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Review Article

Mechanisms of Salt Tolerance in Rice Plants: Reactive Oxygen Species Scavenging-Systems

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Abstract

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In rice plants, oxidative stress is a major determinant involved in salt-induced damage. Accumulation of reactive oxygen species (ROS) during salt stress depends on the balance between the production and the scavenging of ROS. The present review summarizes the major research advance in elucidating the role of ROS-scavenging systems in salt tolerance of rice plants. Evidence shows that the increased tolerance to salt stress in rice plants is linked to an increased ROS-scavenging systems.

Key words: Reactive oxygen species, Rice, Salt stress.

INTRODUCTION

It was projected that world agriculture faces a challenge of producing 70% more food for an additional 2.3 billion people by 2050 (FAO 2009). Crop productivity is largely influenced by various abiotic stresses. Soil salinity is one of the most severe abiotic stresses. About 40% total irrigated lands has been reported to be damaged by salts (Xiong & Zhu 2001). Climate change, rise in sea levels, excessive irrigation without proper drainage in inlands, and underlying rocks rich in harmful salts are believed to be the factors causing the increase of area under salt stress. Salinity is the most common abiotic stress encountered by rice plants, which are considered to be a salt sensitive crop in their early seedling stage (Lutts *et al*. 1995). Thus, it is important to produce salt tolerant rice plants to extend the lands where rice plants can grow even if the lands are salty. Previously, we have described the regulatory roles of compatible solutes, aquaporins, and Na^+ transporters in salt tolerance of rice plants (Kao 2015b, 2015c). In this review, the focus is on the role of reactive oxygen species (ROS)-scavenging systems in salt stress tolerance of rice plants.

ROS IN RICE PLANTS UNDER SALT STRESS

Oxygen (O_2) is essential for life. Reduction of O_2 results in the production of superoxide (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical (• OH). Under normal growth conditions, ROS are mainly produced at low levels in organelles such as chloroplasts, mitochondria, and peroxisomes and/or can be scavenged by various defense mechanisms. During abiotic stresses, the production rate of the ROS is dramatically increased. Accumulation of ROS during abiotic stress mainly depends on the balance between the production and the scavenging of ROS. The accumulated ROS molecules in turn lead to the loss of cellular function (Gill & Tuteja 2010).

Basically, over-reduction of the electron

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transport chain in mitochondria is a main mechanism of ROS generation during stress (Miller *et al*. 2010). In chloroplasts, limitation of CO_2 fixation coupled with over-reduction of electron transport chain is the major cause of ROS production during stress (Miller *et al*. 2010). During photorespiration, the oxidation of glycolate to glyoxylic acid results in the formation of H_2O_2 (Miller *et al*. 2010). Thus, photosynthesis, respiration, and photorespiration are major potential sources of ROS in plants. However, in recent years, another source of ROS has been identified in plasma membrane (Suzuki *et al*. 2011). The activation of plasma membrane-bound NADPH oxidase catalyzes the transfer of electrons from cytoplasmic NADPH to O_2 to form O_2^-, followed by the dismutation of O_2^- to H_2O_2, in cell walls (Pei *et al*. 2000; Suzuki *et al*. 2011).

In rice plants, NaCl treatment results in an increase in H_2O_2 content (Fadzilla *et al*. 1997; Lin & Kao 2001; Hong *et al*. 2009; Hernandez *et al*. 2010; Yamane *et al*. 2012; Wei *et al*. 2013; Hazman *et al*. 2015). Yamane *et al*. (2012) demonstrated that NaCl-induced H_2O_2 accumulation in the chloroplasts, mitochondria, peroxisomes, plasma membrane, and cell walls of rice leaves. Accumulated evidence has shown that NaCl-induced accumulation of H_2O_2 in rice roots could be due to the activation of NADPH oxidase (Hong *et al*. 2009; Wei *et al*. 2013).

ROS-SCVENGING SYSTEMS AND RICE SALT TOLERANCE

Salt stress causes increased production of ROS and it has been shown that in rice plants oxidative stress is a major determinant involved in salt-induced damage (Moradi & Ismail 2007). A correlation between ROS-scavenging systems and salinity tolerance has been reported in rice (Dionisio-Sese & Tobita 1998; Moradi & Ismail 2007; Chawla *et al*. 2013; Mishra *et al*. 2013). Recent work by Hazman *et al*. (2015) also demonstrated that the increased tolerance to salt stress in jasmonic acid-deficient rice mutants is linked to an increased ROS-scavenging systems. In general, ROS-scavenging systems include ROS-scavenging enzymes and antioxidants (Gill & Tuteja 2010). Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR) are the ROS-scavenging enzymes whereas the ROS-scavenging antioxidants include ascorbic acid (AsA) and reduced glutathione (GSH).

Ascorbic acid

Ascorbic acid is the most abundant, powerful and water soluble antioxidant to prevent the damage caused by ROS in plants (Gill & Tuteja 2010). It has been demonstrated that exogenous application of AsA to salt-stressed rice plants increases endogenous AsA content, reduces H_2O_2 content and lipid peroxidation, indicating that exogenous AsA is able to mitigate oxidative damage of rice plants caused by salinity (Wang *et al*. 2014). In higher plants, it is now known that AsA is biosynthesized via D-manose/L-galactose pathway (Kao 2015a). In this pathway, L-galctono 1, 4-lactone dehydrogenase (GalLDH) is an enzyme catalyzing the last step of AsA biosynthesis (Kao 2015a). However, it is not clear whether overexpression of *GalLDH* gene in rice plants through genetic engineering provides a better tolerance to salinity.

The recycling of AsA is one of the approaches to maintain the AsA pool in cells. Monodehydroascorbate reductase (MDHR) and dehydrohyrroascorbate reductase (DHAR) are two enzymes responsible for AsA recycling. Ushimaru *et al*. (2006) reported that expression of rice DHAR in transgenic *Araidopsis thaliana* enhances resistance to salt stress. Recent work by Kim *et al*. (2014) demonstrated that overexpression of *OsDHAR1* increases the DHAR activity, AsA content and the tolerance of rice plants to salt stress. Nguyen *et al*. (2006) isolated a cDNA encoding MDHAR from mangrove (*Acanthus ebracteatus*) plant. Later, Sultana *et al*. (2012) introduced *AeMDHAR* to rice plants and found that the transgenic line MT24, which harbored a single copy of *AeMDHAR*, increased significantly MDHAR enzyme activity and displayed tolerance to salt stress.

Reduced glutathione

Reduced glutathione (GSH; γ-glutamate-cysteine-glycine) is another antioxidant in stress alleviation. It occurs abundantly in plant tissues and is localized in all compartments such as cytosol, mitochondria, chloroplasts, and in apoplast (Gill & Tuteja 2010). It is involved in defense of ROS (Foyer & Noctor 2005). During oxidative stress, GSH is oxidized to glutathione disulfide (GSSG). The ratio of GSH to GSSG is considered as an indicative of cellular redox balance in plants (Foyer & Noctor 2005).

It has been demonstrated that exogenous GSH application increases endogenous GSH content and decreases oxidative damage of salt-treated rice plants (Wang *et al*. 2014). It is well established that GSH is synthesized from two-consecutive ATP-dependent reactions. γ-Glutamylcysteine synthetase (ECS) catalyzes the formation of a peptide bond between the γ-carboxyl group of glutamate and the α-amino group of cysteine. Next, glutathione synthetase catalyzes the formation of a peptide bond between the cysteinyl carboxyl group of γ-glutamylcysteine and the α-amino group of glycine. ECS is the main enzyme regulating GSH biosynthesis in plants. Choe *et al*. (2013) generated transgenic rice plants overexpressing *OsECS* under the control of an inducible promoter (Rab21). These transgenic rice plants increase tolerance to oxidative stress caused by paraquat and salinity.

Reduced glutathione is also a substrate for glutathione S-transferase (GST) and glutathione peroxidase (GPX) which are involved in the removal of ROS (Noctor *et al*. 2012). GSTs, also known as glutathione transferases, and GPXs are GSH-dependent ROS-detoxifying enzymes found in plant cells (Anjum *et al*. 2012). An increased GST activity was found in roots of rice plants under salinity stress (Moons 2003). Sharma *et al*. (2014) demonstrated that overexpressing *OsGSTU* gene in *E. coli* results in a higher GST activity and better growth under salinity stress. Recent findings of Hazman *et al*. (2015) pointed out that increased tolerance to salt stress in jasmonic acid biosynthesis of rice mutants is associated with an increased GST activity. Diao *et al*. (2014) reported the cloning a GPX gene from *Nelumbo nucifera* and found that overexpression of *NnGPX* gene in rice plants was significantly more tolerant to salt stress compared with the wild-type.

Superoxide dismutase

Superoxide dismutase (SOD) catalyzes the conversion of O_2^- to H_2O_2 and O_2. Within a cell, the SOD represents the first line of defense against ROS. O_2^- is known to produce at any location where any electron transport chain is present, and thus O_2^- formation may occur in mitochondria, chloroplasts, and peroxisomes. Phospholipid membranes are not permeable to O_2^- molecules (Takahashi & Asada 1983), thus it is not surprising that SOD is present in the compartments where O_2^- is formed. SOD isoforms are classified by their metal cofactor and subcellular localization: cytosolic CuZn-SOD, chloroplastic CuZn-SOD, peroxidsomal CuZn-SOD, mitochondrial Mn-SOD, and chloroplastic Fe-SOD (Mittler *et al*. 2004).

In rice, NaCl treatment has been demonstrated to be effective in increasing SOD activity in leaves but not in roots (Lee *et al*. 2001). In another work, Tsai *et al*. (2004) observed that NaCl had no effect on the activity of SOD and isoenzymes of SOD in rice roots of 'Taichung Native 1' cultivar. Using 'Nipponbare' rice cultivar, Morita *et al*. (2011) showed that salt stress caused no significant increase in cytosolic SOD transcript. Tanaka *et al*. (1999) were the first to show that overexpression of the yeast mitochondrial Mn-SOD in rice chloroplasts increases total SOD activity and exhibits enhanced tolerance to salt stress, suggesting that high levels of chloroplastic SOD is important for salt resistance in rice. Later work by Badawi *et al*. (2004) showed that targeted rice cytosolic CuZn-SOD to chloroplasts of tobacco results in an enhancement of tolerance to NaCl stress in transformed tobacco plants. Prashanth *et al*. (2008) also reported that overexpression of *Sod1* encoding a cytosolic CuZn-SOD isolated from the mangrove species *Avicennia marina* in *indica* rice cultivar Pusa Basmati-1 confers salt stress tolerance.

Ascorbate peroxidase

Ascorbate peroxidase (APX) belongs to the class I heme-containing peroxidases found in higher plants (Takeda *et al*. 1998) and is thought to play the most important role in scavenging ROS and protecting cells in higher plants. APX catalyzes the conversion of H_2O_2 to H_2O and O_2, utilizing AsA as the specific electron donor. APX has a higher affinity for H_2O_2 than CAT. APX is able to detoxify lower concentrations of H_2O_2 when compared with CAT, thus renders *APX* an ideal candidate for tight regulation of H_2O_2. Eight types of *APX* genes have been described for rice: two cytotolic (*OsAPX1* and *OsAPX2*), two putative peroxisomal (*OsAPX3* and *OsAPX4*), and four chloroplastic isoforms (*OsAPX5*, *OsAPX6*, *OsAPX7*, and *OsAPX8*) (Teixeira *et al*. 2006; Hong *et al*. 2007). We have studied the expression patterns of the gene family of APX in roots of etiolated rice seedlings in response to NaCl stress (Hong *et al*. 2007). Increased APX activity and *OsAPX8* expression were observed in NaCl-treated rice roots (Hong *et al*. 2007). The expression of *OsAPX8* by NaCl is associated with Na^+, but not Cl^- and osmotic component (Hong *et al*. 2007; Hong & Kao 2008). It has also been demonstrated that *OsAPX8* gene expression and APX activity in rice roots induced by NaCl are mediated through abscisic acid but not H_2O_2 (Hong *et al*. 2007). In contrast, Teixeira *et al*. (2006) demonstrated that the expression of *OsAPX8* was drastically down-regulated by NaCl stress. These observed different results may be due to the differences in cultivars, plant age, and growth conditions. Guan *et al*. (2010) have demonstrated that the expression of *OsAPX4* gene in rice leaves and roots is induced by NaCl stress. They also found that overexpression of *OsAPX4* gene in *Arabidopais* and in yeast exhibit greater tolerance to NaCl. However, transgenic Arabidopsis and alfalfa overexpressing *OsAPX2* gene improved salt tolerance (Lu *et al*. 2007; Guan *et al*. 2012; Zhang *et al*. 2014). Recent gene knockout study conducted by Zhang *et al*. (2013) also stressed the importance of rice cytosolic *APX2* in tolerance to various stresses including salinity through scavenging ROS.

Glutathione reductase

Generally, GSH is oxidized to GSSG. Glutathione reductase (GR), a flavor-protein oxidoreductase, catalyzes the reduction of GSSG back to GSH at the expense of NADPH and thus is essential for maintaining the GSH pool. GR has been purified and characterized from rice (Kaminaka *et al*. 1998). Three types of *GR* genes have been described for rice: a cytosolic (*OsGR2*) and two chloroplast/mitochondria co-localized (*OsGR1* and *OsGR3*) (Wu *et al*. 2013). In rice roots, expression of *OsGR2* and *OsGR3* in response to NaCl has been shown to be regulated by H_2O_2, but not by abscisic acid (Hong *et al*. 2009). Kim *et al*. (2012) observed that *OsGR* expression in the yeast cells can reduce the deleterious effect of abiotic conditions, indicating that GR has a role in protecting against ROS. Recently, Wu *et al*. (2015) investigated the role of rice GR3 in salt tolerance using a rice *GR3*-knockout mutant, *gr3*. They demonstrated that knockout of *GR3* reduces GR activity and is more sensitive to NaCl stress. In contrast, functional complementation of *gr3* mutant increases GR activity and NaCl stress tolerance. The results strongly suggest that GR3 plays an important role in salt stress tolerance in rice.

Catalase

Catalase (CAT), a tetrameric heme containing enzyme, directly dismutates H_2O_2 into H_2O and O_2. CAT is required for ROS detoxification during stressed conditions (Gill & Tuteja 2010). It has been shown that NaCl has no effect on CAT activity in shoots (Fadzilla *et al*. 1997) and roots (Tsai *et al*. 2004) of rice. Tsai *et al*. (2004) also demonstrated that NaCl does not affect isoenzymes of CAT in rice roots. On the other hand, decrease in CAT by NaCl has been shown in rice leaves (Dionisio-Sese & Tobita 1998; Lee *et al*. 2001). Overexpression of the CAT gene, *katE*, derived from *E. coli* in rice plants improves salinity stress, suggesting the feasibility of producing salt tolerant transgenic rice plants (Motohashi *et al*. 2010). Of particular interest is the finding of Zhao & Zhang (2006), who demonstrated that co-expression the *Suaeda salsa GST* and *CAT1* in rice leads the increased salt stress protection. Based on their data, they concluded that salt tolerance of *GST* + *CAT1* transgenic rice plants could be resulted from the increased GST, CAT, and SOD activity.

CONCLUSIONS

Salt stress is one of the most serious threats to agriculture and to the environment in many parts of the world. In this review, the role of ROS-scavenging systems in salt tolerance of rice plants is summarized. As described above, the increased salt tolerance in rice plants is indeed linked to increased ROS-scavenging systems in rice plants. However, there are still many questions that are unanswered. It has been suggested that the expression of combinations of antioxidant enzymes in transgenic plants might have synergistic effects on stress tolerance. However, the work described by Zhao & Zhang (2006) is the only report that has been carried out to address ROS-scavenging systems expressing two enzymes in rice plants. Since maximum yield of rice plants under salt conditions is the principal objective, the genes of ROS-scavenging systems incorporated should contribute to salt tolerance not only at the growth stage of interest but also the whole plant levels. In the field, salinity always occur simultaneously with other abiotic stresses. For example, salinity may occur together with drought and/or heat. In order to engineering rice plants more tolerant to field conditions, how these different stress combinations affecting ROS-scavenging systems should be taken into considerations.

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水稻耐鹽之機制：活化氧族清除系統

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摘要

高景輝。2017。水稻耐鹽之機制：活化氧族清除系統。台灣農業研究 66(1):1–8。

氧化逆境是鹽分導致水稻傷害之主因。鹽分逆境下，活化氧族之累積是與形成及清除間之平衡有關 。本文說明活化氧族清除系統在水稻耐鹽機制所扮演角色之主要研究進展。證據顯示，水稻耐鹽性之增加與活化氧族清除系統之增加有關。

關鍵詞：活化氧族、水稻、鹽分逆境。

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