

Influence of Drought Stress on Morphological, Physiological and Biochemical Attributes of Plants: A Review

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Drought poses the most significant environmental constrain that limits the growth and yield efficiency of vegetables around the world. The major challenges lies is to identify potential genetic resources and technology development that improve quality and productivity of vegetable crops under declining land, reducing natural resources and increasing environmental stresses. Varied responses of different crop species/genotypes to water-deficit condition have been studied for a long time, and several morphological, physiological and biochemical characters have been suggested to be responsible for drought tolerance. Understanding the morphological, physiological and biochemical responses to drought is essential for a holistic perception of plant resistance mechanisms to water-limited conditions and also to design screening techniques for drought tolerance that may be employed in crop breeding. Drought stress lead to the overproduction of reactive oxygen species (ROS) in plants which inactivate enzymes and damage important cellular components. The effects of the action of free radicals on membranes include the induction of lipid peroxidation and fatty acid de-esterification. Plants possess very efficient enzymatic and non-enzymatic antioxidant defense systems which work in concert to control the cascades of uncontrolled oxidation and protect plant cells from oxidative damage by scavenging of ROS. In this review the important morphological, physiological and biochemical traits that are influenced by drought stress, and may be important indices for identification/screening of drought tolerant genotypes in vegetable crops has been described.

Keywords: Climate change, Drought stress, Photosynthesis, Electrolytes,
Reactive oxygen species, Antioxidants.

Stress is defined as ‘environmental condition results into functional alteration’. In case of plants, it is the environmental factors which is below or beyond the optimum points so as to impaired plant growth and development. Stresses can be biotic or abiotic in nature, biotic stresses

include the interaction of plants with insect pests and pathogens or microorganisms while abiotic stresses includes drought, chilling, salinity, heat, high light, oxidative stress, heavy metal toxicity, radiations, and UV light. The impact of each biotic and abiotic factor depends upon the quantity,

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intensity, duration and the way of their application on the plants (Ansari *et al.*, 2019; Acquaaah, 2007). Plants are often subjected to extremes of temperatures, water potential, salinity and other stresses that limit their survival and productivity. In agricultural crops, it is simply not a matter of survival of plants but also impacts economic output in terms of yield and quality. The ability of a crop to withstand a particular stress is, directly related to its survival and productivity. As the growing population and changing climatic condition making it more severe due to the considerably mounting demands of food in the future (Battisti and Naylor, 2009). Abiotic stresses are the primary cause of crop loss worldwide, and a rough estimate suggests that ~70% of yield reduction is a direct result of abiotic stresses (Nahakpam and Shah, 2011).

Drought is a meteorological term and is commonly defined as a period without significant rainfall that limits plant productivity. In broad terms, drought is the retard availability of water, reduction in soil water content, or higher water need in quantity. A lot of fresh water resources requires for agricultural production, therefore, with continuously reducing water availability drought stress is becoming a critical issue to agriculture productivity (Ansari *et al.*, 2018; Jaleel *et al.*, 2009). Loss in agricultural yield caused due to water stress is higher than the losses inflicted by all other causes (Rodriguez *et al.*, 2010). Drought stress results into many interactive modification in plants (Table 1) which includes: (1) changes in level of gene expression (up, down or co-expression) of the responsible genes which having role in the life sustenance of plants (Batlang *et al.*, 2013), (2) alteration in protein production and degradation which results either into damaging of plants or act as countering mechanism to protect plants from drought stress (Mohammadi *et al.*, 2012) and (3) varied metabolic pool to channelize the production of new biochemically related metabolites which may confer drought stress tolerance (Kumari *et al.*, 2013).

Present status of drought stress and plants interactions

Approximately 16% of India's geographic area, mostly arid, semi-arid and sub-humid is drought-prone (GoI, 2013). Cattivelli *et al.*, (2008) reported that from the total 140 million hectares of cultivated area, about 68% is vulnerable to drought.

Since 2001, India faced three major droughts, in the years 2002, 2004 and 2009, which severely affects the various sectors and overall economic development of the country. During 2012, United States faced an agricultural drought which results into 12% decrease in corn production compared to the previous year (USDA, 2014). Hampered caused due to drought stress results into decrease in crop production which facilitates enormous economic disruption, therefore the demand of development of drought-tolerant crops is increasing. Plant facing drought makes themselves resistance to water deficit through different strategies i.e. escape, avoidance or tolerance. In most cases, plants combine a range of response types (Ansari *et al.*, 2017; Chaves *et al.*, 2003). Term drought escape is used when plants completes successful reproduction before a severe drought stress is generated, by shortening life cycles with high rates of growth and gas exchange, using maximum available resources. Plants performs drought avoidance by minimizing water loss through closing stomata, reducing light absorbance, and reducing canopy leaf area and peaked water absorption (increasing root distribution, reallocation of nutrients allocated in older leaves, enhanced photosynthesis). Drought tolerance is the outcome of coordination of physiological and biochemical alternation at the cellular and molecular levels. These alterations may involve osmotic adjustment and more rigid cell walls. Abiotic stress causes a series of morphological, physiological, biochemical and molecular changes in plants that adversely affect growth and productivity. In few decades tremendous progress has been made to understand molecular, biochemical, and physiological basis of stress tolerance in plants. Drought stress affects photosynthetic and defense machinery of plants and triggers many reactions such as photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism and growth promoters which ultimately results into retard plant growth (Jaleel *et al.*, 2008). Monakhova and Chernyadev, (2002) reported inhibition of the photochemical activities and reduction in the activities of enzyme of calvin cycle. Abedi and Pakniyat, (2010) studied antioxidant enzyme changes in response to drought stress in *Brassica napus* revealed appearance of new enzymes isoforms under drought that were suggested to

have use as a biochemical marker to differentiate drought tolerant cultivars under drought stress.

The reaction as well as potential to abide drought environment depends on the species and genotype, duration and level of water loss, age and stage of development, organ, cell type, and also type of sub-cellular compartment (Jaleel *et al.*, 2008). The responses to adapt against drought stress can be categorized in to following categories: (i) osmotic homeostasis or osmotic adjustment; (ii) stress damage control and repair, or detoxification; and (iii) growth control (Zhu, 2001). Osmotic stress signalling for the reestablishment of cellular homeostasis under stress conditions, detoxification signalling to control and repair stress damages, and signalling to coordinate cell division and expansion to the levels suitable for specific stress conditions, are the functional categorization of drought stress signaling. Therefore, drought tolerance is a complex trait, which includes interaction of morphological (earliness, reduced leaf area, leaf rolling, wax content, efficient rooting system, stability in yield and reduced tillering), physiological (reduced transpiration, high water-use efficiency, stomatal closure and osmotic adjustment), and biochemical (accumulation of proline, polyamine, trehalose, increased nitrate reductase activity and increased storage of carbohydrate) parameters. However, a high yield potential under drought conditions is an obvious target for improvement strategies, since it contributes to the yield in moderate drought stress conditions (Blum, 1996).

Effects of drought stress on morphological Characteristics

Phenological changes

It has been well-known that drought stress is a critical limiting factor for plant growth and establishment, which affects plant elongation and expansion growth due to the low turgor pressure. Osmotic regulation maintains the cell turgor and assists plants to survive even under severe drought stress conditions in pearl millet (Shao *et al.*, 2008). Wu *et al.*, (2008) reported 25% reduction in water stressed citrus seedlings plant height. A significant affect on *Abelmoschus esculentus* stem length were also reported. Growth of optimal leaf area is vital to photosynthesis and dry matter yield. Drought stress generally reduced leaf growth in number of plant species like *Populus* (Wullschleger *et al.*, 2005), soybean (Zhang *et al.*, 2004) and many other

species (Farooq *et al.*, 2009). Under drought stress Wullschleger *et al.*, (2005) reported significant inter-specific differences between two sympatric *Populus* species in total number of leaves, total leaf area and total leaf biomass. Influence of root system under drought showed significant relation with above ground dry mass. The consequence of root systems in acquiring water has long been accepted. A profuse root structure can give the advantage to maintain accelerated plant expansion through the early crop growth phase and take out water from thin soil layers that is otherwise basically loosed by evaporation. The fall in root dry weight under mild and severe water stress in *Populus* species were identified (Wullschleger *et al.*, 2005). An enhancement in root to shoot proportion under drought environment was associated to ABA content of roots and shoots (Manivannan *et al.*, 2007). Reduction in fresh and dry biomass production is a general adverse effect of water stress on crop plants (Farooq *et al.*, 2009).

In general, shallow-rooted crop species are less drought tolerant than deep-rooted species. Under water stress, some plants maintains short suberized roots, even after top soil becomes dry, which protects plants even under drought by retaining water loss from plant roots. Root-shoot signaling to adapt variable environments plants transduce positive and negative signals amongst roots and shoots to direct growth rate and behavior. The established model for plant responses to dry soil is based on hydraulic signaling together with a decline in root water uptake and then water potential and turgor in the leaves and stomatal closure, decreased leaf elongation, and osmotic adjustment. The impacts of drought stress in the root zone on the shoot can be influenced by interaction between the chemical signals. It is known to be plants growth reduction is an adaptive response of plants to stress rather than as a secondary consequence of resource margination (Rollins *et al.*, 2013).

It is the relations of phenology with the pattern of water use which makes crop to adapt against drought stress (Sekhon *et al.*, 2010). To minimize the water use under drought stress plants limit shoot growth by a decreased number of tillers (Soda *et al.*, 2010). Generally, varieties of short-duration perform better under the stress conditions compared to long-duration varieties, varied root

system of these genotypes are the region. It is the plant size and stomatal conductance which reduce to protect plant against stress, may be major factor for reduced productivity. (Deikman *et al.*, 2012).

Physiological responses to drought stress

Number of physiological parameters responsible for sustained growth of plants under environmental stresses has been identified and their roles towards drought stress tolerance were also confirmed by researchers. Variation in, relative water content, electrolyte leakage, water use efficiency (WUE), stomatal conductance, photosynthesis, transpiration, chlorophyll leaf fluorescence and chlorophyll color index in response to water deficit were reported which serve as measure for drought tolerance (Anyia and Herzog, 2004; Bahadur *et al.*, 2011). The interactive effect of parameters mentioned above depends on species considered, and their ability to resist drought stress.

Physiological parameters noticeably affected by drought stress are discussed below:

Stomatal conductance

When the plants are exposed to water-deficit under field condition the first response of the plants is the stomatal closure to prevent the loss of water through transpiration. Stomatal conductance showed close association with many physiological parameters, like electron transport rate, WUE, respiration, transpiration, and diffusion of CO₂. In response to water-deficit drought-sensitive and drought-tolerant plant exhibit differential stomatal movements. Maintained Stomatal conductance and carbon assimilation are reported in drought-sensitive crops even after the water potential falls (Pinheiro *et al.*, 2011). Over 95% water loss occurs from plants by evaporation (transpiration) through the stomatal pores. Consequently, it is essential for plants to be capable to balance the sum of CO₂ being brought into the plant with the quantity of water evading as an effect of the open stomatal pores (Shimazaki *et al.*, 2007). Stomatal closure of plants due to drought stress causes a restriction in gas exchange between the surroundings and inside of the leaf. Pirouz showed lowest stomatal conductance and seed yield under drought stress (Sapeta *et al.*, 2013). Though stomatal closure due to drought stress is a restraint for photosynthesis, it is considered as an effective mechanism for preventing water loss.

Relative water content (RWC)

Water is an essential factor of plant, which required at all stages of plant growth and development. Leaf water content is an useful indicator of plant homeostasis, presents the relative amount of water available in the plant tissues. A measurement which is referred to as Relative Water content (RWC), measures maximum amount of water tissue can hold, had preferentially removed measurement of water content expressed based on tissue fresh or dry weight basis (Boyer, 1968). Relative water content one of the most appropriate measures of plant water status in terms of the physiological consequence of cellular water-deficit. Grover *et al.*, (2004) reported decline in RWC and decrease in water relations immediately after abiotic stress development in plants. Relative water content (RWC) negatively affected by stresses especially by drought stress is considered as better indicator of water status as compared to water potential achieved by plants under drought stress mitigation (Payam, 2011). Many reports indicate that water-deficit causes reduction in RWC (Sanchez *et al.*, 2006; Sanchez *et al.*, 2010; Rai *et al.*, 2015).

Electrolyte leakage (EL)

Electrolyte leakage measured as an indicator of stress response in plant cells. The electrolyte leakage induced due to stress is often accompanied by enhancement of reactive oxygen species (ROS) which often acts as factor of programmed cell death (PCD) (Demidchik *et al.*, 2014). Stress-induced injury of plants is often measured through electrolyte leakage which acts as an indicator of plant stress tolerance (Lee and Zhu, 2010). The alteration in electrolyte leakage starts almost after the application of a stress factor and lasts for minutes to several hours. Undamaged or unstressed plant cells maintain electrolytes within the cell membrane that are vital for proper cell functioning. Maintenance of their integrity and stability could be quantified by measuring relative conductivity of the leaked ions in water (Rolny *et al.*, 2011). Electrolyte leakage (EL) has been recommended as a valuable parameter for identification of stress tolerant cultivars in several crop species (Singh *et al.*, 2011).

Photosynthesis

Similar to other physiological parameters, photosynthesis is also influenced by drought stress.

Drought has an adverse effect on the photosynthetic apparatus, membrane and enzymes (David *et al.*, 2007). Drought-induced alteration in organelle movement moreover affects photosynthesis to a large extent. Drought stress induced imbalance in hormonal level was reported in plants, which results into declination of the concentrations of many of the key enzymes of photosynthesis. Reduced RWC and water potential of leaves due to drought stress, gradually reduced stomatal conductance, which leads to a decline in CO₂ molar fraction in chloroplasts, decreased CO₂ assimilation, and reduction in rate of photosynthesis. An earliest response of plants subjected to drought stress is stomatal closure which in general understood to be the most important reason of the drought-induced decrease in photosynthesis (Flexas *et al.*, 2008).

Transpiration

Decrease in transpiration and respective increase in foliage temperature also closure of stomata are consequences of drought stress. A strong and positive link exists between yield and rate of transpiration. Stomata regulated decrease in transpiration a general response of plants against drought stress which also supports to increase plant water use efficiency (Bahadur *et al.*, 2011). Transpiration is directly related to the grade of water vapor concentration from the internal evaporation surface to the bulk air outside the leaf, and vice versa to the total resistance to water vapor transport of the air boundary layer and of the leaf (Lopez *et al.*, 2012). The decline in cumulative transpiration under drought conditions is usually linearly related to a reduction of dry matter production. Different crops show varied leaf expansion and transpiration responses to reduced level of available soil water. However, in general, these processes decrease when about a third of the transpirable soil water remains in the soil (Turner, 2001).

Photosynthetic efficiency (F_v/F_m) and chlorophyll concentration index (CCI)

Photosynthetic activity in tissues inhibited under drought stress due to imbalance generated between light capturing and its utilization (Foyer and Noctor, 2000). The declination in the maximum quantum yield of PSII photochemistry F_v/F_m implies a reduced capturing and conversion rate of excitation energy by PSII reaction centers.

Some reports suggested that in *Calluna* F_v/F_m was not altered by drought stress, but in case of *Deschampsia* 1.5%, so far significant decline was noted across the season. Plants develops various mechanism to protect from photo inhibition, which includes non photochemical quenching, transport to molecules other than CO₂, particularly to oxygen, which leads to photorespiration, non-radiative energy dissipation mechanisms and changes in chlorophyll concentration. Now a day F_v/F_m is being used as rapid and non destructive tool for drought stress screening of plants under field condition which provides rapid indication of change in current plant productivity in response to water change. It is easy to discriminate the genotypes either drought tolerant or susceptible based on Chlorophyll fluorescence measurements. Bahadur *et al.*, (2011) reported reduced PSII activity (F_v/F_m) of drought susceptible genotypes compared to drought tolerant, under water-deficit. Rapid, non-destructive estimation of total chlorophyll is a potentially important application for plant researchers. Significant correlations between total chlorophyll and chlorophyll content index values (CCI) obtained using portable chlorophyll meters have been reported for crops, including cabbage, cotton, and pea (Marquard and Tipton, 1987), sorghum and pigeonpea and muskmelon (Azia and Stewart, 2001).

Water use efficiency (WUE)

Improving WUE is necessary for securing environmental sustainability of food production in semiarid areas, where crop production relies on the use of large volumes of water. WUE is generally calculated at the leaf level, accessibility of portable equipment for measuring leaf gas exchange rates facilitates the instantaneous measurement of photosynthesis and transpiration. Scaling up from single-leaf to whole-plant WUE was tested in grapevines in different experiments (Medrano *et al.*, 2015). It was amongst one of the parameter which has been considered a lot because it gives an idea of the genotypes variation in ability to utilize water efficiently under limited water availability. In dry land areas where crops faces unpredictable seasonal rainfall, the maximization of soil moisture use is a critical factor for plant drought resistance (avoidance), which is expressed in terms of lower WUE (Blum, 2005). Genotypic difference in WUE

was determined largely by differential water use rather than by variations in plant produced. Large inconsistency in WUE was reported by Condon *et al.* (2002), among several species as well as within a species including cowpea. Enhanced crop growth is directly related with higher rate of leaf photosynthesis. A combination of elevated photosynthesis and enhanced WUE may play a critical role for yield improvement of crops under drought stress conditions.

Biochemical responses to drought stress

Plants can respond to drought stress by changing the biochemical profile of their tissues: many biochemical parameters are described below.

Proline

Proline strongly associated with plant drought stress, in which free proline can notably enhanced in crops and other plants (Lee *et al.*, 2009). Without disrupting cellular structure proline can accumulate to high concentrations in plant cells as an osmoprotectant. Proline accumulation played an important role in osmotic adjustment, detoxification of ROS and membrane integrity when plants encountered environmental stresses (Zhang *et al.*, 2011). Increase in proline concentration has been used as criteria for stress tolerance study. Protection of plasma membrane integrity, a sink of energy or reducing power, a source for carbon and nitrogen, or hydroxyl radical scavenger are the roles which proposed to be performed by proline other than osmotic adjustment. Increased levels of proline facilitate the plants to retain low water potentials. Accumulation of compatible osmolytes, reduced water potential which allows to take additional water from surrounding to maintain the osmoregulation, thus resist the intervening effect of water-deficit within the organism. Su and Wu, (2004) reported enhanced salt and water-deficit tolerance in transgenic *O. sativa* over expressing *P5CS* cDNA, led to the accumulation of *P5CS* mRNA and proline. Induced expression of abiotic stress tolerance genes involved in proline biosynthesis were reported in transgenic plants.

Hydrogen peroxide (H₂O₂)

Drought stress responses towards the production of H₂O₂ which differ by genotype to genotype, duration of water-deficit and age of plants also played important role. Dual role performed by H₂O₂ in plants, as at low concentration it acts as a

signaling molecule while at high concentrations, it leads to program cell death. H₂O₂ generated due to univalent reduction of O₂. Relatively longer half-life (1 ms) by H₂O₂ whereas, other ROS such as O₂^{•-}, OH[•] and ¹O₂, exhibit much shorter half-life (2-4 μs). H₂O₂ inactivate enzymes by oxidizing their thiol groups. Enhanced accumulation of H₂O₂ in Cu-deficient leaves of *Morus alba* cv. Kanva 2 compared to the plants grown under excess Cu noted by Tewari *et al.*, (2006). H₂O₂ also played as key regulator of physiological processes like senescence, photorespiration and photosynthesis, stomatal movement, cell cycle, growth and development (Gill and Tuteja, 2010). Mechanism by which H₂O₂ helps to sustain the soybean plant under water-deficit was reported.

Lipid peroxidation (LPO)

Most damaging biochemical process occurs under stress condition is lipids peroxidation in every living organisms. Most reliable parameters considered to identifying the genotype as tolerant or susceptible under stress condition is lipid peroxidation. MDA is the product formed during lipid peroxidation (Garg *et al.*, 2009). In both cellular and organelle membranes when ROS level crossed above-threshold limit, lipid peroxidation occurs, which not only impacts on regular cellular functioning, also stimulate the oxidative stress through generation of lipid-derived radicals. Rasool *et al.*, (2013) measured level of lipid peroxidation by estimating malondialdehyde content. Increase in Lipid peroxidation with the increase in NaCl concentration in all genotypes but lesser in salt-tolerant genotypes were recorded compared to susceptible genotypes. Stoilova *et al.*, (2010) studied wheat plants under drought stress in field condition and reported that the weakening of membrane integrity and oxidative damage to lipids were severe in the drought sensitive varieties compared to drought tolerant. In salt and drought stress condition, Pan *et al.*, (2006) reported increase in MDA content in liquorice seedlings (*Glycyrrhiza uralensis* Fisch). The LPO was suggested as an important parameter in selecting tomato genotypes under water-deficit condition. Increased accumulation of MDA has been correlated with decline in RWC and photosynthetic pigment content when plants exposed to prolonged drought (Deeba *et al.*, 2012).

Photosynthetic pigments

Chlorophyll (Chl) is considered to be most important chloroplast components for photosynthesis, and their relative concentration has a positive relationship with photosynthetic rate. Pigment photo-oxidation and chlorophyll degradation due to loss of chloroplast membranes, due to drought stress causes reduction in chlorophyll

content. Drought stress results into a significant injury to photosynthetic pigments also leads to damage of thylakoid membranes (Kannan and Kulandaivelu, 2011). Commonly noted phenomenon under drought stress is the decline in Chl content (Din *et al.*, 2011). However Pirzad *et al.*, (2011) reported enhanced accumulation of Chl under drought stress. In general it is known when

Table 1. Plant traits and mechanisms of drought adaptation

Primary traits		Drought adaptive traits	
Constitutive traits	Induced traits	Secondary traits	Integrated traits
Roots	Osmotic changes	Relative water content	Drought sensitivity index
Phenology	Cell viability	Leaf senescence	Drought tolerance efficiency
Waxes	Membrane integrity	Leaf folding/rolling	Harvest index
Stomatal conductance	Chlorophyll stability	Flowering time Delayed senescence	Recovery growth
Water use efficiency	Protein synthesis Scavenging system Lipid peroxidation Gas exchange		Plant height Leaf area Growth parameters

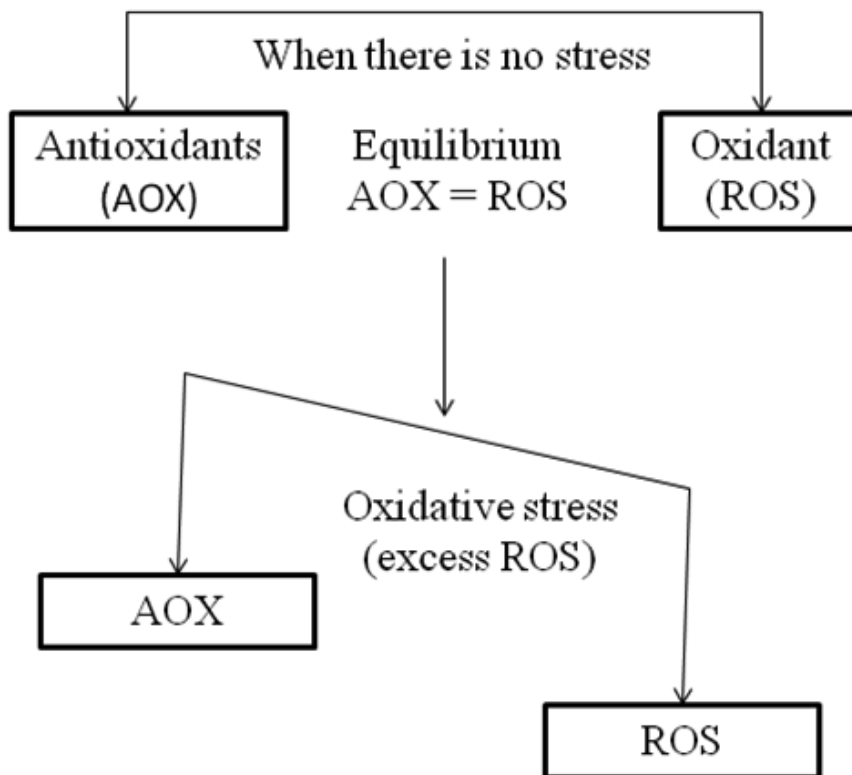


Fig. 1. Altered equilibrium under oxidative stress (Modified from Gill and Tuteja, 2010)

plants were exposed to water-deficit the decrease in Chl b is larger than that of Chl a, thus, transforming the ratio in favor of Chl a (Jain *et al.*, 2010). Carotenoids (Car) are essential for photoprotection of photosynthesis and they play an important role during the plant growth under abiotic/biotic stress. These days, improved Car contents in plants are of significant attention for breeding as well as genetic engineering in different plants. Farooq *et al.*, (2009) reported that drought stress induced the changes in the ratio of chlorophyll 'a' and 'b' and carotenoids. The reduction in sunflower and *Vaccinium myrtillus* chlorophyll content at significant level under water-deficit were observed (Jaleel *et al.*, 2009).

Reactive Oxygen Species

Stress induced Generation of reactive oxygen species (ROS) is most basic responses of plant cells to various environmental stresses. ROS induced cellular damage by oxidizing proteins, inactivating enzymes, changes in the gene expression pattern, and degradation of biomembranes. Also alterations in ROS production acts as signals that alter the transcription of genes thereby participate in the acclimation of plants to abiotic stresses (Mahalingam *et al.*, 2015). Under normal conditions antioxidant enzymes maintained ROS at low levels (Fig. 1). The stability can be affected by lessening of antioxidants or the enhanced generation of ROS, which results in to oxidative stress, and damage to cellular macromolecules and membranes and an enhanced lipid peroxidation (Lushchak, 2011). ROS induced damages confines agricultural productivity globally, deleterious effects of abiotic stresses on agricultural production are responsible for billions of dollars losses annually. Plants developed diverse mechanisms to defend themselves from unfavorable environmental situation, which involves less ROS production coupled with an efficient antioxidant defense, and the activation of different signaling pathways (Jajic *et al.*, 2015). Free radicals like $O_2^{\cdot-}$, OH^{\cdot} and non radicals like H_2O_2 and 1O_2 are the key members of the ROS family. The major centre of ROS production in plants is localized in the chloroplast, mitochondria and peroxisomes. Whereas endoplasmic reticulum, cell membrane, cell wall and the apoplast acts as secondary centre for ROS generation. Plants developed efficient anti oxidant machinery to protect from harmful

effect generated due to ROS, which is categorized into two group, (i) enzymatic antioxidants like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), glutathione reductase (GR), mono dehydro ascorbate reductase (MDHAR), and dehydro ascorbate reductase (DHAR); and (ii) non-enzymatic antioxidants which includes ascorbic acid (AA), reduced glutathione (GSH), α -tocopherol, carotenoids, flavonoids, and proline. Together both antioxidant system work to scavenge ROS (Kaushik and choudhury, 2014).

Antioxidant defense system in plants

Exposure of plants to drought stress can enhance the generation of ROS e.g., 1O_2 , $O_2^{\cdot-}$, OH^{\cdot} and H_2O_2 . To protect plant cells and its organelles, chloroplast, mitochondria and peroxisomes against the generated toxic oxygen intermediates, employed antioxidant defense system. It has been established that the induction of the cellular antioxidant machinery is significant for protection against various stresses. To counter the oxidative damage caused due to ROS under stress, plants have evolved a complex antioxidative defense system comprising of enzymatic and non-enzymatic components. The occurrence of oxygen in the surroundings and various cellular locations where ROS are produced, render oxidant scavengers that essential for plant growth and continued existence. These ROS scavenger forms antioxidative defense system located in different plant cell compartments to scavenge ROS and to check the harmful effects of ROS. Enhanced concentrations and activities of antioxidant molecules under abiotic stresses confer tolerance to plants (Gill and Tuteja, 2010; Manivannan *et al.*, 2014).

Non-enzymatic antioxidants

Molecules such as, glutathione, ascorbate, carotenoids, α -tocopherol, and various phenylpropanoid derivatives (phenolic compounds) such as flavonoids, lignans, tannins and lignins, participate in non-enzymatic antioxidant defense mechanism. Major low molecular weight thiol in plants is tripeptide glutathione (GSH, α -Glu- Cys- Gly). Glutathione is found in all higher plants cells and subcellular compartments contained glutathione. Highest concentrations of glutathione were present in chloroplasts, however its presence in significant quantities also found in the cytosol.

GSH scavenges 1O_2 , $O_2^{\cdot-}$, OH^{\cdot} and H_2O_2 and protects the biomolecules by forming adducts (glutathiolated) or by reducing them in presence of ROS or organic free radicals. GSH also helps in the formation of phytochelatin, which helps to chelate heavy metal ions and thus scavenges another potential source of ROS formation in plants (Choudhury *et al.*, 2012). L-ascorbic acid (vitamin C) is the major and the most widely studied antioxidant compound. It is known to be able to donate electrons to a wide range of enzymatic and non-enzymatic reactions. Most of the ascorbic acid in plant cells is generated due to Smirnoff-Wheeler pathway, catalyzed by L-galactano- α -lactone dehydrogenase in the plant mitochondria, while the remaining generated from D-galacturonic acid. Ascorbate played an essential role in number of physiological processes in plants, which includes growth, differentiation, and metabolism. It reduces many free radicals, thereby minimizes the destruction caused by oxidative stress (Gill and Tuteja, 2010). Carotenoids are a large class of isoprenoid molecules de novo synthesized by both photosynthetic and lots of non-photosynthetic organisms. Carotenoids are divided into the hydrocarbon carotenes, such as lycopene and β -carotene or xanthophylls, typified by lutein. β -carotene, present in the chloroplasts bound to the core complexes of PSI and PSII. To the proper functioning of chloroplast protection is necessary at this site from ROS. β -carotene in photosynthetic tissue directly quenches triplet chlorophyll, which restricts the generation of singlet oxygen and protects from oxidative damage. An increase in carotenoids/chlorophyll ratio might be of a protective value as carotenoids are known to be potent quenchers of ROS, particularly singlet oxygen (Bahadur *et al.*, 2011). One of the important secondary ROS scavenging systems in plants is Flavonoids, experiencing harm to the photosynthetic apparatus, due to the excess excitation energy. Flavonoids also played role in 1O_2 scavenging thereby lessen the damages caused to the outer envelope of the chloroplastic membrane (Agati *et al.*, 2012).

Enzymatic antioxidants

The enzymatic antioxidants include superoxide dismutase (SOD; EC 1.15.1.1), peroxidase (POD; EC 1.11.1.7), catalase (CAT;

EC 1.11.1.6), and the enzymes of AsA-GSH or Halliwell-Asada pathway viz., ascorbate peroxidase (APX; EC 1.1.1.11), glutathione reductase (GR; EC 1.6.4.2), monodehydroascorbate reductase (MDHAR; EC 1.6.5.4) and dehydroascorbate reductase (DHAR; EC 1.8.5.1). These antioxidants enzymes in cells directly detoxify ROS in cells, also catalyze synthesis, degrade, and recycle the antioxidant molecules of the cells.

CONCLUSION

Present review a steps towards to improve our understanding of the impacts, mechanisms of tolerance, and parameters associated with drought stress. Present times required well planned experimental programs aimed at enhancing the tolerance to combinations of different abiotic stresses and particularly related to drought. As we improve our knowledge and quantify the impacts of mild, average and severe water-deficit effects on various morphological, physiological, biochemical, growth, development, yield, and quality of crops, the probability of application of these factors into drought stress study will be improved and should be considered. Improved efficiency of water consumption within agricultural systems is a chief precedence in arable lands of many regions in the world. The elevating threat of declining water resources suggest germplasm identification with enhanced drought tolerance and water-use efficiency.

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