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Insight into the Role of Antioxidant Enzymes for Salt Tolerance in Plants

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Abstract: Salinity toxicity is a worldwide agricultural and eco-environmental problem. Salt stress is one of the major abiotic stresses faced by plants, which adversely affect their productivity. Salt stress causes reduction of crop yield and alterations in plant metabolism, including a reduced water potential, ion imbalances and toxicity and sometimes severe salt stress may even threaten survival. Salinity also leads to oxidative stress in plants due to the production of Reactive Oxygen Species (ROS) such as the super oxide radical, hydrogen peroxide and hydroxyl radical. Oxidative stress is one of the major limiting factors in plant productivity. Reactive Oxygen Species (ROS) generated during metabolic processes damage cellular functions and consequently lead to disease, senescence and cell death. Plants have evolved an efficient defense system by which the ROS is scavenged by antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), Polyphenoloxidase (PPO) and Glutathione Reductase (GR). Attempts to reduce oxidative damages under the salt stress conditions have included the manipulation of ROS scavenging enzymes by gene transfer technology. It is important to maintain and/or increase the productivity (photosynthetic capacity) under stressful environment by developing plants that have well adapted to environmental stress through manipulating antioxidant system. In this study, we discuss the role of antioxidant enzymes for salt tolerance in plants and this study will help to improve the tolerability of plants to salt by enhancing the expression of antioxidant enzymes.

Key words: Salt stress, antioxidant enzymes, oxidative stress, reactive oxygen species, plants

INTRODUCTION

Many arid and semi-arid regions in the world contain soils and water resources that are too saline for most of the common economic crops, which affect plants through osmotic effects, ion specific effects and oxidative stress (Munns, 2002; Pitman and Lauchli, 2002). High concentrations of salt in soil are causing large decreases in yields for a wide variety of crops all over the world (Sekmen *et al.*, 2007). Currently, 20% of the world's cultivated land is affected by salinity, which results in the loss of 50% of agricultural yield (Zhu, 2001; Bartels and Sunkar, 2005). Many crop plants such as barley, maize and rice, are often subject to salinity stress (Sairam and Tyagi, 2004).

Abiotic pressures like salt stress and chemical insultance can impose limitations on crop productivity and also limit land available for farming, often in regions that can ill afford such constraints, thus highlighting a greater need for understanding how plants respond to adverse conditions with the hope of improving tolerance of plants to environmental stress (Joseph *et al.*,

2010). The effects of various environmental stresses in plants are known to be mediated, at least in part, by an enhanced generation of Reactive Oxygen Species (ROS) including $\cdot\text{O}_2^-$, H_2O_2 and $\cdot\text{OH}$ (Hernandez *et al.*, 2000; Benavides *et al.*, 2000). These ROS are highly reactive and can alter normal cellular metabolism through oxidative damage to membranes, proteins and nucleic acids; they also cause lipid peroxidation, protein denaturation and DNA mutation (Imlay, 2003). To prevent damage to cellular components by ROS, plants have developed a complex antioxidant system. The primary components of this system include carotenoids, ascorbate, glutathione and tocopherols, in addition to enzymes such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), peroxidases and the enzymes involved in ascorbate-glutathione cycle (Foyer and Halliwell, 1976), such as ascorbate peroxidase (APX) and glutathione reductase (GR). Many components of this antioxidant defense system can be found in various subcellular compartments (Hernandez *et al.*, 2000).

A comparison of the antioxidant responses of plant genotypes exhibiting differential tolerance to salt stress

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could contribute to the understanding of the physiological and biochemical mechanisms of protection against salt-induced oxidative damage. Therefore, the present study was conducted to investigate the role of the antioxidant-enzymatic system in relation to salt tolerance in plants.

Reactive oxygen species: Reactive Oxygen Species (ROS) are regarded as the main source of damage to cells under biotic and abiotic stresses (Candan and Tarhan, 2003; Gara *et al.*, 2003; Mittler, 2002; Vaidyanathan *et al.*, 2003). ROS's are partially reduced forms of atmospheric oxygen, which are produced in vital processes such as photorespiration, photosynthesis and respiration (Mittler, 2002; Uchida *et al.*, 2002). To produce water in these processes, four electrons are required for perfect reduction of oxygen. But ROS typically results from the transference of one, two and three electrons, respectively, to O_2 to form superoxide ($\cdot O_2^-$), peroxide hydrogen (H_2O_2) and hydroxyl radical ($\cdot OH^-$) (Mittler, 2002). These species of oxygen are highly cytotoxic and can seriously react with vital biomolecules such as lipids, proteins, nucleic acid, etc., causing lipid peroxidation, protein denaturing and DNA mutation, respectively (Breusegem *et al.*, 2001; Scandalios, 1993; Quiles and Lopez, 2004). Evidence suggests that membranes are the primary sites of salinity injury to cells and organelles (Candan and Tarhan, 2003) because ROS can react with unsaturated fatty acids to cause peroxidation of essential membrane lipids in plasmalemma or intracellular organelles (Karabal *et al.*, 2003; Stewart and Bewley, 1980).

Oxidative damage by salt stress: Oxygen is essential for the existence of aerobic life, but toxic reactive oxygen species (ROS), which include the superoxide anion radical ($\cdot O_2^-$), hydroxyl radical ($\cdot OH^-$) and hydrogen peroxide (H_2O_2), are generated in all aerobic cells during metabolic processes (Foyer *et al.*, 1994; Asada, 1999). Injury caused by these ROS is known as oxidative stress, which is one of the major damaging factors to plants exposed to environmental stress. It is well documented that abiotic stresses exert at least in part of their effects by causing oxidative damage (Smirnov, 1995).

Oxidative damages are caused by Reactive Oxygen Species (ROS) and excess amounts of ROS are harmful to many cellular components, including membrane lipids. ROS cause peroxidation of polyunsaturated fatty acids in the membranes (Smirnov, 2005). Production of ROS is increased under saline conditions (Greenway and Munns, 1980; Hasegawa *et al.*, 2000) and ROS-mediated membrane damage has been demonstrated to be a major cause of the cellular toxicity by salinity in rice, tomato and citrus

(Gueta-Dahan *et al.*, 1997; Dionisio-Sese and Tobita, 1998; Mittova *et al.*, 2004). The effects of various environmental stresses in plants are known to be mediated, at least in part, by an enhanced generation of reactive oxygen species (ROS) including $\cdot O_2^-$, H_2O_2 and $\cdot OH^-$ (Hernandez *et al.*, 2000; Benavides *et al.*, 2000).

Regulation of Reactive Oxygen Species (ROS) at normal environment: Under normal growth conditions, low amounts of ROS such as superoxide radical ($\cdot O_2^-$), hydrogen peroxide (H_2O_2), hydroxyl radical ($\cdot OH^-$) and singlet oxygen (1O_2) are metabolic byproducts of plant cells (Cai-Hong *et al.*, 2005). Plants have developed the scavenging mechanism of ROS categorized as enzymatic and non-enzymatic (Reddy *et al.*, 2004; Demiral and Turkan, 2005). When ROS increases, chain reactions start, in which superoxide dismutase (SOD) catalyzes the dismutation of O_2^- radicals to molecular O_2 and H_2O_2 (Meloni *et al.*, 2003). The H_2O_2 is then detoxified in the ascorbate-glutathione cycle (Asada, 1999; Mittler, 2002), which involves the oxidation and re-reduction of ascorbate and glutathione through the ascorbate peroxidase (APX) and Glutathione Reductase (GR) action (Noctor and Foyer, 1998). If there is a serious imbalance in any cell compartment between the production of Reactive Oxygen Species (ROS) and antioxidant defense, oxidative stress and damage occurs (Mittler, 2002). When a plant faces harsh conditions, ROS production will overcome scavenging systems and oxidative stress will burst. In these conditions, ROS attack vital biomolecules and disturb the cell metabolism and ultimately the cell causes its own death (Sakihama *et al.*, 2002).

Scavenging of reactive oxygen species by plants under salt stress condition: Salt stress induces cellular accumulation of ROS which can damage membrane lipids, proteins and nucleic acids (Hernandez *et al.*, 1993, 1999; 2000; Mansour *et al.*, 2005; Ben-Amor *et al.*, 2007; Eyidogan and Oz, 2007). Much of the injury to plants exposed to stress is connected with oxidative damage at the cellular level (Foyer and Noctor, 2003). During oxidative stress, the excess production of ROS causes membrane damage that eventually leads to cell death. For protection against ROS, plants contain antioxidant enzymes as well as a wide array of non-enzymatic antioxidants (Blokhina *et al.*, 2003).

Fortunately, plants have developed various protective mechanisms to eliminate or reduce ROS, which are effective at different levels of stress-induced deterioration (Beak and Skinner, 2003). The enzymatic antioxidant system is one of the protective mechanisms including superoxide dismutase (SOD: EC 1.15.1.1), which

can be found in various cell compartments and it catalyses the disproportion of two $\cdot\text{O}_2^-$ radicals to H_2O_2 and O_2 (Scandalios, 1993). H_2O_2 is eliminated by various antioxidant enzymes such as catalases (CAT: EC 1.11.1.6) (Kono and Fridovich, 1983; Scandalios, 1993) and peroxidases (POX: EC 1.11.1.7) (Gara *et al.*, 2003; Jablonski and Anderson, 1982) which convert H_2O_2 to water. Other enzymes that are very important in the ROS scavenging system and function in the ascorbate-glutathione cycle are glutathione reductase (GR: EC 1.6.4.2), monodehydro ascorbate reductase (MDHAR: EC 1.6.5.4) and dehydroascorbate reductase (DHAR: EC 1.8.5.1) (Candan and Tarhan, 2003; Yoshimura *et al.*, 2000).

Role of antioxidant enzymes for salt tolerance in plants:

To minimize the effects of oxidative stress, plant cells have evolved a complex antioxidant system, which is composed of low-molecular mass antioxidants (glutathione, ascorbate and carotenoids) as well as ROS-scavenging enzymes, such as: superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX) and glutathione reductase (GR) (Apel and Hirt, 2004).

One of the well-known mechanisms, that how the antioxidants work properly at the onset of oxidative stress is the water-water cycle (Asada, 1999; Fig. 1). The most important function of this cycle is a rapid, immediate

scavenging of superoxide anion radical and hydrogen peroxide at the site of generation prior to their interaction with target molecules. SOD, APX (thylakoid-bound and stroma), monodehydro ascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and Glutathione Reductase (GR) were participated in this cycle. However, this antioxidative mechanism seems to be not enough to protect plants from the elevated environmental stresses. To maintain the productivity of plants under the stress condition, it is important to fortify the antioxidative mechanism of the chloroplasts by manipulating the antioxidant enzymes and small antioxidant molecules in the chloroplast (Kwon *et al.*, 2001).

Kartashov *et al.* (2008) studied the activities of principal antioxidant enzymes and the accumulation of sodium ions and proline. Moreover, plants with the high activity of peroxidase and active proline accumulation could acclimate to salts stress (100 mM NaCl, 24 h) independently of SOD activity (Kartashov *et al.*, 2008). Several studies have pointed out that salt-tolerant species increased their antioxidant enzyme activities and antioxidant contents in response to salt treatment, whereas salt-sensitive species failed to do so (Shalata *et al.*, 2001; Demiral and Turkan, 2005). The scavenging of ROS by increased activation of antioxidant enzymes can improve salt tolerance (Alscher *et al.*, 2002). A relationship between salt tolerance and increased

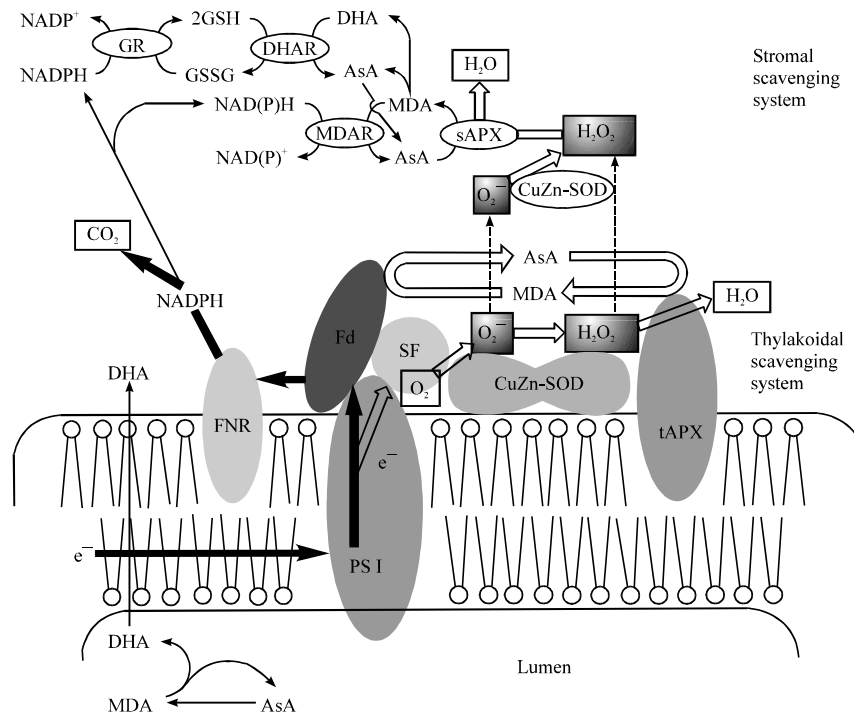


Fig. 1: The water-water cycle and microcompartmentalization of the participating enzymes (Asada, 1999)

activation of antioxidant enzymes has been demonstrated in *Plantago* (Sekmen *et al.*, 2007), pea (Hernandez *et al.*, 2000), rice (Dionisio-Sese and Tobita, 1998), tomato, maize (Neto *et al.*, 2005), sorghum (Costa *et al.*, 2005; Heidari, 2009), soybean (Cicek and Cakirlar, 2008) and mulberry (Harinasut *et al.*, 2003).

The generation of ROS and increased activity of many antioxidant enzymes during salt stress have been reported in cotton (Desingh and Kanagaraj, 2007), mulberry (Sudhakar *et al.*, 2001; Harinasut *et al.*, 2003), wheat (Sairam *et al.*, 2002), tomato (Mittova *et al.*, 2002), rice (Vaidyanathan *et al.*, 2003) and sugar beet (Bor *et al.*, 2003). In general, the activities of antioxidant enzymes were increased in the root and shoot under saline stress. But the increase was more significant and consistent in the root (Kim *et al.*, 2005). The activities of antioxidant enzymes were increased in the root and shoot under saline stress in barley seedlings treated with 200 mM NaCl (Kim *et al.*, 2005).

The quantitative and qualitative aspects of changes are often related to the levels of resistance to salinity. In tomato and citrus, salt-tolerance is attributed to the increased activities of SOD, APX and CAT (Gueta-Dahan *et al.*, 1997; Mittova *et al.*, 2004). Further supporting evidence on the involvement of antioxidant enzymes in salt tolerance has been provided by transgenic plants with a reduced or an increased expression of antioxidant enzymes (Willekens *et al.*, 1997). Increased protection to salt stress has been demonstrated by the over expression of cytosolic APX (Torsethaugen *et al.*, 1997). Jaleel (2009) carried out an experiment with different concentrations of sodium chloride (NaCl) in *alba* and *rosea* varieties of *Catharanthus roseus* (L.) to determine the changes that occurring in antioxidant enzymes in various plant parts and reported that, *C. roseus* is an ideal plant for cultivation in salt affected areas in order to obtain plants with high antioxidant and medicinal values.

Superoxide Dismutase (SOD): The Superoxide Dismutase (SOD) (EC 1.15.1.1) is a metalloprotein that catalyzes the initial step in the water-water cycle in chloroplasts, the dismutation of superoxide to H₂O₂ and molecular oxygen (Scandalios, 1993; Bowler *et al.*, 1991; Allen *et al.*, 1997; Asada, 1999). The subsequent reduction of H₂O₂ to water through the cycle in the chloroplast uses reducing equivalents from NADPH (Foyer *et al.*, 1994). The increased SOD activities in leaves of *Ulmus pumila* presented an increased trend at salt concentrations less than 1.5%, the growth of seedlings did not decline and tress and leaves had no symptom of injury, while the salt concentrations exceeded 1.5%, SOD activities sharply

decreased (Song *et al.*, 2006). In rice, the salt-tolerant varieties have higher SOD activity and lower lipid peroxidation than the salt-sensitive varieties (Dionisio-Sese and Tobita, 1998). It was suggested that the ratio between superoxide dismutase and H₂O₂-scavenging enzyme activities could be used as a working hypothesis for a biochemical marker for salt tolerance in sorghum (Costa *et al.*, 2005).

Catalase (CAT): Catalase is a common enzyme found in nearly all living organisms that are exposed to oxygen, where it functions to catalyze the decomposition of hydrogen peroxide to water and oxygen. It is a tetramer of four polypeptide chains, each over 500 amino acids long (Chelikani *et al.*, 2004). Salt stress was associated with an increase of the antioxidant enzyme response and induction of new CAT isoforms in rice (Srivalli *et al.*, 2003). Salt-tolerant cotton cultivars exhibited significantly greater in CAT, APX and SOD activities as compared to the salt-sensitive ones (Gossett *et al.*, 1994). Nagamiya *et al.* (2007) introduced *katE*, a catalase gene of *Escherichia coli*, into japonica rice cultivar. Catalase activity in the transgenic rice plants was 1.5 to 2.5 fold higher than non-transgenic rice plants.

Peroxidase (POX) and Polyphenol Oxidase (PPO): Meratan *et al.* (2008) studied the effects of salinity on antioxidant enzymes in three *Acanthophyllum* species. *A. glandulosum* showed a remarkable increase in POX and PPO between 50 to 200 mM NaCl. In *A. sordidum*, POX and PPO activities increased at 50 mM NaCl and then decreased at higher salinities. Their results showed that the differences in the antioxidant enzyme activities of seedling may, at least in part explain the greater tolerance of *A. glandulosum* comparing to *A. sordidum* and *A. laxiusculum*. Sreenivasulu *et al.* (1999) studied the effect of NaCl on total peroxidase activity, induction of isoperoxidases and lipid peroxidation in 5-day-old seedlings of two contrasting genotypes of *Setaria italica* L. Total peroxidase activity increased under NaCl salinity and the degree of elevation in the activity was salt concentration dependent.

Aspartate Peroxidase (APX): The H₂O₂ produced via the disproportionation of O₂⁻ catalyzed with SOD is reduced to water by APX (E.C. 1.11.1.11), which use ascorbate as the electron donor in chloroplasts. APX is a heme peroxidase and uses two molecules of ascorbate to reduce H₂O₂ to water, with the generation of two molecules of monodehydroascorbate (MDHA). It distributed in at least four distinct cell compartments, the stroma (sAPX) and thylakoid membrane (tAPX) in chloroplasts, the

microbody (mAPX) and the cytosol (cAPX) (Yoshimura *et al.*, 2000). In addition, Zhang *et al.* (1997) identified an APX associated with the glyoxysomal membranes. Allen *et al.* (1997) reported that transgenic tobacco plants expressing gene constructs for either cytosolic APX or a chimeric chloroplast-targeted cytosolic APX from pea have the increased protection from photo oxidative stress.

Role of antioxidant enzymes in rice plants: Rice is one of the most important crops all over the world. But the rice agriculture is often threatened by abiotic stresses, including salinity. Many researches have focused on this problem, with the aim to find the mechanism of salt tolerance and the critical elements that may confer the tolerance to salinity. Some studies have shown that salt stress arouses many aspects of protective reaction, such as accumulation of small osmotic molecules, enhanced selective ion transport, increased reactive oxygen species (Csonka and Hanson, 1991). The responses of the antioxidant enzymes in the resistance to salt stress were determined in the rice (*Oryza sativa* L. cv. Dongjin) plant. In the leaves of the rice plant, salt stress preferentially enhanced the content of H₂O₂ as well as the activities of the superoxide dismutase (SOD), ascorbate peroxidase (APX) and peroxidase specific to guaiacol, whereas it induced the decrease of catalase activity (Lee *et al.*, 2001). The superoxide dismutase activity in roots and glutathione reductase activity in both shoots and roots were decreased significantly under high salinity levels in rice plant (Kumar and Shriram, 2009).

Strategies to improve salt stress tolerance: Recent advances in plant genome mapping and molecular biology techniques offer a new opportunity for understanding the genetics of salt stress-resistance genes and their contribution to plant performance under salt stress. These biotechnological advances will provide new tools for breeding in salt stress environment. Molecular genetic maps have been developed for major crop plants, including rice, wheat, maize, barley, sorghum and potato, which make it possible for scientists to tag desirable traits using known DNA landmarks. Molecular genetic markers allow breeders to track genetic loci controlling stress resistance without having to measure the phenotype, thus reducing the need for extensive field-testing over time and space. Moreover, gene pyramiding or introgression can be done more precisely using molecular tags. Together, molecular genetic markers offer a new strategy known as marker assisted selection. Another molecular strategy which depends on gene cloning and plant transformation technology, is genetic engineering of selected genes into

elite breeding lines. What makes a particular goal attainable or unattainable in genetic engineering experiments is the availability of the following three inputs: (1) the gene of interest, (2) an effective technique for transferring the desired gene from one species to another and (3) promoter sequences for regulated expression of that gene. Amongst these, the first is considered a rate-limiting factor. Arrays of salt stress-induced genes have been isolated. Salt stress-responsive genes can be analysed following targeted or non-targeted strategy. The targeted approach relies upon the availability of relevant biochemical information (i.e., in terms of defined enzyme, protein, a biochemical reaction or a physiological phenomenon). The non-targeted strategy to obtain a desired gene is indirect. This strategy, for instance, includes differential hybridization and shotgun cloning. The list of genes, whose transcription is upregulated in response to stress, is rapidly increasing. Understanding of the mechanisms which regulate gene expression and the ability to transfer genes from other organisms into plants will expand the ways in which plants can be utilized. To exploit the full potential of these approaches, it is essential that the knowledge is applied to agriculturally and ecologically important plant species.

CONCLUSION AND FUTURE PROSPECTS

Salinity in the soil and irrigation water is an environmental problem and a major constraint for crop production. Salt stress (NaCl) has both osmotic (cell dehydration) and toxic (ion accumulation) effects on plants. Although, a wide range of genetic adaptations to saline conditions has been observed and a number of significant physiological responses have been associated with tolerance, underlying mechanisms of salt tolerance in plants are still poorly understood.

The ROS, especially hydrogen peroxide, have been proved as a central component of plant adaptation to biotic and abiotic stresses (Mittler, 2002; Karpinski *et al.*, 1999). Under the stress conditions, ROS may play in damaging the cellular components or signaling the activation of defense responses. To allow for these different roles, cellular levels of ROS must be tightly controlled. In first, precise understanding the roles of each ROS scavenging enzyme and small molecular antioxidants in stress adaptation and accurate characterization of the complex stress tolerance phenotypes is necessary to develop stress tolerant plants. However, this antioxidative mechanism seems to be not enough to protect plants from the elevated environmental stresses such as salinity. To maintain the

productivity of plants under the salt stress condition, it is important to fortify the antioxidative mechanism of the chloroplasts by manipulating the antioxidant enzymes and small antioxidant molecules in the chloroplast.

Cloned plant genes and transgenic plants have become a standard tool in plant-stress biology. These technologies have mainly been applied to model systems and have greatly enlarged the knowledge of mechanisms of tolerance. The various abiotic stresses cause changes in plant processes at all levels of organization (morphological, physiological, biochemical and molecular). In recent years, attention has focused on alterations in gene expression. The list of genes whose transcription is upregulated in response to stress is rapidly increasing. Functions for some of these polypeptides are close to being identified and their likely role in stress physiology is being determined. The understanding of mechanisms that regulate gene expression and the ability to transfer genes from other organisms into plants will expand the ways in which plants can be utilized. The exploitation of cloned genes to alter the function of gene products in transgenic plants provides novel opportunities to assess their biological role in a salt stress response.

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