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Antioxidative Responses to Drought and Salinity Stress in Plants, A Comprehensive Review

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ABSTRACT

Environmental stresses are one of the most important reducing factor for plant’s growth and productivity worldwide. Among them, salinity and drought are known as the most harmful. Reactive oxygen species (ROS) production is a frequent consequence of most stresses, including salinity and drought. These free radicals cause serious damages to plant’s structure by oxidizing membrane lipids, proteins and nucleic acids. During the evolution process, plants acquire an antioxidative system consisting of nonenzymatic antioxidants, such as β-carotenes, ascorbic acid (AA), α-tocopherol (α-toc), and antioxidant enzymes, such as catalase (CAT), superoxide dismutase (SOD), and peroxidase (POX). Considering the fact that ROS production is an outcome of plant metabolism, controlling the ROS levels is highly vital for plant cells survive. There are considerable numbers of scientific researches regards to the antioxidative responses of plants grown under drought and salinity. These responses highly depend on plant species, other environmental conditions, growth stage and other factors. In this review, the biochemistry of enzymatic and non-enzymatic antioxidants and plant’s antioxidative system changes in response to drought and salinity were expansively evaluated.

Key words: Antioxidative system; Free radicals; Stress tolerance

INTRODUCTION

Under both natural and agricultural conditions, plants are frequently exposed to a wide range of biotic and abiotic stresses. Some environmental factors, such as air and temperature, can become harmful in just a few minutes; others (such as soil salinity and soil water content) may take longer periods of time to become stressful (Taiz and Zeiger, 2006). A large group of studies have shown that environmental stresses, such as salinity, drought and cold stress, could enhance reactive oxygen species (ROS) formation (Mittler et al., 2004). These free radicals, including superoxide radicals (O2), hydrogen peroxide (HO2) and hydroxyl radicals, following an injury to the electron transport chain, and cause serious damages to plant’s structure by oxidizing membrane lipids, proteins and nucleic acids. During the evolution process, plant cells possess an antioxidative system consisting of nonenzymatic antioxidants, such as β-carotenes, ascorbic acid (AA), α-tocopherol (α-toc), and antioxidant enzymes, such as catalase (CAT), superoxide dismutase (SOD), and peroxidase (POX). Considering the fact that ROS production is an outcome of plant metabolism, controlling the ROS levels is highly vital for plant cells survive. Therefore, the development of strategies to alleviate adverse effects of salinity stress on plants has received considerable attention. In this review, the antioxidative responses of plants to drought, salinity and cold stress and the ameliorative strategies to alleviate these harmful effects are comprehensively discussed.

ROS BIOCHEMISTRY AND PRODUCTION

It has been estimated that 1-2% of O2 consumption leads to the ROS production in plant tissues (Bhattachrjee 2005). Throughout a range of chemical reactions, O2 leads to the formation of H2O2, OH- and other ROS.
Regards to their oxygenic conditions and the abundance of the photosensitizers and PUFA in chloroplast envelope, photosynthesizing plants are specifically at the risk of oxidative damage. In light the chloroplasts and peroxisomes are the main sources of ROS formation (Foyer and Noctor, 2003). In darkness, the mitochondria are known as the main ROS producers. It has been estimated that 1-5% of O2 consumption of isolated mitochondria results in ROS production (Moller, 2001).

**SALINITY AND ANTIOXIDATIVE RESPONSE**

Soil and water salinity is one of the most important agricultural constraints which increasing gradually worldwide (Abdel Latef, 2010). Presently, about 77 million hectares (5%) of cultivated lands are affected by saline condition (Sheng et al., 2008). Salt stress has been found to act as a disrupting factor for several physiological processes which leads to reduce growth and productivity (Yurtseven et al., 2005). Salinity affects many physiological activities related to the ion's accumulation (Lee et al., 2008). Salinity often leads to increased uptake of Na+ or decreased uptake of Ca2+ and K+ in plant tissue which causes nutritional imbalances (Neel et al., 2002). Saline condition induces osmotic stress by limiting water absorption, and ionic stress within plant cells (Kohler et al., 2009). The mechanism of salinity tolerance varies at cellular, molecular and the whole-plant levels (Munns and Tester, 2008).

An increased production of reactive oxygen species (ROS) is one of the most common consequences of all environmental stresses, including salinity (Sairam et al., 2005). A close correlation between the antioxidant capacity and NaCl tolerance has been demonstrated in numerous crops, such as pea (Hernandez et al., 2000), cotton (Gossett et al., 1998), rice (Dionisio-Sese and Tobita, 1998) and foxtail millet (Sreenivasula et al., 2000). In addition, recent reports on the responses of plant antioxidant enzyme to salinity showed varying activity patterns according to the species and analyzed tissues.

**DROUGHT AND ANTIOXIDATIVE RESPONSE**

Due to the growth of population and expansion of the agricultural, energy, and industrial sectors, the demand for water has increased extensively, and water scarcity has been occurring almost every year in many parts of the world. Drought is known as a major abiotic factor that limits plant’s growth and production (Saeidinejad et al., 2013). Although the general effects of drought on plant growth are fairly well known, the primary effects of water deficit at the biochemical and molecular levels are not well understood (Bhatnagar-Mathur et al., 2009).

Plants respond to drought stress through physiological, biochemical and metabolic adjustments occurring in all plant organs. Much of the injury to plants caused by stress exposure is associated with oxidative damage at the cellular level. However in certain tolerant crop plants morphophysiological and metabolic changes occur in response to drought, which contribute towards adaptation to such unavoidable environmental constraints (Sairam & Sirvastava, 2001).

**ANTIOXIDATIVE DEFENSE SYSTEM ACTIVITY**

Environmental stressful conditions including drought, salinity, air pollutants, nutrient deficiency, cold and heat stress and heavy metals could enhance the production of reaction oxygen species as free radicals. Plant cells and structures are evolved a highly efficient antioxidant defense systems to protect plants in response to the mentioned stress conditions (Tuteja, 2007., Khan and Singh, 2008., Singh et al., 2008). This proficient system is include enzymatic (SOD, CAT, APX, MDHAR, DHAR and GR) and non-enzymatic (carotenoids, tocopherols, AA and GSH) antioxidants (Schutzendubel and Polle, 2002).

Recent works showed that salt tolerance is closely related to the efficiency of antioxidant enzymes (Rout and Shaw, 2001; Arbona et al., 2003; Shalata et al., 2001; Muscolo et al., 2003). SOD, CAT and POD are among the major antioxidant enzymes involved in scavenging AOS (Broetto et al., 2002).

**4-1-Enzymatic antioxidants**

**4-1-1- Superoxide dismutase (SOD)**

Superoxide dismutase is known as the most effective intracellular enzymatic antioxidant and provides the first defense line against the harmful effects of increased levels of ROS and thus plant stress tolerance induction. The main SOD role is to removes O-2 and so decreases the risk of OH- formation. SODs are classified according to their metal cofactors into three types: the copper/zinc (Cu/Zn-SOD), the manganese (Mn-SOD) and the iron (Fe-SOD), which are localized in different cellular compartments (Mittler, 2002).

The subcellular distribution of these isozymes is also typical. Mn-SOD type is found in the mitochondria and peroxisomes (Del Rio et al., 2003), some Cu/Zn-SOD isozymes are found in the cytosolic fractions, and also in chloroplasts of higher plants (del Rio et al., 2002). The Fe-SOD isozymes, often not detected in plants (Ferreira et al., 2002) are usually associated with the chloroplast compartment when present (Alscher et al., 2002).

Regulation of SODs production in oxidative stress caused by biotic and abiotic stress is implicated and critical in plant’s survival under stress conditions. A great deal of research has established that a considerable increase in
SOD activity has been observed in a variety of plants under salt stress, such as mulberry (Harinasut et al., 2003), C. arietinum (Kukreja et al., 2005), and Lycopersicon esculentum (Gapi et al., 2008). A significant increase in activities of Cu/ZnSOD and MnSOD in C. arietinum under salt stress was reported (Eydigogan and Oz, 2005). A significant increase in SOD activity in Glycyrrhiza uralensis which grown under salinity and drought stress was also observed (Pan et al., 2006). Cao et al. (2005) demonstrated on the basis of molecular, physiological and genetic approaches the elevation in antioxidant enzymes was the consequence of enhanced expression of DET2 gene, which enhanced the resistance to oxidative stress in Arabidopsis.

In a study, antioxidant responses of Crithmum maritimum as a perennial halophyte to salinity was evaluated and it was shown that the highest SOD activity was recorded on shoots at optimal salt concentration (50 mMNaCl), whereas no significant effect was noted at 200 mM NaCl. SOD isozymes separation confirmed the evolution of the spectrophotometric activities and three SOD isoforms were detected including two Mn-SODs and one CuZn-SOD. Only two CuZn-SOD isoforms, denominated CuZn-SOD1 and CuZn-SOD2, were identified in shoots (Ben Amor et al., 2005).

Since Mn-SOD is, generally, found in mitochondria, Fe-SOD in chloroplasts and CuZn-SOD in chloroplasts and cytosol, compartment-specific responses of the antioxidative response system can be distinguished. Data of this study suggest that mitochondrial and cytosolic compartments are crucial in the protection of roots against superoxide formation when plants deal with moderate salinity. However, scavenging of superoxide radicals was found to be more important in the chloroplastic compartment in shoots, owing to the presence of two CuZn-SOD isoforms (Ben Amor et al., 2005).

In Another study by Tuna et al. (2008), antioxidant enzyme activities of maize plants which grown under salinity in combined with gibberellic acid treatment was experimented and it was well documented that SOD activity was enhanced under salinity stress. Similar increases in the activity of SOD enzymes have been reported in cotton cultivars (Meloni et al., 2003), in Cassia angustifolia plants (Agarwal and Pandey, 2004) and Beta maritime and Beta vulgaris cv. Ansa (Bor et al., 2003) subjected to salt stress. Enhancement of SOD activity under salt stress could increase the ability of the seedlings scavenging activity of O2 radicals, which could cause membrane damage (Agarwal and Pandey, 2004). However, some conflict results are available in the literature for SOD activity under saline conditions. For example, in pea (Hernandez et al., 1995) and in rice (Dionisio-Sese and Tobita, 1998), NaCl stress caused a reduced SOD activity.

It was comprehensively studied and documented that drought could enhance SOD activity and this effect is more visible on drought-tolerant plants. For instance, the effects of water deficit on physiological properties and antioxidant activity of barley was evaluated and it was shown that activity of SOD increased by the effect of drought treatments in the leaves of drought-resistant varieties as compared to sensitive variety. The drought treatment resulted in a 418 % and 59 % increase in SOD activity in resistant varieties at the end of the 12th day of experimental period (Acar et al., 2001). In another study, it was observed that SOD activity of groundnut leaves reduced during the early drought stress period, but along with the stress continuing, SOD activity increased and it was stronger in tolerant genotype than that in susceptible genotype (Jiang and Ren, 2004). Fu and Huang (2001) reported that SOD activity enhanced when Kentucky bluegrass (Poa pratensis L) and tall fescue (Festuca arundinacea Schreb.) were exposed to drought stress when in was applied by surface drying and full drying. They stated this raise as a mechanism which makes them capable of surviving surface soil drying.

When effect of salt and drought stress on antioxidant enzymes activities and SOD isoenzymes of liquorice (Glycyrrhiza uralensis Fisch) was investigated, the result showed that activity of SOD and was up-regulated by salt and drought stress. The data also showed that although the activity of SOD was differentially influenced by drought and salinity, the changes of antioxidant enzyme activities subjected to drought stress follow a pattern similar to that subjected to salt stress, indicating that similar defensive systems might be involved in the oxidative stress injury in liquorice (Pan et al., 2006).

Another experiment by Yu and Rengel (2009) which studied drought and salinity effects on activities of superoxide dismutase (SOD) forms in Lupinus angustifolius L. showed that activity of total SOD increased by 21%, Cu/ZnSOD by 33% and FeSOD by 50% after 2 days of withholding water; further increases were noted with an increase in severity of drought stress.

4-1-2- Catalase (CAT)

The metabolism of H2O2 is dependent on various antioxidant enzymes such as catalases and peroxidases, which decompose H2O2 from stressed cells (Kim et al. 2005). The results of study the antioxidants activity of canola under salinity stress demonstrated that catalase (CAT) and ascorbate peroxidase (APX) activities were considerably increased (Heidari, 2010). Thus, this and other similar findings suggest that CAT and APX activities coordinated with SOD activity play a vital protective role in O2- and H2O2 scavenging process (Bardawi et al. 2004).

CAT has one of the highest turnover rates for all enzymes and it plays a critical role in removing of H2O2 which
generated in peroxisomes by fatty acids oxidation and photorepiration. CAT isozymes have been studied comprehensively in higher plants (Polidoros and Scandalias, 1999) such as 2 for H. vulgare (Azevedo et al., 1998), 4 in Helianthus annus cotyledons (Azpicueta et al., 2007) and 12 in Brassica (Frugoli et al., 1996).

Evaluation of Salinity stress on antioxidant enzyme activities of pearl millet showed that Salt stress remarkably enhanced CAT antioxidant enzyme activity at both vegetative and reproductive stages (Heidari and Jamshidi, 2011).

In the present study, changes in SOD, POD, GR, CAT enzyme activity on 1-month old salt stressed Catharanthus roseus seedlings suggests that oxidative stress may be an influential component of possible environmental stresses on C. roseus. Higher enzyme activity was observed in all plant tissue parts under saline conditions, and most markedly in the roots (Misra and Gupta, 2006), these results are in contrast to the opposite trend which was previously observed in wheat (Meneguzzo et al., 1999). It was also shown that CAT activity was raised in response to saline condition in Pennisetum glaucum (Borde et al., 2011). In another study (Abdel Latef and Chaoxing, 2011), it was reported that salinity stress stimulated the activity of antioxidants system, including CAT in tomato. A higher CAT activity was also observed on mustard cultivars under salinity stress (Khan et al., 2009).

When drought tolerance of wheat was examined, results showed that in comparison with non-stressed seedlings, the catalase (CAT) activity was upregulated by more than 50% in the roots of water-stressed seedlings in drought-tolerant genotypes (Devi et al., 2012). CAT activity was also significantly increased at ~0.4 MPa osmotic potential in melon seedlings cultivars which exposed to drought stress levels (Kavas et al., 2012).

4-1-3- Ascorbate peroxidases (APX)

APX is considered to have the most critical role in ROS scavenging and protecting cells under oxidative stress. APX has a higher affinity for H2O2 than CAT and POD and thus it may have a more essential role in the ROS induced stress management. APX is consists of five different isoforms, including thylakoid (tAPX) and glyoxisome membrane forms (gmAPX), cytosolic form (cAPX) and chloroplast stromal soluble form (sAPX) (39). There is a large number of reports regards to an increased activity of APX in plants which grown under stress conditions, such as salinity. For instance, Roychoudhury et al. (2010) reported that APX activity was enhanced in three varieties of indica rice differing in their level of salt tolerance were exposed to salinity stress. In another experiment, when alfalfa seedling was treated with salinity condition (200 mM), the activity of APX in shoots and roots of both cultivars sharply increased (Wang et al., 2009). Lower levels of lipid peroxidation are associated with higher APX activity in drought- or salt tolerant tomato (Shalata and Tal, 1998), sugar beet (Bor et al., 2003), and rice (Demiral and Turkan, 2005) plants.

Water deficit stress led to the upregulation of APX activity in the endosperms of wheat (Devi et al., 2012). In evaluation the antioxidative response of perennial grass species, Kentucky bluegrass (Poa pratensis) to drought stress, it was observed that The transcript level of APX was significantly enhanced, suggesting that SOD and APX could be involved in scavenging oxidative stress-induced reactive oxygen species in kentucky bluegrass through changes in the level of gene expression (Xu et al., 2011).

4-1-4- Glutathione reductase (GR)

The role of glutathione in H2O2 scavenging in plant cells has been well established (Tausz et al., 2004; Srivalli and Khanna-Chopra, 2008; Szalai et al., 2009). Glutathione takes part in the removal of excess H2O2 and lipid peroxides keeping ROS under control (Rausch et al., 2007). GR catalyzes the rate-limiting last step of ascorbate-glutathione cycle and maintains high ratio of reduced to oxidized glutathione (Noctor and Foyer, 1998). It is localized predominantly in chloroplasts, but small amount of this enzyme has also been found in mitochondria and cytosol (Greissen et al., 1994).

An increased activity of GR in the leaf tissue (Eyidogan and Oz, 2005) and also roots tissue (Kukreja et al., 2005) of C. arietinum under salinity stress was previously reported. It was also observed that drought stress treatment at ~0.4 MPa osmotic potential in melon seedling (Kırkağac cultivar) caused a significant increase in GR activity (P < 0.05), while this activity in Galia cultivata at ~0.2 MPa osmotic potential was approximately 2-fold higher than in the control. It can be suggested that GR are important elements fighting oxidative stress in shoot tissues of both cultivars under drought stress conditions (Kavas et al., 2013).

4-1-5- Other enzymatic antioxidants (Guaiacol peroxidase, Monodehydroascorbate reductase, Dehydroascorbate reductase, Glutathione transferases, Glutathione peroxidase)

Guaiacol peroxidase (GPOX) could be differed from APX according to the physiological functions. GPOX decomposes indole-3-acetic acid (IAA) and has a role in the biosynthesis of lignin and defense against biotic stresses by consuming H2O2 (ROS paper). The activity of GPOX varies considerably depending upon plant species and stresses condition. It was reported that GPOX activity in leaf and root tissues of Vigna radiate (Panda, 2001) and O. sativa (Koji et al., 2009) was enhanced under salinity stress.

MDHAR exhibits a high specificity for monodehydro
Glutathione peroxidase (GPX) are the last group of enzymatic antioxidants which protect plant cells from oxidative damages by using GSH to reduce H2O2 and organic and lipid hydroperoxides (Noctor et al., 2002). Similarly with GT, a considerable increase in GPX activity was observed in L. esculentum roots under saline condition (Gapinska et al., 2005).

4-2-1- Ascorbic acid

As a highly vital substance, ascorbic acid performs essential metabolic functions in plants. The endogenous level of ascorbic acid been suggested to be important in regulation of developmental senescence (Pavet et al. 2005). Plants have several L-AA biosynthetic pathways including routes via L-galactose and L-gulose (Wolucka and Van Montagu 2003), and the contribution of each pathway varies between different species (Cruz-Rus et al. 2011). It was well documented that AA plays a very crucial role in the protection of plants against several environmental stresses, such as salinity (Shalata and Neumann 2001, Vwioko et al. 2008).

Ascorbic acid is the most abundant, studied and powerful non-enzymatic antioxidant which protect plants cells from oxidative damage. Ascorbate is known as a magnificent scavenger because of its ability to donate electrons in a number of enzymatic and non-enzymatic reactions. It is able to scavenge the O2 and OH- and by regenerate a-tocopherol from tocopheroxyl radical, directly, and protect membranes (Smirnoff, 2005). It was approved that enhanced AA concentration is a response to salinity and drought stress. For instance, AA concentrations increased twofold after 15 days of drought, and maximum values were attained after 50 days of drought, when Cistus clusii plants were exposed to drought stress (Hernandez et al., 2004).

4-2-2- Tocopherols (Vitamin E)

α-Tocopherol, which belongs to the vitamin E group of compounds, is a lipophilic antioxidant that has a number of functions in plants. α-Tocopherol is synthesized in the envelope of plastids (Arango and Heise, 1998), and is stored in plastoglobuli of the chloroplast stroma, and in thylakoid membranes (Fryer; 1992; Havaux, 1998) Most of the α-tocopherol synthesized is partitioned between the chloroplastic envelope and the thylakoids and is stored in plastoglobuli only in some cases. In spinach chloroplasts, one-third of the total α-tocopherol is located in envelope membranes, and the remaining two-thirds in thylakoids (Wise and Naylor, 1987). The antioxidant activity of tocopherols and tocotrienols as free-radical scavengers is associated with the ability to donate its phenolic hydrogen to lipid free radicals, and with specific requirements of the molecule.

It can be assessed that stress-tolerant plants usually display increase tocopherol levels, but the most sensitive ones show net tocopherol loss under stress, which leads to oxidative damage and cell destruction (Munne-Bosch and Alegre, 2002; Munne-Bosch, 2005). The role of α-Tocopherol in salinity tolerance induction was observed by some researchers, for instance, Srivastava et al. (2005) reported a general induction in α-tocopherol content in A. dolioleum under NaCl and Cu stress.

Several observations support this state, e.g., α-tocopherol increases remarkably by water deficit in spinach and pea leaves (Tanaka et al., 1990; Moran et al., 1994), in wheat (Bartoli et al., 1999), in Mediterranean shrubs such as rosemary and lavender (Munne-Bosch et al., 1999; Munne-Bosch et al., 2001), and in European beech seedlings (Garcia-Plazaola and Becerril, 2000). However an interesting observation can be also taken; the changes in α-tocopherol level during plant responses to environmental stress are characterized by two phases. In the first phase, there is an increase in tocopherol synthesis, which is followed by a second phase of net tocopherol loss (Munne-Bosch, 2005).

4-2-3- Glutathione

GSH is necessary to maintain the normal reduced state of cells as an interaction to the inhibitory effects of produced ROS (Meyer, 2008). It is a potential scavenger of O2, H2O2 and OH (Briviba, 1997). Additionally, GSH plays a key role in the antioxidative defense system by regenerating another potential water soluble antioxidant like ASH, via the ASH-GSH cycle (Foyer and Halliwell, 1976).

It was observed that the amount of GSH was increased in leaves and petals of two different drought resistance marigold cultivars (Tagetes erecta L. cv. Chokdee and Tagetes erecta L. cv. Discovery) (Tian et al., 2012).

4-2-4- Flavonoids and Carotenoids (Car)

Flavonoids are among the most bioactive plant secondary metabolites. Flavonoids serve as ROS scavengers by locating and neutralizing radicals before they damage the
cell thus important for plants under adverse environmental conditions. Antioxidative activity of flavonoid compounds depends on the reduction potentials of their radicals. Many flavonoid biosynthetic genes are induced under stress conditions. It has been found that there is considerable increase in flavonoid levels following biotic and abiotic stresses (Lovdal et al., 2010).

Carotenoids are lipid soluble antioxidants which found in plants and microorganisms and play a series of functions in plant metabolism, including oxidative stress tolerance (Gill and Tuteja, 2010).

Increase level of flavonoids compounds in plants under stress conditions, such as drought was previously reported (Hernandez et al., 2004).

4-2-5-Proline

Plants exposed to saline conditions accumulate a number of metabolites which known as compatible solutes since there is no interfere with plant metabolic process. Among them, Proline accumulation is one of the most frequently reported modifications induced by salt stress in plants, and it is considered have a critical role in stress resistance induction. Proline also acts as a energy sink in order to adjust redox potentials. It protects plants from free radicals damage by singlet oxygen quenching (Matysik et al., 2002).

Proline metabolism depends on two key enzymes including g-glutamyl kinase and g-glutamyl phosphate reductase which known as P-5-C synthetase enzyme complex and the regulation of proline biosynthesis is mainly controlled by the activity of P-5-C synthase (Khan et al., 2003). Proline oxidase also influences the level of proline accumulation as it degrades proline to glutamate. Salt treatment dramatically increased proline synthesis from glutamate and its utilization by oxidation and for protein synthesis was decreased by 50 and 60%, respectively, in barley under salinity stress (Buhl and Stewart, 1983). The higher accumulation of proline could be due to enhanced activities of ornithine aminotransferase (OAT) and pyrroline-5-carboxylate reductase (P-5-CR), the enzyme involved in proline biosynthesis as well as due to inhibition of proline oxidase and proline dehydrogenase (PDH), proline catabolizing enzymes (Kandpal et al., 1981). The enhanced concentration of proline in response to environmental stress including salinity and drought was previously observed and reported (Mohammadkhan and Heidari, 2008).

CONCLUSION

Based on the evaluation of research's results, it is well documented that ROS production is a very common consequence of abiotic stresses which leads to the oxidative damage in plant cell structures. In this review, the role of enzymatic and non-enzymatic antioxidants on biochemical protection of plants was assessed and the mechanism of action of these compounds was demonstrated. The importance of antioxidative system in environmental stress tolerance induction especially in salinity and drought stress was also shown in detail. It could be concluded that plants with higher antioxidative potential will have a higher level in future investigations regards to the production of more tolerable plants.

REFERENCES


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