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Review

Drought and oxidative stress

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Drought, a natural stress factor has the highest percentage with 26%, when the usable areas on the earth are classified in view of stress factors. Biotic and abiotic stress factors may cause yield loss in plants and affect human and animal nutrition. Amount of lacking yield due to biotic and abiotic stress factors ranged between 65 and 87%. The best option for crop production, yield improvement and yield stability under soil moisture deficient conditions is to develop drought tolerant crop varieties (Siddique et al., 2000). A physiological approach would be the most attractive way to develop new varieties rapidly. Only few studies highlighted the importance of antioxidant enzymes during drought stress. The antioxidant defenses appear to provide crucial protection against oxidative damage in cellular membranes and organelles in plants grown under unfavorable conditions. Thus, plants are equipped with complex and a highly efficient antioxidative defense system which can respond and adapt to drought stress. This system is composed of protective nonenzymatic and enzymatic protection mechanisms. They interrupt the uncontrolled oxidation and serve to maintain the antioxidants in their reduced functional state, that efficiently scavenge ROS (reactive oxygen species) and prevent damaging effects of free radicals. Balance at aerobic metabolism is defined as free radical generation and rapid removal by antioxidant systems. The structure of cells and functional changes of systems, may be damaged by the formation of irreversible oxidative stress. Redox signalling and antioxidative defense systems are very important for protection towards uncontrolled and cascade damage of biotic and abiotic stress factors. In this review, drought, drought types and antioxidative defense system components will be discussed.

Key words: Antioxidative defense system, ascorbate peroxidase, catalase, drought types, glutathione reductase, oxidative stress, superoxide dismutase.

STRESS AND STRESS TYPES

Any inappropriate environmental factor for living organisms is termed “stress” and ability of living against unfavourable environmental conditions is called "stress resistance" by scientists (Cirak and Esendal, 2006; Levitt, 1980). In nature, a wide range of biotic and abiotic environmental factors cause stress in plants. Abiotic factors can be grouped as physical and chemical environmental factors (Kacar et al., 2009). Stress factors cause a rise of tension in organisms. The tension factor cause reversible physical and chemical changes called "elastic tension" which is not significant for agriculture because of disappearing by the removal of stress factor. However, prolonged and ongoing stress creates an irreversible tension called “plastic tension” which is important for agriculture (Cirak and Esendal, 2006).

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Stress affects growth and development negatively by important physiological and metabolic changes. Stress also causes death of the plant and plant organs, decrease in product quality and quantity (Kacar et al., 2009). Biotic and abiotic stress factors cause the loss of plant productivity and affect human and animal nutrition negatively. Lose of productivity by biotic and abiotic stress factors ranged from 65 to 82%. Stress factors that cause yield lost can be defined as drought, salinity, heat, chilling, biogenic, oxidative, air polutants stress, light and ultraviolet light intensity and water flood (Kacar et al., 2009).

DROUGHT STRESS AND TYPES

Plant growth and productivity is adversely effected by nature’s wrath in the form of various biotic and abiotic stress factors. Water deficit is one of the major abiotic

stresses which adversely affects crop growth and yield (Jaleel et al., 2009). On dry farming areas, an important part of annual precipitation falls between November and April. As a result of insufficient and irregular precipitation, the cultivation of wheat in dry farming areas becomes a big problem. Drought seems at different development stages of plant and induces effects especially at the grain filling period . At drought conditions, water potential of soil and plant decreases, at advanced stages of plant growth, turgor pressure decreases, stomata close, leaf growth and photo-synthesis rate reduce (Ozturk, 1998; Monti, 1986). Drought stress is synonymous with water stress, it happens when water lost as vapor (transpiration) is more than water taken (Sade, 2000), so a competition starts between plants for water because of the negative pressure.

In other words, balance among plant organs is disrupted during drought (Kacar et al., 2009). It is not possible defining drought exactly. However, in general locations where annual rainfall amount is lower than 400 mm or does not take enough precipitation, during rapid plant development, soil moisture is under pailing point which is defined as “dry zone” (Cirak and Esendal, 2006; Eris, 1990). Generally, drought stress occurs when the available water in the soil reduces and atmospheric conditions cause continuous loss of water by transpiration or evaporation (Jaleel et al., 2009; Anonymous, 2010a). It is also possible to define drought as a natural event that causes negative effect on land, water resources and hydrological balance as a result of falling below the normal levels. Drought types are classifed as; meteorological, agricultural, hydrologic and physiologic drought.

Meteorological drought

Meteorological drought is defined as the deviation of values from normal rainfall for a specific period (at least 30 years). These definitions are usually territorial and based on understanding of the regional climatology. Under normal conditions, meteorological measurements are used as an indicator of expressing drought. An ongoing meteorological drought could be stronger quickly or finished suddenly (Anonymous, 2010a).

Agricultural drought

Agricultural drought is related with various characteristics of meteorological drought and is defined as the absence of water needs of plant, seen during limitation of water resources and in moisture periods. In this kind of drought, falling period is more important than amount of precipitation. It will be usefull if rainfall comes in the right stage of plant development. Amount of precipitation may not be much, but if the time of precipitation is suitable for plant development, meteorological drought may occur but agricultural drought does not seem because of plant’s water procurement (Anonymous, 2010b).

Hydrologic drought

Hydrological drought means absence of earth and undergroung water resources due to long-lasting reduction of precipitation. The kind of drought may be traced by measurement of lakes, reservoirs and underground water levels. Generally, hydrological measurements are not the only indicator of drought. It is possible to see hydrological drought after a long time of meteorological drought (Anonymous, 2010a). The frequency and severity of hydrological drought is often defined on a watershed basin scale. Although, climate is a primary contributor to hydrological drought, other factors such as changes in land use, land degradation, and the construction of dams also affect the hydrological characteristics of water resources (Anonymous, 2010b).

Physiologic drought

Physiological drought is defined as a state of water expressed by the water content limiting the plant production in the soil root zone. The expression physiological drought seems to be a better characteristic to specify the water deficiency for plants. Its relation to different types of drought is not unambiguous; even if the meteorological drought exists, it does not necessarily mean physiological or hydrological drought. Accordingly, the stage of physiological drought depends on the plant type, especially on the ontogenesis stage of a particular plant (Novak, 2008). During physiological drought, plant cannot use water in the soil because of the unsuitable formation. Due to the low temperature or freezing of soil, water plants cannot take water by roots; when plants are faced with physiological drought, they try to keep water by removing their leaves (Anonymous, 2010b).

EFFECTS OF DROUGHT STRESS ON PLANTS

Various management strategies have been proposed to cope with drought stress. Drought stress causes reducing leaf size, stem extension and root proliferation, water use efficiency, and disturbing plant water relations. Different kinds of plants display physiological and biochemical responses at cellular and whole organism towards prevailing drought stress. CO_2 assimilation by leaves is reduced mainly by stomatal closure, membrane damage and disturbed activity of various enzymes, especially those of CO_2 fixation and ATP (adenosine triphosphate) synthesis by drought stress (Farooq et al., 2008). The antioxidant defenses appear to provide crucial protection

against oxidative damage in cellular membranes and organelles in plants grown under unfavourable conditions (Al-Ghamdi, 2009; Kocsy et al., 1996).

Thus, plants are equipped with a complex and highly efficient antioxidative defense system which can respond and adapt to drought stress, composed of protective non-enzymatic and enzymatic mechanisms to interrupt the cascades of uncontrolled oxidation in some organelles (Al-Ghamdi, 2009; Noctor and Foyer, 1998). Plants maintain the antioxidants in their reduced functional state, that efficiently scavenge ROS and prevent damaging effects of free radicals (Al-Ghamdi, 2009; Schwanz et al., 1996). Only few studies highlighted the importance of antioxidant enzymes during drought stress.

Mechanical effect

Mechanical effect of drought occurs when turgor reduces as a result of extreme water lost. The structure of the plasma membrane is a consequence of the aqueous environment of the cell; the hydrophobic phospholipid tails in the membrane are repelled by water forming the bilayer (Liquid-crystalline phase). As water leaves the cell, the structure of the membrane alters, the hydrophilic head groups of the phospholipids approach to each other and membranes become compact (Gel phase). In the phase, the membrane lipids have less kinetic energy and lateral and rotational motion compared with the liquid crystalline phase due to water loss, cell volume begins to decrease, resulting in plasmolysis, where the plasma membrane withdraws from the cell wall, remaining attached only at the plasmodesmata. The collapse places the plasma membrane and tonoplast under tension, in that it can cause the tearing of either the plasma membrane, or the tonoplast can cause a release of hydrolytic enzymes (Kalefetoglu and Ekmekci, 2005) which separate organic molecules from one or more components and autolysis of the cytoplasm (Anonymous, 2010c). This damage inevitably disrupts, often permanently, the normal cellular metabolism (Kalefetoglu and Ekmekci, 2005).

Metabolic effect

Plants give 99% of water taken by roots to the atmosphere by transpiration and use the remaining 1% for metabolic activities. Water is used as a source of electron to the pigment of photosystem II in photosynthesis light reactions. For this reason, water is very important for ongoing photosyntetic reactions (Sade, 2000). Because of the functional properties of water and as a result of its loss, the regulation of normal cell metabolism is disrupted and cannot continue. Ion accumulation originates from the water loss of the cell, can damage the cell, disrupts membranes and causes protein denaturation (Kalefetoglu and Ekmekci, 2005).

Oxidative effect

Many abiotic environmental stresses including salinity, drought stress, temperature extremes, and metal toxicity disrupt the redox homeostasis of cells and exert a wide range of adverse effects on plant growth and metabolism (Maheswari and Dubey, 2009). These stressful conditions induce overproduction of ROS such as $O_2^{\bullet 2}$ (singlet oxygen), the (OH^-) (hydroxyl radical) and H_2O_2 (hydrogen peroxide), which can cause oxidative damage to vital cellular components, such as membrane lipids, proteins, enzymes, pigments and nucleic acids (Maheswari and Dubey, 2009; Dat et al., 2000). ROS damage DNA, proteins, chlorophyll and membrane function are produced by oxidative meta-bolism in chloroplasts, mitochondria and peroxisomes (Keles and Unyayar, 2004; Asada, 1996).

ROS production is further enhanced in response to various abiotic stresses, such as drought (Keles and Unyayar, 2004; Rubio et al., 2002), salt, extreme temperatures. Numerous studies show that the level of antioxidant enzymes increases when plants are exposed to biotic or abiotic stresses. Higher plants employ defense strategies under environmental stresses (Keles and Unyayar, 2004; Pastori and Foyer, 2002). Effectively, in order to survive, plants need to respond to environmental stresses through a variety of biochemical reactions (Keles and Unyayar, 2004; Bonnet et al., 2000). Plant cells are also equipped with oxygen radical detoxifying enzymes, such as superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR) and catalase (CAT) (Keles and Unyayar, 2004; Alscher et al., 2002).

FREE RADICALS

Oxygen toxicity is an inherent feature of aerobic life, since it has been estimated that 1% of the oxygen consumed by plants is diverted to produce activated oxygen (Carlos et al., 1999; Asada and Takahashi, 1987) in various subcellular loci. The univalent reduction of dioxygen occurs in almost all aerobic cells (Keles and Unyayar, 2004; Behera et al., 2002). Free radicals are the chemicals which have an uncoupled electron. All free radicals are reactive oxygen species but every reactive oxygen species are not free radicals. These chemicals are capable of reacting rapidly (Antmen, 2005). The first product is superoxide radical anion, O_2^-. Subsequently, other toxic chemical entities such as H_2O_2 and hydroxyl radical, OH^-, are formed. Superoxide radicals resulting in H_2O_2 formation are detoxified by SOD (Keles and Unyayar, 2004; Alscher et al., 2002). The removal of H_2O_2 is achieved by APX which oxidises ascorbate to

monodehydro Ascorbate radicals (Keles and Unyayar, 2004; Rubio et al., 2002). Dehydroascorbate is reduced to ascorbate by glutathione. Glutathione, which is oxidised in this process to glutathione disulfide, is recycled by glutathione reductase (GR) consuming NADPH. Antioxidant defense capacity of cells is determined by the pool size of the antioxidant compounds and antioxidant enzyme activities. Changes of these parameters reflect the impact of environmental stresses on plant metabolism (Keles and Unyayar, 2004; Herbinger et al., 2002).

Free radical effects

The effects on DNA and nucleic acids

A wide variety of oxidative damage products are induced in DNA by hydroxyl radicals, superoxide, and nitric oxide (Britt, 1996; Demple et al., 1985). Some of these damaged bases, including thymine glycol and its degradation product, urea, act as blocks to DNA synthesis but are not particularly mutagenic. Significant extracellular sources of activation include air pollutants such as ozone or perhaps radicals produced by neighboring cells during the hypersensitive response. Very high levels of UV-B radiation can also induce oxidative damage in DNA (Britt, 1996). In some cases, free radicals can cause DNA mutations by effecting cells. Chromosomal and other changes in DNA cause cytotoxic effects due to modificational changes. Hydroxyl radical can react as deoxyribose and other base modifications. Hydrogen peroxide can easily pass cell membranes and reach to nucleus and cause DNA damage by dysfunction of cells and cell death (Antmen, 2005; Meram and Aktaran, 2002).

The effects on proteins

Oxidative attack on proteins results in site-specific amino acid modifications, fragmentation of the peptide chain, altered electrical charge and increased susceptibility to proteolysis. The amino acids in a peptide differ in their susceptibility to attack, and the various forms of activated oxygen differ in their potential reactivity. Primary and secondary protein structures alter the relative susceptibility of certain amino acids. In spite of this complexity, generalisations can be made. Amino acids containing sulphur, and thiol groups specifically, are very susceptible sites. Activated oxygen can abstract a H atom from cysteine residues to form a thiyl radical that will transform to a second thiyl radical to form disulphide bridges. Alternatively, oxygen can add to a methionine residue to form methionine sulphoxide derivatives. Reduction of both may be accomplished in microbial systems by thioredoxin and thioredoxin reductase (Anonymous, 2010c; Farr and Kogama, 1991). A protein-methionine-S-oxide reductase has been measured in pea chloroplasts (Anonymous, 2010d; Ferguson and Burke, 1992). This enzyme reduces the methionyl sulfoxide back to methionyl residues in the presence of thioredoxin (Anonymous 2010d; Brot and Weissbach, 1982). In some instances, this enzyme has restored the biological activity of a protein, but this function in plants has not been described. Other forms of free radical attack on proteins are not reversible. For example, superoxide with enzymatic function destroys oxidation of iron-sulphur (Anonymous, 2010d; Gardner and Fridovich, 1991). Many amino acids undergo specific irreversible modifications when a protein is oxidised.

For example, tryptophan is readily transformed to form bityrosine products (Anonymous, 2010d; Davies, 1987). Histidine, lysine, proline, arginine, and serine form carbonyl groups on oxidation. The oxidative degradation of protein is enhanced in the presence of metal cofactors that are capable of redox cycling, such as Fe. In these cases, the metal binds to a divalent cation binding site on the protein. The metal then reacts with hydrogen peroxide in a Fenton reaction to form a hydroxyl radical that rapidly oxidises an amino acid residue at or near the cation binding site of the protein. This site-specific alteration of an amino acid, usually inactivates the enzyme by destruction of the cation binding site. Oxidative modification of specific amino acids is one mechanism of marking a protein for proteolysis (Anonymous, 2010d; Stadtman, 1986). In *Escherichia coli*, there are specific proteases that degrade oxidised proteins (Anonymous, 2010d; Farr and Kogoma, 1991) and similar specificity is expected in plants. It is well documented that the various peptide components of photosystem II turnover at different frequencies (Anonymous, 2010d; Barber and Andersson, 1992).

The effects on lipids

The occurrence of malondialdehyde (MDA), a secondary end product of the oxidation of polyunsaturated fatty acids, is considered a useful index of general lipid peroxidation (Hodges et al., 1998). Lipid is an important component surrounding cells and cellular organelles. Oxidative degradation of membrane lipids is defined as lipid peroxidation known as unsaturated fat acids' distortion and occurrence of lipid hydroperoxides at cell membrane. Lipid peroxidation is the only way of producing MDA at biological systems (Dogan, 2005; Horton and Fairhurst, 1987).

RESISTANCE MECHANISMS TO OXIDATIVE STRESS

The antioxidant defenses appear to provide crucial protection against oxidative damage in cellular membranes

and organelles in plants grown under unfavorable conditions (Al-Ghamdi, 2009; Kocsy et al., 1996). Cellular antioxidative defense system, which keeps AOS (active oxygen species) under control and functions as a reductant for many free radicals, minimizes the damage caused by oxidative stress (Al-Ghamdi, 2009; Noctor and Foyer, 1998). Plants possess a complex antioxidant system, which consists of ascorbic acid, glutathione and enzymes that protect the plant against oxidative damage induced by environmental stresses. Ascorbate (ASC), a ubiquitous soluble antioxidant in photosynthetic organisms, is the most important reducing substrate for hydrogen peroxide detoxification (Chen et al., 2007). An antioxidant system consists of low molecular weight antioxidants such as ascorbate, glutathione, α-tocopherol and carotenoids, as well as several enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR) (Feng et al., 2004). Superoxide dismutase (SOD) is a group of metalloenzymes that catalyse the disproportionation of superoxide to H_2O_2 and O_2.

Thus, SOD constitutes the first line of defense against superoxide derived oxidative stress in the plant cell. Cellular H_2O_2 is detoxified by CAT and in chloroplasts by ascorbate-glutathione cycle with its key enzymes APX and GR. Environmental stresses exert their effects on plant growth and development indirectly through formation of ROS (Arora et al., 2002). Enhanced activities of antioxidants are associated with resistance to environmental stresses. In sunflower seedlings, it was reported that there was an induction of defense enzyme activities and an increase in glutathione content when plants reached a moderate level of water deficit stress. Wheat plants subjected to water stress (Carlos et al., 1999) showed that ascorbate/glutathione cycle allowed the plants to maintain hydrogen peroxide at the control level, despite a greater capacity of the thylakoid membranes to leak electrons towards oxygen (Szechynska et al., 2007; Loschiavo et al., 1989; Vergara et al., 1990). Oxidative stress causes an imbalance between reactive oxygen species (ROS) generation and antioxidant capacity of cells (Szechynska et al., 2007; Cutler et al., 1991; Papadakis et al., 2001). It has been proposed that water-stress conditions may trigger formation of the superoxide radical and hydrogen peroxide, which can directly attack membrane lipids and inactivate SH- containing enzyms (Carlos et al., 1999). The control of H_2O_2 levels is complex and dissection of H_2O_2 is difficult, particularly in biotechnogical researches like *in vitro* culture. The principal H_2O_2 scavenging enzyme in plants is catalase (CAT), which is located in peroxisomes/glyoxysomes and in mitochondria. Alternative H_2O_2 scavenging mechanisms may compensate for a reduced catalase activity, as shown by increased peroxidases (PODs) (Szechynska et al., 2007; Willekens et al., 1997).

They are found primarily in the cytosol, chloroplasts and cell walls (Szechynska et al., 2007; Karpinski et al., 1999). Higher antioxidant enzyme activities were observed in regenerating protoplasts in comparison with non-regenerating protoplasts (Szechynska et al., 2007; Siminis et al., 1993). Another soluble antioxidant, reduced glutathione (GSH), is a disulfide reductant that protects thiols of enzymes. It can regenerate ASC and react with singlet oxygen, hydrogen peroxide and hydroxyl radical. Changes in ASC and GSH pools including the increases in ASC and GSH levels, ASC/ dehydroAscorbate (DHA) and GSH/oxidized glutathione (GSSG) ratios, and activities of the enzymes related to their biosynthesis and metabolism, are tightly related to the responses of plants to a wide range of stresses. Levels and redox status of ASC and GSH also regulate expression of genes and activities of the redox sensitive transcription factors and enzymes (Chen et al., 2007).

ENZYMATIC ANTIOXIDANTS

Catalase

Catalase is an antioxidative defense system enzyme which transforms H_2O_2 to H_2O and O_2. H_2O_2 damages cell by transforming to hydroxyl radical which is very dangerous for cell and DNA structure. Those kind of dangerous reactive oxygen species are detoxyfied by ascorbate-glutathione cycle (Arora, 2002). Catalase is a critical enzyme for maintaining the redox balance during oxidative stress. Catalase controls peroxisomal H_2O_2 without limiting its production (Willekens et al., 1997). It was observed that catalase injected into the intercellular space of the leaf, can compensate for peroxisomal catalase deficiency. It was suggested that catalase functionally protects cells against H_2O_2 that is produced at a distant location. This would imply that catalase could be involved in the removal of H_2O_2 from subcellular compartments other than the peroxisomes (Willekens et al., 1997).

Ascorbate peroxidase

Ascorbate has been found in the chloroplast, cytosol, vacuole and extra-cellular compartments of the cell. About 20 to 40% of the ascorbate is in chloroplast of leaf mesophyll cell. The chloroplast contains all the enzymes to regenerate reduced ascorbate from its oxidised products. Some researchers proposed that hydrogen peroxide was dissipated in the chloroplast by the coupling of ascorbate and glutathione redox cycling (Anonymous, 2010d). APX is a very important enzyme in the ascorbate-glutathione cycle. The enzyme transforms H_2O_2 to H_2O and O_2 (Antmen, 2005). This sequence of reactions is also named as the Halliwell-Asada pathway. It was illuminated that chloroplasts produce superoxide and hydrogen peroxide on the thylakoids, most commonly PSI (protein structure initiative). Superoxide is

converted into hydrogen peroxide by either spontaneous dismutation or the SOD enzyme (Koc and Ustun, 2008). Hydrogen peroxide is scavenged by ascorbate and the enzyme ascorbate peroxidase.

The monodehydroascorbate has two routes of regeneration, one via monodehydroascorbate reductase, the other via dehydroascorbate reductase and glutathione. The terminal electron donor is NADPH (Keser, 2005). This pathway serves two functions. One is the detoxification of hydrogen peroxide, otherwise it participates in Fenton reactions, and oxidizes NADPH. The latter function is an apparently energy-consuming, wasteful process analogous to photorespiration.

The chloroplast contains catalase and dissipates hydrogen peroxide without "wasting" NADPH. However, it should be realized that favoring conditions for electron transfer from PSI to oxygen, generally causes a high redox potential like high NADPH/NADP ratio. By reducing this redox potential through the Halliwell-Asada pathway, the tendency of PSI to reduce oxygen is minimized (Anonymous, 2010d).

Superoxide dismutase

SOD, the first enzyme in the detoxifying process, converts radicals to H_2O_2. Cu/Zn SOD isoforms are found primarily in chloroplasts and in the cytosol, and Mn SODs are located in the mitochondria (Gupta et al., 1993; Rabinowitch and Fridovich, 1983). Peroxisomal localization of Mn/SOD has also been reported in pea (Gupta et al., 1993; Sandalio et al., 1987). Tobacco plants contain chloroplast-localized Fe/SOD (Gupta et al., 1993; Bowler et al., 1992; Van Camp et al., 1990).

Glutathione reductase

Glutathione reductase converts GSSG/2 (oxidized glutathione) by various nonenzymic and enzymic (that is dehydroascorbate reductase) reactions back to the reduced form GSH (free glutathione) in a short time (Keser, 2005).

One of the main functions of GSH is to protect –SH (sulphur) groups in enzymes and structural proteins against oxidation, either by acting as a scavenger for oxidizing substances or by repairing the -SH groups via the GSH-disulfide exchange reaction. The GSSG formed in both cases is reduced rapidly by the action of GR. According to the -SH hypothesis, freezing tolerance in plants involves an increase in the resistance toward oxidation of -SH groups in proteins.

The theory, however, supposes that an effective system is operating in the leaves of frost-resistant plants which maintains the -SH containing proteins in the reduced state during the frost period (Esterbauer and Dieter, 1977).

NON-ENZYMATIC ANTIOXIDANTS

Ascorbic acid (vitamin C)

ASC can directly scavenge OH^- and regenerate tocopherol from tocopheroxyl radical, thus, providing membrane protection. ASC also acts as cofactor of violaxanthin de-epoxidase, thus sustaining dissipation of excess excitation energy (Ahmad et al, 2008; Smirnoff, 2000). It can react indirectly by regenerating c-tocopherol or in the synthesis of zeaxanthin in the xanthophylls cycle. ASC plays a great role in minimizing the damage caused by oxidative process. This is performed by its synergistic action with other antioxidants (Ahmad et al, 2008; Foyer and Noctor, 2005).

Tocopherols

c-Tocopherols prevent lipid auto-oxidation and this makes it an effective free radical trap. The increase in tocopherols in conjunction with ASC has been implicated as one of the primary responses of water deficit conditions in rice (Ahmad et al, 2008; Boo and Jung, 1999). Oxidative stress activates the expression of genes responsible for the synthesis of tocopherols in higher plants (Ahmad et al, 2008; Wu et al., 2007). Antioxidants including c-tocopherol and ascorbic acid have been reported to increase following triazole treatment in tomato and these may have a role in protecting membranes from oxidative damage, thus contributing to chilling tolerance (Ahmad et al, 2008; Shao et al., 2007). Increase in tocopherol during water stress in plants has been demonstrated by many workers (Ahmad et al, 2008; Wu et al., 2007; Shao et al., 2007; Pourcel et al., 2007) have shown that drought stress led to an increase of 1 to 3-fold of c-tocopherol concentration in some grass species.

CONCLUSION AND FUTURE PERSPECTIVE

It is very important to understand mechanism of drought and oxidative stress, especially for breeding. For this aim, physiological approaches will be more effective. At this manuscript, drought effects are disscussed at this way. Antioxidative defence is very important to detoxify biotic and abiotic stresses' harmful effects. Precautions should be taken to be preserved from those factors. Current observations suggest that increasing the level of stress tolerance by reinforcing the plant's defence system with new genes is an attanable goal (Arora, 2002).

There are different ways of triggering gene expression like pre-treatment of seeds with different solutions called priming. There are also moleculer and genetic approaches like gene transfer. ROS detoxifying gene expression is an effective way also. Especially, pretreatment of seeds with H_2O_2 solutions trigger antioxidative

defence system components. Redox regulation of gene expression by oxidants is emerging as a vital mechanism in the growth and development of the plant (Shao et al., 2007). ROS serve as a common factor in regulating various signalling pathways (Ahmad et al., 2008). It is very important finding more ways to trigger antioxidative defence components for providing plant protection from the lethal effects of stress factors.

REFERENCES

Ahmad P, Sarwat M, Sharma S (2008). Reactive oxygen species, antioxidants and signaling in plants. J. Plant Biol. (3): 167-173.

Al-Ghamdi A (2009). Evalution of oxidative stres tolerance in two wheat (*Triticum aestivum*) cultivars in response to drought, Int. J. Agric. Biol. (11): 7-12.

Alscher RG, Erturk N, Heath LS (2002). Role of superoxide dismutases (SODs) in control ling oxidative stress in plants. J. Exp. Bot.. (53): 1331-1341.

Anonymous (2010a). Government meteorology management. http://www.meteor.gov.tr (Accessed 11.11.2010).

Anonymous (2010b.) Pasific diseaster centre. http://www.pdc.org (Accessed 11.11.2010)

Anonymous (2010c). Plant stress. http://www.plantstress.com (Accessed 11.11.2010).

Anonymous (2010d). Naturel disaster center. http://afetmerkezi.com (Accessed 01.02.2011).

Antmen ŞE (2005). Oxidative stress at Beta talasamide. Cukurova Uni. Pub.

Arora A, Sairam RK, Srivastava GC (2002). Oxidative stress and antioxidative system in plants. Curr. Sci. (82): p. 10.

Asada K, Takahashi M (1987). Production and scavenging of active oxygen in photosynthesis. Elsevier. pp. 227-287.

Asada K (1996). Radical production and scavenging in chloroplasts. In: Baker NR (ed) Photo synthesis and environment, Kluwer Aca. Pub. pp. 123-150.

Barber J, Andersson B (1992). Too much of a good thing light can be bad for photosynthesis. Trends Biochem. Sci. (17): 61-66.

Behera RK, Mishra PC, Choudhury NK (2002). High irradiance and water stress induce al terations in pigment composition and chloroplast activities of primary wheat leaves. J. Plant Physiol. (159): 967-973.

Boo YC, Jung J (1999). Water deficit induced oxidative stress and antioxidative defense in rice plants. J. Plant Physiol. (51): 255-261.

Bonnet M, Camares O, Veisseire P (2000). Effects of zinc and influence of *Acremonium lolii* on growth parameters, chlorophyll a fluorescence and antioxidant enzyme activities of ryegrass (*Lolium perenne* L.cv Apollo). J. Exp. Bot. (51): 945-953.

Bowler C, Van Montagu M, Inze D (1992). Superoxide dismutase and stress tolerance. Annu. Rev. Plant Physiol. Plant Mol. Biol. p. 43.

Britt BA (1996). DNA damage and repair in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. (47): 75–100.

Brot N, Weissbach H (1982). The biochemistry of methionine sulfoxide residues in proteins. Trends Biochem. Sci. (7): 137-139.

Carlos GB, Simontacchi M, Tambussi E, Beltrano J, Montaldi E, Puntarolo S (1999). Drought and watering-dependent oxidative stres: effect on antioxidant content *Triticum aestivum L.* Leaves. J. Exp. Bot. (50): 375-383.

Chen KM, Gong HJ, Wang SM, Zhang CL (2007). Antioxidant defense system in *Phragmites communis* Trin. Ecotyp. Biol. planta. (4): 754-758.

Cırak C, Esendal E (2006). Drought stres of soybean, Ondokuz Mayıs Univ. J. Faculty Agric. (21): 231-237.

Cutler A, Saleem M, Wang H (1991). Cereal protoplast recalcitrance, *In vitro* Cell Dev. Biol. (27): 104–111.

Dat J, Vandenabeele S, Vrabova E, Van M, Inze D, Van Breusegem F (2000). Dual action of the active oxygen species during plant stress responses. Cell. Mol. Life. Sci. (57): 779-795.

Davies KJA (1987). Protein damage and degradation by oxygen radicals. I General Aspects. J. Biol. Chem. (162): 9895-9901.

Dogan M (2005). Physiological and morphological effects of cadmium chloride, sodium chloride and their combinations in *Ceratophyllum demersum* L. PhD Thesis. Cukurova Uni. Sci. Instit. pp. 23-26.

Eris A (1990). Horticulture plant physiology. Uludag Uni. Agric. Engin. Faculty Publishing.

Esterbauer H, Dieter G (1977). Seasonal variation of glutathione and glutathion reductase in needles of *Picea abies*. Plant Physiol. (61): 119-121.

Farooq M, Wahid A, Kobayashi D, Basra SMA (2008). Plant drought stress effects, mechanisms and management. Agron. Sustainable Dev. (29): 185-212.

Farr SB, Kogoma T (1991). Oxidative stress responses in *Escherichia coli* and *Salmonella typhimurium*. Microbiol. Rev. (55): 561-585.

Feng Z, Jin-Kui G, Ying-Li Y, Wen-Liang H, Li-Xin Z (2004). Changes in pattern of antiozidant enzyms in wheat exposed to water deficit and rewatering. Acta Physiol. Planta. (26): 345-352.

Ferguson DL, Burke JJ (1992). A new method of measuring protein methionine Soxide reductase activity. Plant Physiol. (100): 529-532.

Foyer CH, Noctor G (2005). Redox homeostis and antioxidant signaling A metabolic interface between stress perception and physiological responses. Plant Cell. (17): 1866-1875.

Gardner PR, Fridovich I (1991). Superoxide sensitivity of *Escherichia coli*. phosphogluconate dehydratose. J. Biol. Chem. (266): 1478-1483.

Gupta AS, Webb RP, Holaday AS, Allen RD (1993). Overexpression of superoxide dismutase protects plants from oxidative stress. Plant Physiol. (103): 1067-1073.

Herbinger K, Tausz M, Wonisch A, Soja G, Sorger A, Grill D (2002). Complex interactive effects of drought and ozone stress on the antioxidant defense systems of two wheat cultivars. Plant Physiol. Biochem. (40): 691-696.

Hodges D, DeLong JM, Forney CF, Prange RK (1998). Improving the thiobarbituric acid reactive substances assay for estimating lipid peroxidation in plant tissues containing anthocyanin and other interfering compounds. Planta, (207): 604-611.

Horton A, Fairhurst A (1987). Lipid peroxidation and mechanism of toxicity. Critical Rev. Toxicol. (18): 27-79.

Jaleel CA, Manivannan P, Wahid A, Farooq M, Al-Juburi HJ, Somasundaram R, Vam RP (2009). Drought stres in plants a review on morphological characteristics and pigments composition. Int. J. Agric. Biol. (11): 100-105.

Kacar B, Katkat V, Ozturk S (2009). Plant physiology, Book. Nobel Publishing. ISBN:975-591-833-7.

Kalefetoglu T, Ekmekci Y (2005). The effects of drought on plants and tolerance mechanisms. Gazi Univ. J. Sci. (18): 723-740.

Karpinski S, Reynolds H, Karpinska B, Wingsle G, Creissen G, Mullineaux P (1999). Systemic signalling and acclimatisation in response to excess excitation energy in Arabidopsis. Sci. (284): 654–657.

Keles Y, Unyayar S (2004). Responses of antioxidant defense system of *Helianthus annus* to absisic acid under drought and waterlogging. Acta Physiol. Planta, (26): 149-156.

Keser G (2005). Effects of lead on the activities of stress related enzymes, contents of mineral and chlorophyll, and growth in *Nasturtium officinale* R. Br. PhD Thesis. Cukurova Univ. Sci. Instit. pp. 12-23.

Kocsy G, Brunner M, Ruegsegger A, Stamp P, Brunold C (1996). Glutathione synthesis in maize genotypes with different sensitivities to chilling. Planta, (198): 365–370.

Koc E, Ustun AS (2008). Defence against pathogen in plants and antioxidants. Erciyes Uni. Sci. Instit. J. (24): 82–100.

Levitt J (1980). Responses of plants to environmental stresses. Academic Press.

Loschiavo F, Pitto L, Giuliano G, Torti G, Nuti Ronchi V, Marazziti D, Vergara R, Orselli S, Terzi M (1989). DNA methylation of embryogenic carrot cell cultures and its variation as caused by mutation, differentiation, hormones and hypomethylating drugs. Theor. Appl. Genet. (77): 325–331.

Maheshwari R, Dubey RS (2009). Nickel induced oxidative stres and the role of antioxidant defense in rice seedlings. Plant Growth Regul.

(59): 37-49.
Meram I, Aktaran S (2002). Effects of free radicals on biomolecules. Archive. 11: p. 299.
Monti LM (1986). Breeding plants for drought resistance the problem and its relevance, drought resistance in plants. Meeting Held in Amalfi. pp.1-8.
Noctor G, Foyer CH (1998). Ascorbate and glutathione keeping active oxygen under control. Annu. Rev. Plant Physiol. Plant Mol. Biol.(49): 249–279.
Novak V (2008). Using the sensitivity of biomass production to soil water for physiological drought evaluation. Soil Water Res.(3): 116–122.
Ozturk A (1998). The effect of drought on the growth and yield of winter wheat. Trends J. Agric. For. (23): 531-540.
Papadakis AK, Siminis I, Roubelakis K (2001). Reduced activity of antioxidant machinery is correlated with suppression of totipotency in plant protoplasts. Plant Physiol. (126): 434–444.
Pastori GM, Foyer CH (2002). Common components, net works, and path ways of cross tolerance to stres. The central role of “redox” and abscisic acid mediated con trols. Plant Physiol. (129): 460-468.
Pourcel L, Routaboul JM, Cheynier V (2007). Flavonoid oxidation in plants from biochemical properties to physiological functions. Trends Plant. Sci. (12): 29-36.
Rabinowitch HD, Fridovich I (1983). Superoxide radicals, superoxide dismutases and oxygen toxicity in plants. Photochem. Photobiol. (37): 679-690.
Rubio MC, González EM, Minchin FR, Webb KJ, Arrese Igor C, Ramos J, Becana M (2002). Effects of water stress on antioxidant enzymes of leaves and nodules of transgenic alfalfa overexpressing superoxide dismutases. Physiol. Plant. (115): 531-540.
Sade B (2000). Plant physiology. Book. Selcuk University, Agriculture Faculty Publishing No:29.
Siddique MRB, Hamid A, Islam MS (2000). Drought stres effects on water relations of wheat. Bot. Bull. Acad. Sin. (41): 35-39.
Sandalio L, Palma J, De1 Rio L (1987). Localization of manganese superoxide dismutase in peroxisomes isolated from *Pisum satiuum* L. Plant Sci.(51): 1-8.
Schwanz P, Picon C, Vivin P, Dreyer E, Guehl J, Polle A (1996). Responses of antioxidative systems to drought stress in pendunculate oak and maritim pine as modulated by elevated CO_2. Plant Physiol. (110): 393–402.
Shao HB, Chu LY, Wu G, Zhang JH, Lu ZH, Hu YC (2007). Changes of some anti-oxidative physiological indices under soil water deficits among 10 wheat *(Triticum aestivum* L.) genotypes at tillering stage. Biointerface, (59): 113-119.
Siminis C, Kanellis A, Roubelakis Angelakis K (1993). Differences in protein synthesis and peroxidase isoenzymes between recalcitrant and regenerating protoplasts. Physiol Plant. (87): 263–270.
Smimoff N (2000). The role of active oxygen in the response of plants to water deficit and desiccation. New Phytol. (1125): 27-58.
Stadtman ER (1986). Oxidation of proteins by mixed-function oxidation systems implication in protein turnover, aging and neutrophil function. Trends Biochem. Sci. (11): 11-12.
Szechynska M, Skrzypek E, Dabrowska G, Biesaga-Koscielniak J, Filek M, Wedzony M (2007). The role of oxidative stress induced by growth regulators in the regeneration process of wheat. Acta Physiol. Plant. (29):327-337.
Van Camp W, Bowler C, Villarroel R, Tsang E, Van Montagu M, Inze D (1990). Characterization of iron superoxide dismutase cDNAs from plants obtained by genetic complementation in *Escherichia coli*. Proc. Natl. Acad. Sci. USA. (87): 9903-9907.
Vergara R, Verde F, Pitto L, Loschiavo F, Terzi M (1990). Reversible variations in the methylation pattern of carrot DNA during somatic embryogenesis. Plant Cell Rep. (8): 697–700.
Willekens H, Chamnongpol S, Davey M, Schraudner M, Langebartels C, Montagu M, Inze D, Van Camp W (1997). Catalase is a sink for H_2O_2 and is indispensable for stres defense in C_3 plants. Embo. J. (16): 4806–4816.
Wu G, Wei ZK, Shao HB (2007). The mutual responses of higher plants to environment: physiological and microbiological aspects. Biointerface, (59): 113-119.