebelá, 2008. Ornithine deltaaminotransferase: an enzyme implicated in salt tolerance in higher plants. *Plant Signal. Behav.*, 3: 929–935
- Sun, S.J., S.Q. Guo, X. Yang, Y.M. Bao, H.J. Tang, H. Sun, J. Huang and H.S. Zhang, 2010. Functional analysis of a novel Cys2/His2-type zinc finger protein involved in salt tolerance in rice. *J. Exp. Bot.*, 61: 2807–2818
- Takasaki, H., K. Maruyama, S. Kidokoro, Y. Ito, Y. Fujita, K. Shinozaki, K. Yamaguchi-Shinozaki and K. Nakashima, 2010. The abiotic stress-responsive NAC-type transcription factor OsNAC5 regulates stress-inducible genes and stress tolerance in rice. *Mol. Genet. Genom.*, 284: 173–183
- Tao, H., H. Brueck, K. Dittert, C. Kreye, S. Lin and B. Sattelmacher, 2006. Growth and yield formation for rice (*Oryza sativa* L.) in the water-saving ground cover rice production system (GCRPS). *Field Crops Res.*, 95: 1–12
- Tao, Z., Y. Kou, H. Liu, X. Li, J. Xiao and S. Wang, 2011. OsWRKY45 alleles play different roles in abscisic acid signalling and salt stress tolerance but similar roles in drought and cold tolerance in rice. *J. Exp. Bot.*, 62: 4863–4874
- Teixeira, F.K., L. Menezes-Benavente, V.C. Galvão, R. Margis and M. Margis-Pinheiro, 2006. Rice ascorbate peroxidase gene family encodes functionally diverse isoforms localized in different subcellular compartments. *Planta*, 224: 300–314
- Thapa, G., M. Dey, L. Sahoo and S.K. Panda, 2011. An insight into the drought stress induced alterations in plants. *Plant Biol.*, 55: 603–613
- Turrall, H., J. Burke and J.M. Faurès, 2011. *Climate Change, Water and Food Security*. FAO, Rome
- Van Breusegem, F. and J.F. Dat, 2006. Reactive oxygen species in plant cell death. *Plant Physiol.*, 141: 384–390
- Varshikar, D. and F.C. Tan, 2016. Salt and drought stress affects electron transport chain genes in rice. *Int. J. Adv. Appl. Sci.*, 4: 106–110
- Vellosillo, T., J. Vicente, S. Kulasekaran, M. Hamberg and C. Castresana, 2010. Emerging complexity in reactive oxygen species production and signaling during the response of plants to pathogens. *Plant Physiol.*, 154: 444–448
- Voothuluru, P., H.J. Thompson, S.A. Flint-Garcia and R.E. Sharp, 2013. Genetic variability of oxalate oxidase activity and elongation in water-stressed primary roots of diverse maize and rice lines. *Plant Signal. Behav.*, 8: 23454
- Wang, F.Z., Q.B. Wang, S.Y. Kwon, S.S. Kwak and W.A. Su, 2005b. Enhanced drought tolerance of transgenic rice plants expressing a pea manganese superoxide. *J. Plant Physiol.*, 162: 465–472
- Wang, L., Z. Pei, Y. Tian and C. He, 2005a. OsLSD1, a rice zinc finger protein, regulates programmed cell death and callus differentiation. *Mol. Plant Microbe Interact.*, 18: 375–384
- Wu, K.L., Z.J. Guo, H.H. Wang and J. Li, 2005. The WRKY family of transcription factors in rice and *Arabidopsis* and their origins. *DNA Res.*, 12: 9–26
- Xie, Q., G. Frugis, D. Colgan and N.H. Chua, 2000. *Arabidopsis* NAC1 transduces auxin signal downstream of TIR1 to promote lateral root development. *Genes Dev.*, 14: 3024–3036
- Yang, J.C., K. Liu, S.F. Zhang, X.M. Wang, Z.Q. Wang and L.J. Liu, 2008. Hormones in rice spikelets in responses to water stress during meiosis. *Acta Agron. Sin.*, 34: 111–118

- Yang, P.M., Q.C. Huang, G.Y. Qin, S.P. Zhao and J.G. Zhou, 2014. Different drought-stress responses in photosynthesis and reactive oxygen metabolism between autotetraploid and diploid rice. *Photosynthetica*, 52: 193–202
- Ye, N.H., G.H. Zhu, Y.G. Liu, Y.X. Li and J.H. Zhang, 2011. ABA controls H₂O₂ accumulation through the induction of *OsCATB* in rice leaves under water stress. *Plant Cell Physiol.*, 52: 689–698
- Yin, X., L. Huang, M. Wang, Y. Cui and X. Xia, 2017. *OsDSR-1*, a calmodulin-like gene improves drought tolerance through scavenging of reactive oxygen species in rice (*Oryza sativa* L.). *Mol. Breed.*, 37: 75
- Yin, X.M., L.F. Huang, X. Zhang, M.L. Wang, G.Y. XuXin and J. Xia, 2015. *OsCML4* improves drought tolerance through scavenging of reactive oxygen species in rice. *J. Plant Biol.*, 58: 68–73
- You, J., H. Hu and L. Xiong, 2012. An ornithine δ -aminotransferase gene *OsOAT* confers drought and oxidative stress tolerance in rice. *Plant Sci.*, 197: 59–69
- You, J., W. Zong, X. Li, J. Ning, H. Hu, X. Li, J. Xiao and L. Xiong, 2013. The *SNAC1*-targeted gene *OsSRO1c* modulates stomatal closure and oxidative stress tolerance by regulating hydrogen peroxide in rice. *J. Exp. Bot.*, 64: 569–583
- Zhang, Z., Q. Zhang, J. Wu, X. Zheng, S. Zheng, X. Sun, Q. Qiu and T. Lu, 2013. Gene knockout study reveals that cytosolic ascorbate peroxidase 2 (*OsAPX2*) plays a critical role in growth and reproduction in rice under drought, salt and cold stresses. *Plos One*, 8: 57472
- Zlatev, Z., 2009. Drought-induced changes in chlorophyll fluorescence of young wheat plant. *Biotechnology*, 23: 437–441
- Zhou, L., Z. Liu, Y. Liu, D. Kong, T. Li, S. Yu, H. Mei, X. Xu, H. Liu, L. Chen and L. Luo, 2016. A novel gene *OsAHL1* improves both drought avoidance and drought tolerance in rice. *Sci. Rep.*, 6: 30264
- Zhu, Y., J. Yan, W. Liu, L. Liu, Y. Sheng, Y. Sun, Y. Li, H.V. Scheller, M. Jiang, X. Hou, L. Ni and A. Zhang, 2016. Phosphorylation of a NAC transcription factor by *ZmCCaMK* regulates abscisic acid-induced antioxidant defense in maize. *Plant Physiol.*, 171: 1651–1664
- Zulfugarov, I.S., A. Tovuu, Y.J. Eu, B. Dogsom, R.S. Poudyal, K. Nath, M. Hall, M. Banerjee, U.C. Yoon, Y.H. Moon, G. An, S. Jansson and C.H. Lee, 2014. Production of superoxide from Photosystem II in a rice (*Oryza sativa* L.) mutant lacking *PsbS*. *BMC Plant Biol.*, 14: 242

(Received 14 June 2017; Accepted 15 February 2018)