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An overview of plant responses to the drought stress at morphological, physiological and biochemical levels

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Abstract. Agricultural production is continuously constrained by number of biotic and abiotic stresses. Among all, water deficit is one of the major abiotic stresses, which adversely affects crop growth and productivity. Drought impairs normal growth, reduces leaf expansion, stem extension and root proliferation, disrupts water relation and water use efficiency. It interferes with the synthesis of photosynthetic pigments, resulting in the decline of light harvesting, generation of reducing power, and reduction of gas exchange and carbon fixation, which in turn, leads to the decline in plant growth and productivity water relations and reduces water-use efficiency in plants and it finally leads to biomass and final yield reduction of crop plants. However, plants develop some mechanisms of drought tolerance, avoidance or escape. This review presents some aspects of changes in plant at morphological, physiological and biochemical levels induced by drought.

Keywords: drought stress, growth, yield, gas exchange, photosynthetic pigments, antioxidative system, osmolytes.

INTRODUCTION

Water scarcity during growing season is the major factor limiting crop growth, development and final yield, especially in arid and semi-arid regions, where plants are exposed to drought stresses. The drought is one of the main causes of crop losses all over the world, it reduces the average yields by even more than 50% (Wang et al., 2003; Du et al., 2010; Bray et al., 2000, Anjum et al., 2011; Hussain et al., 2019). Most crop plants show a wide genotypic variability and wide range of crop damage in response to drought stress (Hasanuzzaman et al., 2012). The sensitivity of yield to water shortage depends on the type of harvested agricultural products, such as roots, shoots, leaves, fruits or seeds and occurrence of drought during specific phases of crop development may have particularly strong effects on yield (Farooq et al., 2009; Basu at al., 2016).

Reduction of crop yield is a result of many drought-induced morphological, physiological, and metabolic changes that occur in plants. Drought primary effects on reduction of plant growth, which depends on cell division and cell enlargement, and involves genetic, physiological, and morphological events, and their complex interactions. These actions are seriously impaired by drought stress, which negatively affects many important physiological and biochemical processes in plants, including osmotic adjustment, water relations, photosynthesis and respiration and membrane functions. The mechanism of yield reduction under water stress condition is linked to the reduced light absorption, disturbances in membrane electron transport, low photosynthetic rates, water use efficiency and damages caused by reactive oxygen species (Anjum et al., 2011; Hussain et al., 2019; Hasanuzzaman et al., 2013; Kumar et al., 2018).

However, plants have evolved strategies to prevent water loss, optimize water supply to vital organs, maintain cell water content, and persist in dry periods. The ability of a plant to detect first signals of water deficiency and initiate strategies to survive is defined as drought resistance. Drought resistance is a complex trait that proceeds through several mechanisms: escape - acceleration of plant reproductive phase before stress occurrence, avoidance - endurance with increased internal water content and prevention of tissue damage, and tolerance - endurance with low internal water content while sustaining growth over the drought period (Basu at al., 2016). Plants realizes these strategies by shortening their life cycles, reducing water loses and/or increasing water uptake, maintaining cell turgor through osmotic adjustment and cellular elasticity, and initiating reactive oxygen species scavenging system. This paper discusses effects of drought on morpho-physiological and biochemical activities of plants and shows some responses of plants to adapt under drought conditions.

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MORPHOLOGICAL RESPONSES

Drought stress affects the morphological traits of plants. These effects may occur at different growth and development stages, starting from germination through the elongation growth, flowering to grain filling stage. Drought stress causes changes in plant height, fresh weight, dry weight, total biomass as well as yield and yield components.

Growth

Germination disturbance is the first and primary effect of drought, which has been confirmed in many studies (Harris et al., 2002; Okçu et al., 2005; Zeid, Shedeed, 2006; Li et al., 2009; Queiroz et al., 2019; Patanè et al., 2013; Qayyum et al., 2011). Drought stress results in impaired germination and poor stand establishment of rice (Harris et al., 2002). The study on pea (Okçu et al., 2005), wheat (Qayyum et al., 2011), sorghum (Queiroz et al., 2019; Patanè et al., 2013) and maize (Li et al., 2009; Avramova et al., 2015), showed that drought limits not only germination but also the early seedling growth. Furthermore, glycol-induced drought in alfalfa reduced its germination potential and hypocotyl length (Zeid, Shedeed, 2006).

Growth is a very complex process accomplished through cell division and enlargement, and depends on genetic, physiological and environmental events. Cell growth is considered as one of the most drought-sensitive physiological processes due to the reduction in turgor pressure (Zeid, Shedeed, 2006). The reduction of cell turgor and relative water content is a result of the water decrease in soil. Under severe water deficiency, cell elongation of higher plants can be inhibited by interruption of water flow from the xylem to the surrounding elongating cells (Nonami, 1998). In the studies on maize (Premachandra et al., 1991) and Kentucky bluegrass (Wang, Huang, 2004) a significant decline of cell membrane stability under water deficiency was observed. Moreover, impaired mitosis, cell elongation and expansion caused by drought resulted in the reduction of growth and yield traits (Fig. 1) (Harris et al., 2002; Avramova et al., 2015). Effects of drought reflect in reduced accumulation of a plant mass, changes in water use, early senescence and premature death. The rates of growth and of water use are both influenced by the allocation of biomass to the different organs and by the physiological and morphological properties of these organs. The influence of physiological traits on water use efficiency depends on the balance between the effects on growth and on water use. Plant traits that increase water use efficiency may conflict with those that promote growth rate (Zlatev, Lidon, 2012). Under mild drought conditions, biomass allocation into roots usually increases. Higher biomass allocation to roots benefits in increased ability to water uptake, but it is at the expense of the biomass allocation to the above ground tissues. Nejad, (2011) established that under drought stress conditions, plant growth of shoot regions is reduced and roots are expanded, hence an increased root : shoot ratio is observed. Drought stress affects plant morphological traits, such as height, stem diameter and leaf area. Under drought conditions many authors have observed the reduction of height and stem diameter of maize (Khan et al., 2001; Ge, 2012), sorghum (Asgharipour, Heidari, 2011), soybean (Specht et al., 2001), sunflower (Kaya et al., 2006) and potato (Deblonde, Ledent, 2001). Disturbances in normal height of plants can be attributed to impaired cell elongation due to low water availability (Kaya et al., 2006). The number of leaves per plant and their individual size under water deficit conditions is reduced. The expansion of leaf area depends on leaf turgor, temperature and assimilates required for growth. Leaf area reduction caused by drought is attributed to the limitation of leaf expansion due to photosynthesis reduction (Anjum et al., 2011; Anjum et al., 2017b).

Drought affects crop phenology mostly by shortening the crop growth cycle. Limitation of water supply triggers a signal to cause an early switching of plant from the vegetative growth to reproductive development phase (Farooq et al., 2012). For example, total growth duration of both wheat and barley under drought conditions decreased which resulted in yield reduction (Dolferus, 2014). The effect of drought depends on the phase when it occurs. For instance, drought at the pre-anthesis delays flowering of quinoa (Geerts et al., 2008). Similarly, drought at anthesis delays flowering of rice (Pantuwan et al., 2002). Drought at grain filling of soybean fastened its maturity (Specht et al., 2001). Drought stress influences different crops differently. Exposure to drought delays the flowering of maize, quinoa and rice, whereas in the case of soybean, wheat, and barley, drought accelerates flowering and physiological maturity (Dolferus, 2014; Geerts et al., 2008; Pantuwan et al., 2002; Specht et al., 2001).

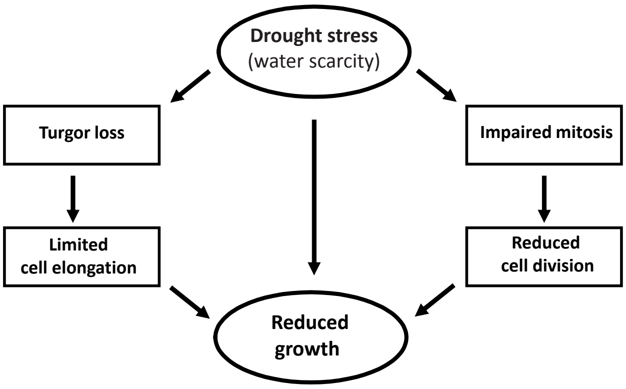

Figure 1. Possible mechanisms of growth limitation under drought stress (Jaleel et al. (2009), modified).

Yield

Water stress affects many yield-determining processes. Yield integrates many of these physiological processes in a complex way. Thus, it is difficult to interpret how plants accumulate, combine and display the ever-changing and indefinite physiological processes over the entire life cycle of crops (Farooq et al., 2009). Plant reaction after stress removal depends on the severity, duration and timing of the stress. When drought occurs during the vegetative period of crop growth, it may substantially decrease final yield. Drought stress during reproductive and grain filling phases is more devastating. For example, drought in pre-anthesis shortened the time to anthesis, while at post-anthesis, it decreased grain-filling period of triticale genotypes (Estrada-Campuzano et al., 2008). In the case of barley, post-anthesis drought stress was detrimental to grain yield irrespective of stress severity. Grain yield decreased due to the reduction of the number of tillers, spikes and grains per plant and individual grain weight (Samarah, 2005; Pecio, Wach, 2015). In maize, drought during reproductive stages greatly reduced grain yield, which was dependent on the level of defoliation (Kamara et al., 2003; Monneveux et al., 2006). Ghooshchi et al., (2008) reported that drought during pre-anthesis-silking period significantly decreased grain yield, 1000 grain weight, and grain number per ear, which was attributed to the lower pollen and filament development and the decreased filament fertility. Similarly, Ge et al. (2012) observed that prolonged and increased water stress negatively affected biomass accumulation and translocation in stem tissue related to grain growth, which suggested that a reduction of yield was linked to decreased stem diameter. Drought at flowering stage generally leads to barrenness. A main cause of this, but not the only one, is the reduction of assimilate flux to the developing ear below some threshold level necessary to sustain optimal grain growth (Farooq et al., 2009). Drought at flowering is critical as it can increase pollen sterility resulting in hampered grain set. In sunflower, under drought at flowering, achene yield declined primarily due to the lower number of achenes (Hussain et al., 2008). In maize, water deficit at anthesis caused loss of silk receptivity, which resulted in embryos abortion, and number of kernel decreased markedly. At the same time, the intermediates involved in starch synthesis were depleted and the ovary starch was lost during abortion (Ge et al., 2012). Akram (2011) reported that in wheat, drought stress during anthesis reduced pollination and thus a lower number of grains per spike were formed which resulted in the grain yield reduction. Grain filling in cereals is a process of starch biosynthesis from simple carbohydrates. It is known that four enzymes play key roles in this process: sucrose synthase, adenosine diphosphate-glucose-pyrophosphorylase, starch synthase and starch branching enzyme (Taiz, Zeiger, 2006; Prathap, Aruna, 2020). Decline in the rate of grain growth resulted from the reduced sucrose synthase activity, while the cessation of growth resulted from inactivation of adenosine diphosphate-glucose-pyrophosphorylase in the water-stressed wheat and rice (Ahmadi, Baker, 2001). Summarizing, water deficit reduces plant growth and development of plants, drought leads to hampered flower production and grain filling resulting in smaller and less grains. The grain filling decrease is a result of reduction of the assimilate partitioning and of the activities of sucrose and starch synthesis enzymes.

Table 1. Grain yield reduction by drought stress in some representative field crops (Farooq et al., 2009 modified).

Crop	Yield reduction [%]	References
Maize	63–87	Kamara et al. (2003)
Maize	79–81	Monneveux et al. (2006)
Maize	12–42	Ghooshchi et al. (2008)
Wheat	8–22	Akram (2011)
Wheat	46	Keyvan (2010)
Wheat	12–59	Pour-Aboughadareh et al. (2017)
Rice	48–94	Lafitte et al. (2007)
Rice	93	Kumar et al. (2009)
Sorghum	12–59	Asgharipour Heidari (2011)
Sunflower	16–25	(Hussain et al. (2008)
Barley	49–57	Samarah (2005)
Barley	38–47	Pecio Wach (2015)

PHYSIOLOGICAL RESPONSES

Root signaling

Plants are able to conduct positive and negative signals between roots and shoots to coordinate growth rate and behavior, and adapt to variable environments. When environmental stresses impair shoot growth, their functions may also be reduced as an effect of root-shoot signaling (Novák et al., 2012). A number of plant hormones such as abscisic acid (ABA), auxin, cytokines, ethylene, gibberellins, and other factors have been implicated in the regulation of physiological processes as signal molecules under environmental stresses. The descent of the soil water potential induces the generation of such signals as the production of ABA in root tissues. ABA has been recognized as a major chemical root-to-shoot stress signal. During soil drying, ABA is synthesized in roots and transported in the xylem vessels to the shoot, where it inhibits leaf expansion and induces stomatal closure, which is an important adaptation to the limited soil water supply. ABA promotes the efflux of K+ ions from the stomata of guard cells. As a result the turgor, pressure is decreasing and the stomata are closing (Anjum et al., 2011; Lipiec et al., 2013). According to some authors (Guerrero, Mullet, 1986), dehydration of plants causes ABA level increase up to 50-fold due to the loss of cell turgor or cell membrane perturbation. ABA has a crucial function in lateral root formation, root branching, and root hair formation. A role of ABA in root development links well with its function as a stress hormone. Regarding roots, ABA also promotes the elongation of the primary root responding to drought (Van Hengel et al., 2004). Generally, under conditions of the limited soil water availability, the root : shoot ratio in plants increases, due to a smaller sensitivity of roots than shoots to the growth limitation caused by low water potential (Anjum et al., 2011).

Photosynthesis

A major effect of drought is the reduction of photosynthesis, caused by a decrease in leaf expansion, impaired photosynthetic system, premature leaf senescence, and the associated reduction in food production (Wahid, Rasul, 2005). The direct impact of drought on photosynthetic apparatus affects essentially by disrupting all major components of photosynthesis including the thylakoid electron transport, the carbon reduction cycle and the stomatal control of the CO_2 supply, together with an increased accumulation of carbohydrates, peroxidative destruction of lipids an disturbance of water balance (Anjum et al., 2011). The decreased photosynthetic rate is a result of stomatal and non-stomatal limitation (Flexas et Medrano, 2002; Kamanga et al. 2018). Drought influence on photosynthesis is presented at Figure 2.

Under drought conditions, carbon fixation, especially in C3 plants, may be declined by photorespiration, process that consumes reducing power and oxygen, and generates carbon dioxide. Rubisco, the key enzyme in CO_2 assimilation, due to its dual nature, may act as carboxylase or oxygenase depending on leaf internal concentration of CO_2 or O_2. During drought, Rubisco functions as oxygenase due to higher internal O_2 than CO_2 contents as consequence of stomatal closure, and increase photorespiration at the expense of carbon-fixation. Under acute water deficit, photorespiration may be beneficial in three ways: (1) it is involved in energy dissipation and consequently reduces photoinhibition, (2) it produces glycine (amino acid) that is used for glutathione synthesis, a component of antioxidant defense, and (3) it enhances the ribulose 1,5-biphosphate (RuBP) supply to Calvin cycle. In parallel to these benefits, photorespiration amplifies oxidative stress in photosynthetic tissues with the elevated production of H_2O_2 in the peroxisome through glycolate oxidase; and more than 70% of H_2O_2 generation in C_3 plants under drought is related to photorespiration (Farooq et al., 2012; Kamanga et al., 2018; Sharma et al., 2020).

Stomatal closure, as it was presented above, limits CO_2 absorption, which leads to decreased photosynthetic activity (Nayyar, Gupta, 2006). Limitations of CO_2 absorption imposed by stomatal closure may promote an imbalance between photochemical activity of photosystem II (PSII) and the electron requirement of the Calvin-Benson cycle, leading to an excess of the absorbed excitation energy and subsequent photoinhibitory damage to PSII reaction centers (Foyer, Noctor, 2000; Souza et al., 2004). Many researchers showed its effects in changes of the chlorophyll fluorescence parameters under unfavorable environmental conditions (Foyer, Noctor, 2000; Souza et al., 2004; Zlatev, Yordanov, 2004; Živčák et al., 2008; Efeoğlu et al., 2009; Pour-Aboughadareh et al., 2017; Kamanga et al., 2018). In the studies on bean plants, under severe drought stress, the minimal fluorescence level from the dark-adapted leaves (F_0) increased, while the maximal fluorescence level from the dark-adapted leaves (F_M) decreased (Zlatev, Yordanov, 2004). Minimal fluorescence (F_0) increase can be attributed to the reduction of plastoquinone acceptor (Q_A^-), being un-

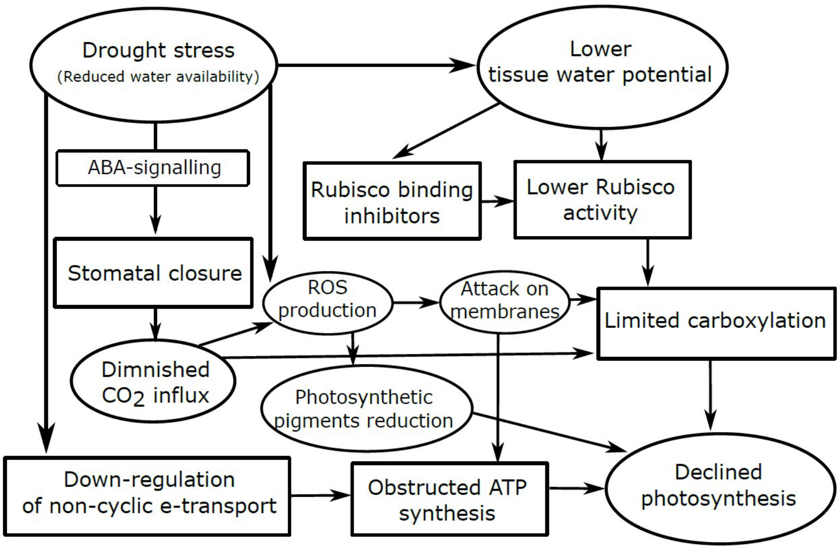

Figure 2. Photosynthesis under drought (Farooq et al. (2009) modified).

able to be oxidized completely because of retardation of the electron flow through PSII. The decrease of the maximal fluorescence (F_M) may be associated with processes related to a decrease in the activity of the water-splitting enzyme complex and perhaps a concomitant cyclic electron transport within or around PSII (Zlatev, Lidon, 2012). In the studies on cowpea (Souza et al., 2004), common bean (Zlatev, Yordanov, 2004) and wheat (Živčák et al., 2008), the quantum efficiency of open PSII reaction centers in the dark-adapted state (F_V/F_M) showed small and mostly not significant reduction under drought conditions. It confirms that plant primary processes of PSII are quite resistant to water deficit (Oukarroum et al., 2009). Under drought stress conditions, Zlatev and Yordanov (2004), Efleoglu et al., (2009) and Ruban (2016) observed the rise of non-photochemical quenching, which was the result of the increased light energy dissipation through heat emission to prevent photoinhibition of PSII or the gathering of reactive oxygen species.

Water relations

Relative water content (RWC), leaf water potential, stomatal resistance, rate of transpiration, leaf temperature and canopy temperature are important indices that influence plant water relations. Relative water content is considered as a measure of plant water status, reflecting the metabolic activity in tissues and used as a most meaningful index for dehydration tolerance (Farooq et al., 2009). RWC measures the volumetric water content relative to water concentration at full turgor concentration. Decline in RWC during drought stress was observed in different plant species by a number of authors (Nayyar, Gupta, 2006; Oukarroum et al., 2007; Živčák et al., 2008; Efeoğlu et al., 2009; Kamanga et al., 2018). The exposure of plants to the drought decreases leaf water potential, relative to water content and transpiration rate, while leaf temperature rises, that finally leads to the disturbances in CO_2 assimilation and photosynthetic electron transport (Nayyar, Gupta, 2006; Oukarroum et al., 2007; Živčák et al., 2008; Efeoğlu et al., 2009; Feller 2016; Pour-Aboughadareh et al., 2017). However, water use efficiency (WUE), other parameter describing water relations in plants, usually increased in plants tolerant or resistant to the drought. Increase in WUE calculated as a ratio of net assimilation rate and transpiration rate was observed in wheat cultivars under drought stress (Shangguan et al., 2000). However, Ge et al. (2012) found that in maize cultivars, WUE varied dependent on growth stage and stress severity. In fact, although the components of plant water relations are affected by the reduced availability of water, stomatal opening and closing is more strongly affected. Drought-tolerant species maintain water-use efficiency by reducing the water losses. However, under circumstance when plant growth was hindered largely, water-use efficiency was also reduced significantly (Farooq et al., 2009).

BIOCHEMICAL RESPONSES

Pigment contents

Photosynthetic pigments are important to plants, mainly for light harvesting and production of reducing power. Chlorophyll is one of the major chloroplast components for photosynthesis, and relative chlorophyll content has positive relationships with photosynthetic rate. The decrease in chlorophyll content under drought stress has been considered a typical symptom of oxidative stress and may be the result of pigment photo-oxidation and chlorophyll degradation. Both the chlorophyll a and b are prone to soil dehydration (Farooq et al., 2009). Many researchers reported a decreased or unchanged chlorophyll level in different species under drought conditions, depending on the severity and duration of drought (Nayyar, Gupta, 2006; Efeoğlu et al., 2009; Asgharipour, Heidari, 2011; Xiang et al., 2013; Karimpour, 2019). Chlorophyll content decreased significantly due to the increase of stress intensity with a greater impact on wheat than maize. Wheat losses equaled to 42% chlorophyll relative to 31% losses of maize over their respective controls (Nayyar, Gupta, 2006). The chlorophyll contents (*a*, *b*, *a*+*b*) of all maize cultivars were significantly reduced under stress, but they increased and reached the control values during recovery. The strong drought-induced decrease of the chlorophyll *a* content indicates that the drought stress induced a strong loss of photosynthetic reaction centers (PSI and PSII). The rapid recovery of the plants following rewatering also suggests that the reaction center loss may has play a regulatory role and did not just represent the damage (Efeoğlu et al., 2009). Low concentrations of photosynthetic pigments can directly limit photosynthetic potential, and hence primary production. From a physiological perspective, leaf chlorophyll content is a parameter of significant interest, while the induction of pigment synthesis or modification of pigment biosynthesis pathways may enhance plant tolerance to drought (Anjum et al., 2011; Jaleel et al., 2009; Kapoor et al., 2020).

Reactive oxygen species

Reactive oxygen species (ROS) are produced as a normal product of plant cellular metabolism. Various environmental stresses lead to the excessive production of ROS causing progressive oxidative damage and ultimately cell death (Sharma et al., 2012). ROS are a group of free radicals, reactive molecules, and ions that are derived from O_2, including superoxide anion radicals ($O_2^{\bullet -}$), hydroxyl radicals ($OH^{\bullet}$), hydrogen peroxide (H_2O_2), alkoxy radicals ($RO^{\bullet}$) and singlet oxygen ($^1O_2$). ROS are always formed by the unavoidable leakage of electrons onto O_2 from the electron transport activities of chloroplasts, mitochondria, and plasma membranes or as a byproduct of various metabolic pathways located in different cellular compartments

(Sharma et al., 2012). The reaction centers of PSI and PSII in chloroplast thylakoids are major generation site of ROS. Under drought conditions, the stomatal closure prevents the diffusion of CO_2 to the carboxylation site, which avoids its utilization by Rubisco. In this situation, NADPH and ATP are not consumed in the Calvin-Benson cycle and can be over-accumulated. In such situation, drought results in the saturation of the photosynthetic electron transport (especially under high intensity of light) which causes the excess of excitation energy in chloroplasts. At the level of the photosystems (PSI and PSII), energy can be transferred from triplet state chlorophyll (excited chlorophyll; $^3Chl^*$) directly to O_2 in its basal state (triplet; $^3O_2$) to yield $^1O_2$. At the reducing side of the PSI, in the so-called Mehler reaction, membrane-bound photosynthetic electron transporters, such as reduced ferredoxin (Fd_{red}), can transfer one electron to O_2, generating $O_2^{\bullet -}$ (Hernandez et al., 2012). The formation of $O_2^{\bullet -}$ by O_2 reduction is a rate-limiting step. Once formed $O_2^{\bullet -}$ generates more aggressive ROS. It may be protonated to $HO_2^{\bullet}$ on the internal, "lumen" membrane surface or dismutated enzymatically by superoxide dismutase (SOD) or spontaneously to H_2O_2 on the external "stromal" membrane surface. At Fe-S centers, where Fe^{2+} is available, H_2O_2 may be transformed through the Fenton reaction into the much more dangerous $OH^{\bullet}$ (Sharma et al., 2012).

ROS, as natural byproduct of the normal metabolism of oxygen, play an important role in cell signaling. However, during environmental stress such as drought, ROS level increases dramatically resulting in oxidative damage to proteins, DNA and lipids, and impairing the normal functions of cells (Apel, Hirt, 2004). The ROS such as $O_2^{\bullet -}$, H_2O_2, and $OH^{\bullet}$ can directly attack membrane lipids and increase lipid peroxidation (Mittler, 2002). It results in the increased content of malondialdehyde (MDA), which is one of the final products of the peroxidation of unsaturated fatty acids in phospholipids and is responsible for cell membrane damage. The content of MDA is an indicator of oxidative damage (Møller et al., 2007). Nayyar and Gupta (2006) reported that contents of H_2O_2 and MDA have been highly correlated in maize and wheat. Under mild drought stress conditions, both species did not differ significantly in oxidative damage (H_2O_2, MDA content). However, the differences between the species became evident as the degree of the stress increased to moderate and higher levels, where wheat experienced more stress injury leading to higher growth reduction.

Antioxidative defense system

Plants are equipped with complex antioxidative defense system comprising of nonenzymatic and enzymatic components to scavenge ROS. Nonenzymic components of the antioxidative defense system include the major cellular redox buffers ascorbate (AsA) and glutathione (γ-glutamyl-cysteinyl-glycine, GSH) as well as tocopherol, carotenoids, and phenolic compounds. They interact with numerous cellular components and in addition to crucial roles in defense and as enzyme cofactors, these antioxidants influence plant growth and development by modulating processes from mitosis and cell elongation to senescence and cell death. Apart their obvious role as enzyme substrates, they can react chemically with almost all forms of ROS (Foyer, Noctor, 2005). The enzymatic components of the antioxidative defense system comprise several antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GPX), enzymes of ascorbate-glutathione (AsA-GSH) cycle, ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). These enzymes operate in different subcellular compartments and respond in concert when cells are exposed to oxidative stress. Their role is either to quench toxic compounds or regenerate antioxidants with the help or reducing power provided by the photosynthesis. Under sufficient water supply conditions, potentially toxic oxygen metabolites are generated at a low level and there is an appropriate balance between production and quenching of ROS. The balance between production and quenching of ROS may be perturbed by a number of adverse environmental factors, giving rise to rapid increases in intracellular ROS levels, which can induce oxidative damage to lipids, proteins, and nucleic acids. In order to avoid the oxidative damage, higher plants raise the level of endogenous antioxidant defense (Apel, Hirt, 2004; Møller et al., 2007; Sharma et al., 2012; Zlatev, Lidon, 2012; Kumar et al., 2018).

Major ROS-scavenging mechanisms of plants include SOD, APX and CAT. The balance between these enzyme activities in cells is crucial for determining the steady-state level of superoxide radicals and hydrogen peroxide. SOD acts as the first line of defense converting $O_2^{\bullet -}$ into H_2O_2, while APX and CAT reduce H_2O_2 to H_2O. SOD is involved in the water-water cycle and the ascorbate–glutathione cycle in chloroplasts, cytosol, mitochondria, apoplast and peroxisomes. In contrast, CAT is only present in peroxisomes, but it is indispensable for ROS detoxification during stress, when high levels of ROS are produced (Mittler, 2002). Many researchers reported the increased activities of antioxidant enzymes under drought conditions (Zlatev et al., 2005; Nayyar, Gupta, 2006; Yang et al., 2009; Avramova et al., 2015; Kamanga et al., 2018). The increased activity of antioxidant enzymes acts as damage control system and provides protection from oxidative stress.

Osmolytes

Osmolytes play an important role in increasing plant tolerance to abiotic stresses, including drought. Osmoprotectants or compatible solutes are small molecules having low molecular weight, electrically neutral, highly soluble and non-toxic at molar concentrations that increase the cell capability to hold water without hindering normal metabolism. Osmoprotectants can be divided to three groups depending on compound character. Osmoprotectants containig ammonium compounds (ex. polyamines, glycine betaine), osmoprotectants containing sugars and sugar alcohols (ex. trehalose, fructan, mannitol, sorbitol) and osmoprotectants containing amino acids (ex. proline, ectoine) (Singh et al., 2015; Blum, 2017). The main role of these organic metabolites is the regulation of osmotic adjustment. They help plants to survive in extreme osmotic environment (Singh et al., 2015). These particles stabilize the osmotic differences between cell's surrounding and cytosol (Wani et al., 2013). Osmolytes take part in protecting cell membranes and membrane proteins against stress factor on cellular metabolism, such as increased ROS production (Alia et al., 1993; Yancey, 1994). Different studies show that plants are able to accumulate high amounts of these osmoprotectants against abiotic stresses, including drought (Singh et al., 2015). Under different environmental stresses synthesis and accumulation of polyamines in plants increase (Hussain, 2011). Moreover, application of exogenous poliamines enhance plant growth and provides protection against drought (Yamaguchi et al., 2007; Kubiś et al., 2014). According to Ashraf and Foolad (2007) plant resistance to drought (and other abiotic stress) was enhanced as effect of increased accumulation of glycine betaine and proline. Furthermore, exogenous application of these osmolytes, effectively improve the osmotic regulation ability, photosynthesis and ROS removing in maize (Anjum et al., 2017a), wheat (Raza et al., 2014) and barley (Wang et al., 2019).

Osmotic regulation also has its limitations, it can only temporarily increase the drought tolerance of plants. In addition, it has a limited effect on the resistance of plants to drought. When drought stress is severe, the turgor pressure of the plants cannot be maintained. The effects of drought occur even within osmotic regulation of the water potential. Osmotic regulation can only mitigate the damage to plants caused by drought to a certain degree.

SUMMARY

Water deficit is worldwide problem, limiting crop production and quality, and under recent global climate changes, the situation is more serious. Drought stress impedes various morphological and physiological processes in different crops. Generally it impairs plant growth and development, leading to disorder in dry matter accumulation, flower production, grain filling, finally resulting in harvestable yield decrease. Timing, duration, severity and speed development undoubtedly have crucial roles in determining plant responses to the water deficit. Decreasing availability of water supply in soil induces production of signals in roots, and these signals cause stomatal closure. It results in the decline of net photosynthesis, water use efficiency, photosynthetic pigments content and fluorescence parameters. Protective responses at leaf level must then be triggered quickly to prevent the irreversible damage of photosynthetic machinery. ROS scavenging systems, osmoregulation, cell membrane stability and stress proteins are essential mechanisms of plant drought tolerance.

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