

Review

Morphological, physiological and biochemical responses of plants to drought stress

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Plants in nature are continuously exposed to several biotic and abiotic stresses. Among these stresses, drought stress is one of the most adverse factors of plant growth and productivity and considered a severe threat for sustainable crop production in the conditions on changing climate. Drought triggers a wide variety of plant responses, ranging from cellular metabolism to changes in growth rates and crop yields. Understanding the biochemical and molecular responses to drought is essential for a holistic perception of plant resistance mechanisms to water-limited conditions. This review describes some aspects of drought induced changes in morphological, physiological and biochemical changes in plants. Drought stress progressively decreases CO₂ assimilation rates due to reduced stomatal conductance. It reduces leaf size, stems extension and root proliferation, disturbs plant water relations and reduces water-use efficiency. It disrupts photosynthetic pigments and reduces the gas exchange leading to a reduction in plant growth and productivity. The critical roles of osmolyte accumulation under drought stress conditions have been actively researched to understand the tolerance of plants to dehydration. In addition, drought stress-induced generation of active oxygen species is well recognized at the cellular level and is tightly controlled at both the production and consumption levels, through increased antioxidative systems. This review focuses on the ability and strategies of higher plants to respond and adapt to drought stress.

Key words: Drought stress, growth, yield, gas exchange, photosynthetic pigments, antioxidative system.

INTRODUCTION

Food productivity is decreasing due to detrimental effects of various biotic and abiotic stresses; therefore minimizing these losses is a major area of concern to ensure food security under changing climate. Environmental abiotic stresses, such as drought, extreme temperature, cold, heavy metals, or high salinity, severely impair plant growth and productivity worldwide. Drought, being the most important environmental stress, severely impairs plant growth and development, limits plant production and the performance of crop plants, more than any other environmental factor (Shao et al., 2009). Plant experiences drought stress either when the water supply to roots becomes difficult or when the transpiration rate becomes very high. Available water resources for successful crop production have been decreasing in

recent years. Furthermore, in view of various climatic change models scientists suggested that in many regions of world, crop losses due to increasing water shortage will further aggravate its impacts.

Drought impacts include growth, yield, membrane integrity, pigment content, osmotic adjustment water relations, and photosynthetic activity (Benjamin and Nielsen, 2006; Praba et al., 2009). Drought stress is affected by climatic, edaphic and agronomic factors. The susceptibility of plants to drought stress varies in dependence of stress degree, different accompanying stress factors, plant species, and their developmental stages (Demirevska et al., 2009). Acclimation of plants to water deficit is the result of different events, which lead to adaptive changes in plant growth and physio-biochemical processes, such as changes in plant structure, growth rate, tissue osmotic potential and antioxidant defenses (Duan et al., 2007). It has become imperative to elucidate the responses and adaptation of crops to water deficit,

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and take actions to improve the drought resistance ability of crop plants and to ensure higher crop yields against unfavorable environmental stresses. This article attempted to provide an overview of morpho-physiological and biochemical responses of plants to drought stress.

MORPHOLOGICAL RESPONSES

Environmental stresses trigger a wide variety of plant responses, ranging from altered gene expression and cellular metabolism to changes in growth and productivity.

Growth

To ensure that food supplies keep pace with population growth, a complete understanding of the processes involved in crop growth and development is required to inform agronomic practices. The optimization of plant performance and crop sustainability under variable environmental stress conditions will be dependent on the degree to which plant vegetative and reproductive growth patterns can be regulated. Plant growth is a function of complex interplay between sources and sink limitations of the two main organs of a plant, the root system and the shoot, establishing functional equilibrium. The permanent or temporary water deficit severely hampers the plant growth and development more than any other environmental factor.

The first and foremost effect of drought is impaired germination and poor stand establishment (Harris et al., 2002). Cell growth is considered one of the most drought-sensitive physiological processes due to the reduction in turgor pressure. Growth is the result of daughter-cell production by meristematic cell divisions and subsequent massive expansion of the young cells. 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). Drought caused impaired mitosis; cell elongation and expansion resulted in reduced growth and yield traits (Hussain et al., 2008). Water deficits reduce the number of leaves per plant and individual leaf size, leaf longevity by decreasing the soil's water potential. Leaf area expansion depends on leaf turgor, temperature, and assimilating supply for growth. Drought-induced reduction in leaf area is ascribed to suppression of leaf expansion through reduction in photosynthesis (Rucker et al., 1995). A common adverse effect of water stress on crop plants is the reduction in fresh and dry biomass production (Zhao et al., 2006). Khan et al. (2001) conducted a study comprising of six treatments, namely, control (six irrigations), five, four, three, two and one irrigation in maize. It was concluded that plant height, stem diameter, leaf area decreased noticeably with increasing water stress. The reduction in plant height could be attributed to

decline in the cell enlargement and more leaf senescence in the plant under water stress (Manivannan et al., 2007a). Drought led to substantial impairment of growth-related traits of maize in terms of plant height, leaf area, number of leaves/plant, cob length, shoot fresh and dry weight/plant. Furthermore, Kamara et al. (2003) revealed that water deficit imposed at various developmental stages of maize reduced total biomass accumulation at silking by 37%, at grain-filling period by 34% and at maturity by 21%.

Yield

Many yield-determining processes in plants respond to water stress. Yield integrates many of these processes in a complex way. Thus, it is difficult to interpret how plants accumulate, combine and display the ever-changing and indefinite processes over the entire life cycle of crops. Grain yield is the result of the expression and association of several plant growth components. The deficiency of water leads to severe decline in yield traits of crop plants probably by disrupting leaf gas exchange properties which not only limited the size of the source and sink tissues but the phloem loading, assimilate translocation and dry matter partitioning are also impaired (Farooq et al., 2009). Drought stress inhibits the dry matter production largely through its inhibitory effects on leaf expansion, leaf development and consequently reduced light interception (Nam et al., 1998). Drought at flowering commonly results in barrenness. A major cause of this, though not the only one, was a reduction in assimilate flux to the developing ear below some threshold level necessary to sustain optimal grain growth (Yadav et al., 2004). When maize plants were exposed to drought stress at teaseling stage, it led to substantial reduction in yield and yield components such a kernel rows/cob, kernel number/row, 100 kernels weight, kernels/cob, grain yield/plant, biological yield/plant and harvest index (Anjum et al., 2011a). Drought-related reduction in yield and yield components of plants could be ascribed to stomatal closure in response to low soil water content, which decreased the intake of CO₂ and, as a result, photosynthesis decreased (Chaves, 1991; Cornic, 2000; Flexas et al., 2004). In summary, prevailing drought reduces plant growth and development, leading to hampered flower production and grain filling and thus smaller and fewer grains. A reduction in grain filling occurs due to a reduction in the assimilate partitioning and activities of sucrose and starch synthesis enzymes.

PHYSIOLOGICAL RESPONSES

Root signaling under drought stress

An extensive root system is advantageous to support

plant growth during the early crop growth stage and extract water from shallow soil layers that is otherwise easily lost by evaporation. There are controversial evidences on effect of drought stress on root growth. An increased root growth due to water stress was reported in *Catharanthus roseus* (Jaleel et al., 2008). However, the root growth was not substantially inhibited under water stress in maize (Sacks et al., 1997). Generally, when water availability is limited, the root: shoot ratio of plants increases because roots are less sensitive than shoots to growth inhibition by low water potentials (Wu and Cosgrove, 2000). Under drought stress conditions roots induce a signal cascade to the shoots via xylem causing physiological changes eventually determining the level of adaptation to the stress. Abscisic acid (ABA), cytokinins, ethylene, malate and other unidentified factors have been implicated in the root–shoot signaling. This drought-induced root-to-leaf signalling through the transpiration stream results in stomatal closure, which is an important adaptation to limited water supply in the field. ABA promotes the efflux of K^+ ions from the guard cells, which results in the loss of turgor pressure leading to stomata closure. Dehydration of plants has been shown to cause ABA level increase up to 50-fold due to loss of cell turgor or cell membrane perturbation (Guerrero and Mullet, 1986). In addition, the dominant role of ABA as a root to shoot signal has been challenged by experiments showing that the ABA concentrations of xylem sap from drought stressed plants were much lower than the concentrations of exogenous ABA required to close stomata in detached leaves (Munns and King, 1988). Overall, ABA is a dominant signal in controlling growth and transpiration, but other factors could also be important. Cytokinins could also be an important signal traveling from roots to the shoots. Root-produced cytokinins are clearly involved in responses to nutrient deprivation Schachtman and Shin (2007) and, as they are produced mainly in roots, could be important in drought responses. Although recent data show decreased cytokinin concentrations in the xylem under drought stress, it is still not clear that all plant species respond in the same way to cytokinin at the concentrations found in the leaf and guard cells (Dodd, 2003).

Photosynthesis

Environmental stresses have a direct impact on the photosynthetic apparatus, 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 and disturbance of water balance (Allen and Ort, 2001).

The ability of crop plants to acclimate to different environments is directly or indirectly associated with their

ability to acclimate at the level of photosynthesis, which in turn affects biochemical and physiological processes and, consequently, the growth and yield of the whole plant (Chandra, 2003). Drought stress severely hampered the gas exchange parameters of crop plants and this could be due to decrease in leaf expansion, impaired photosynthetic machinery, premature leaf senescence, oxidation of chloroplast lipids and changes in structure of pigments and proteins (Menconi et al., 1995). Anjum et al. (2011a) indicated that drought stress in maize led to considerable decline in net photosynthesis (33.22%), transpiration rate (37.84%), stomatal conductance (25.54%), water use efficiency (50.87%), intrinsic water use efficiency (11.58%) and intercellular CO_2 (5.86%) as compared to well water control.

Many studies have shown the decreased photosynthetic activity under drought stress due to stomatal or non-stomatal mechanisms (Ahmadi, 1998; Del Blanco et al., 2000; Samarah et al., 2009). Stomata are the entrance of water loss and CO_2 absorbability and stomatal closure is one of the first responses to drought stress which result in declined rate of photosynthesis. Stomatal closure deprives the leaves of CO_2 and photosynthetic carbon assimilation is decreased in favor of photorespiration. Considering the past literature as well as the current information on drought-induced photosynthetic responses, it is evident that stomata close progressively with increased drought stress. It is well known that leaf water status always interacts with stomatal conductance and a good correlation between leaf water potential and stomatal conductance always exists, even under drought stress. It is now clear that there is a drought-induced root-to-leaf signaling, which is promoted by soil drying through the transpiration stream, resulting in stomatal closure. The "non-stomatal" mechanisms include changes in chlorophyll synthesis, functional and structural changes in chloroplasts, and disturbances in processes of accumulation, transport, and distribution of assimilates.

Chlorophyll contents

Chlorophyll is one of the major chloroplast components for photosynthesis, and relative chlorophyll content has a positive relationship 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. Photosynthetic pigments are important to plants mainly for harvesting light and production of reducing powers. Both the chlorophyll a and b are prone to soil dehydration (Farooq et al., 2009). Decreased or unchanged chlorophyll level during drought stress has been reported in many species, depending on the duration and severity of drought (Kpyoarissis et al., 1995; Zhang and Kirkham, 1996). Drought stress caused a large decline in the chlorophyll a content, the

chlorophyll b content, and the total chlorophyll content in different sunflower varieties (Manivannan et al., 2007b). Exposure of two olive cultivars to reduced irrigation led to lower Chl (a + b) contents. These reductions were 29 and 42% for Chemlali and Chetoui, respectively (Guerfel et al., 2009). Loss of chlorophyll contents under water stress is considered a main cause of inactivation of photosynthesis. Furthermore, water deficit induced reduction in chlorophyll content has been ascribed to loss of chloroplast membranes, excessive swelling, distortion of the lamellae vesiculation, and the appearance of lipid droplets (Kaiser et al., 1981). 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 in its own right. Studies by majority of chlorophyll loss in plants in response to water deficit occurs in the mesophyll cells with a lesser amount being lost from the bundle sheath cells.

Water relations

Relative water content (RWC), leaf water potential, stomatal resistance, rate of transpiration, leaf temperature and canopy temperature are important characteristics that influence plant water relations. Relative water content is considered a measure of plant water status, reflecting the metabolic activity in tissues and used as a most meaningful index for dehydration tolerance. RWC of leaves is higher in the initial stages of leaf development and declines as the dry matter accumulates and leaf matures. RWC related to water uptake by the roots as well as water loss by transpiration. A decrease in the relative water content (RWC) in response to drought stress has been noted in wide variety of plants as reported by Nayyar and Gupta (2006) that when leaves are subjected to drought, leaves exhibit large reductions in RWC and water potential. Exposure of plants to drought stress substantially decreased the leaf water potential, relative water content and transpiration rate, with a concomitant increase in leaf temperature (Siddique et al., 2001). When two poplar species were submitted to progressive drought stress, the decrease of RWC in the water-stressed cuttings was 23.3% in *Populus cathayana*, whereas it was 16% in *Populus kangdingensis*. RWC was affected by the interaction of severity, duration of the drought event and species (Yang and Miao, 2010).

In fact, although components of plant water relations are affected by reduced availability of water, stomatal opening and closing is more strongly affected. Moreover, change in leaf temperature may be an important factor in controlling leaf water status under drought stress. Drought-tolerant species maintain water-use efficiency by reducing the water loss. However, in the events where plant growth was hindered to a greater extent, water-use efficiency was also reduced significantly.

Osmolyte accumulation

Plants accumulate different types of organic and inorganic solutes in the cytosol to lower osmotic potential thereby maintaining cell turgor (Rhodes and Samaras, 1994). Under drought, the maintenance of leaf turgor may also be achieved by the way of osmotic adjustment in response to the accumulation of proline, sucrose, soluble carbohydrates, glycinebetaine, and other solutes in cytoplasm improving water uptake from drying soil. The process of accumulation of such solutes under drought stress is known as osmotic adjustment which strongly depends on the rate of plant water stress. Wheat is marked by low level of these compatible solutes and the accumulation and mobilization of proline was observed to enhance tolerance to water stress (Nayyar and Walia, 2003). Of these solutes, proline is the most widely studied because of its considerable importance in the stress tolerance. Proline accumulation is the first response of plants exposed to water-deficit stress in order to reduce injury to cells. Progressive drought stress induced a considerable accumulation of proline in water stressed maize plants. The proline content increase as the drought stress progressed and reached a peak as recorded after 10 days stress, and then decreased under severe water stress as observed after 15 days of stress (Anjum et al., 2011b).

Proline can act as a signaling molecule to modulate mitochondrial functions, influence cell proliferation or cell death and trigger specific gene expression, which can be essential for plant recovery from stress (Szabados and Savoure, 2009). Accumulation of proline under stress in many plant species has been correlated with stress tolerance, and its concentration has been shown to be generally higher in stress-tolerant than in stress-sensitive plants. It influences protein solvation and preserves the quaternary structure of complex proteins, maintains membrane integrity under dehydration stress and reduces oxidation of lipid membranes or photoinhibition (Demiral and Turkan, 2004). Furthermore, it also contributes to stabilizing sub-cellular structures, scavenging free radicals, and buffering cellular redox potential under stress conditions (Ashraf and Foolad, 2007).

BIOCHEMICAL RESPONSES

Reactive oxygen species (ROS)

The generation of reactive oxygen species (ROS) is one of the earliest biochemical responses of eukaryotic cells to biotic and abiotic stresses. The production of ROS in plants, known as the oxidative burst, is an early event of plant defense response to water-stress and acts as a secondary messenger to trigger subsequent defense reaction in plants. ROS, which include oxygen ions, free radicals and peroxides, form as a natural by product of

the normal metabolism of oxygen and have important role in cell signaling. However, during environmental stress such as drought, ROS levels increase dramatically resulting in oxidative damage to proteins, DNA and lipids (Apel and Hirt, 2004). Being highly reactive, ROS can seriously damage plants by increasing lipid peroxidation, protein degradation, DNA fragmentation and ultimately cell death.

Drought induces oxidative stress in plants by generation of reactive oxygen species (ROS) (Farooq et al., 2009). The ROS such as O_2^- , H_2O_2 and $\bullet OH$ radicals, can directly attack membrane lipids and increase lipid peroxidation (Mittler, 2002). Drought-induced overproduction of ROS increases the content of malondialdehyde (MDA). The content of MDA has been considered an indicator of oxidative damage (Moller et al., 2007). MDA is considered as a suitable marker for membrane lipid peroxidation. A decrease in membrane stability reflects the extent of lipid peroxidation caused by ROS. Furthermore, lipid peroxidation is an indicator of the prevalence of free radical reaction in tissues. Moreover, oxygen uptake loading on the tissues as both processes generate reactive oxygen species, particularly H_2O_2 that produced at very high rates by the glycolate oxidase reaction in the peroxisomes in photorespiration. Yang and Miao (2010) noted the increments of the MDA and H_2O_2 concentrations in the water-stressed cuttings were 88.9 and 99.7% in *P. cathayana*, respectively, whereas they were only 44 and 63.6% in *P. kangdingensis*. In pea (*Pisum sativum*) plants, levels of lipid peroxidation in leaves increased two to four fold with an increase in drought stress, and this was highly correlated with protein peroxidation (Moran et al., 1994).

Antioxidant enzymes

There is a defensive system in plants, that is to say, plants have an internal protective enzyme-catalyzed clean up system, which is fine and elaborate enough to avoid injuries of active oxygen, thus guaranteeing normal cellular function (Horváth et al., 2007). The balance between ROS production and activities of antioxidative enzyme determines whether oxidative signaling and/or damage will occur (Moller et al., 2007). To minimize the affections of oxidative stress, plants have evolved a complex enzymatic and non-enzymatic antioxidant system, such as low-molecular mass antioxidants (glutathione, ascorbate, carotenoids) and ROS-scavenging enzymes (superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX) (Apel and Hirt, 2004). Non-enzymatic antioxidants cooperate to maintain the integrity of the photosynthetic membranes under oxidative stress. The enzymatic components may directly scavenge ROS or may act by producing a non-enzymatic antioxidant. Yang et al. (2009) exhibited that as compared with 100% field capacity, at 25% field capacity the increased activities of

CAT, SOD, POD, APX and GR were 4.3, 103, 172, 208 and 56% in *P. cathayana*, respectively, whereas they were 8.1, 125, 326, 276 and 78% in *P. kangdingensis*. Efficient destruction of O_2^- and H_2O_2 in plant cells requires the concerted action of antioxidants. O_2^- can be dismutated into H_2O_2 by SOD in the chloroplast, mitochondrion, cytoplasm and peroxisome. POD plays a key role in scavenging H_2O_2 which was produced through dismutation of O_2^- catalyzed by SOD. CAT is a main enzyme to eliminate H_2O_2 in the mitochondrion and microbody (Shigeoka et al., 2002) and thus help in ameliorating the detrimental effects of oxidative stress. It is found in peroxisomes, but considered indispensable for decomposing H_2O_2 during stress. Maintaining a higher level of antioxidative enzyme activities may contribute to drought induction by increasing the capacity against oxidative damage (Sharma and Dubey, 2005). The capability of antioxidant enzymes to scavenge ROS and reduce the damaging effects may correlate with the drought resistance of plants.

CONCLUSIONS

Abiotic stress signaling is an important area with respect to increase in plant productivity. Drought is a worldwide problem, constraining global crop production and quality seriously, and recent global climate change has made this situation more serious. Drought stress affects the growth, dry matter and harvestable yield in plants. Timing, duration, severity and speed of development undoubtedly have pivotal roles in determining how a plant responds to water deficit. Following drought, stomata close progressively with a parallel decline in net photosynthesis and water-use efficiency. In addition to other factors, changes in photosynthetic pigments are of paramount importance to drought tolerance. Protective responses at the leaf level must then be triggered quickly in response to the stress effectors to prevent the photosynthetic machinery being irreversibly damaged. Scavenging of reactive oxygen species by enzymatic and non-enzymatic systems, cell membrane stability, expression of aquaporins and stress proteins are vital mechanisms of drought tolerance.

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REFERENCES

- Allen DJ, Ort DR (2001). Impact of chilling temperatures on photosynthesis in warm climate plants. *Trends Plant Sci.*, 6: 36-42.

- Ahmadi AA (1998). Effect of post-anthesis water stress on yield regulating processes in wheat (*Triticum aestivum* L.). Ph.D. Thesis. University of London, Wye College, Wye, Ashford, U.K.
- Anjum SA, Wang LC, Farooq M, Hussain M, Xue LL, Zou CM (2011a). Brassinolide application improves the drought tolerance in maize through modulation of enzymatic antioxidants and leaf gas exchange. *J. Agron. Crop Sci.*, doi:10.1111/j.1439-037X.2010.00459.x.
- Anjum SA, Wang LC, Farooq M, Khan I, Xue LL (2011b). Methyl jasmonate-induced alteration in lipid peroxidation, antioxidative defense system and yield in soybean under drought. *J. Agron. Crop Sci.*, doi:10.1111/j.1439-037X.2010.00468.x.
- Apel K, Hirt H (2004). Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu. Rev. Plant Biol.*, 55: 373-399.
- Ashraf M, Foolad MR (2007). Roles of glycinebetaine and proline in improving plant abiotic stress resistance. *Environ. Exp. Bot.*, 59: 206-216.
- Benjamin JG, Nielsen DC (2006). Water deficit effects on root distribution of soybean, field pea and chickpea. *Field Crops Res.*, 97: 248-253.
- Chandra S (2003). Effects of leaf age on transpiration and energy exchange of *Ficus glomerata*, a multipurpose tree species of central Himalayas. *Physiol. Mol. Biol. Plants*, 9: 255-260.
- Chaves MM (1991). Effects of water deficits on carbon assimilation. *J. Exp. Bot.*, 42: 1-16.
- Cornic G (2000). Drought stress inhibits photosynthesis by decreasing stomatal aperture - not by affecting ATP synthesis. *Trends Plant Sci.*, 5: 187-188.
- Del Blanco IA, Rajaram S, Kronstad WE, Reynolds MP (2000). Physiological performance of synthetic hexaploid wheat-derived populations. *Crop Sci.*, 40: 1257-1263.
- Demiral T, Turkan I (2004). Does exogenous glycinebetaine affect antioxidative system of rice seedlings under NaCl treatment? *J. Plant Physiol.*, 161: 1089-1110.
- Demirevska K, Zashva D, Dimitrov R, Simova-Stoilova L, Stamenova M, Feller U (2009). Drought stress effects on Rubisco in wheat: changes in the Rubisco large subunit. *Acta Physiol. Plant.*, 31: 1129-1138.
- Dodd IC (2003). Hormonal interactions and stomatal responses. *J. Plant Growth Regul.*, 22: 32-46.
- Duan B, Yang Y, Lu Y, Korpelainen H, Berninger F, Li C (2007). Interactions between drought stress, ABA and genotypes in *Picea asperata*. *J. Exp. Bot.*, 58: 3025-3036.
- Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA (2009). Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev.*, 29: 185-212.
- Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD (2004). Diffusive and metabolic limitations to photosynthesis under drought and salinity in C₃ plants. *Plant Biol.*, 6: 1-11.
- Guerrero F, Mullet JE (1986). Increased abscisic acid biosynthesis during plant dehydration requires transcription. *Plant Physiol.*, 80: 588-591.
- Guerfel M, Baccouri O, Boujnah D, Chaibi W, Zarrouk M (2009). Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Sci. Horticult.*, 119: 257-263.
- Harris D, Tripathi RS, Joshi A (2002). On-farm seed priming to improve crop establishment and yield in dry direct-seeded rice, in: Pandey S., Mortimer M., Wade L., Tuong T.P., Lopes K., Hardy B. (Eds.), *Direct seeding: Research Strategies and Opportunities*, International Research Institute, Manila, Philippines, pp. 231-240.
- Horváth E, Pál M, Szalai G, Páldi E, Janda T (2007). Exogenous 4-hydroxybenzoic acid and salicylic acid modulate the effect of short-term drought and freezing stress on wheat plants. *Biol. Plant.*, 51: 480-487.
- Hussain M, Malik MA, Farooq M, Ashraf MY, Cheema MA (2008). Improving drought tolerance by exogenous application of glycinebetaine and salicylic acid in sunflower. *J. Agron. Crop Sci.*, 194: 193-199.
- Jaleel CA, Gopi R, Sankar B, Gomathinayagam M, Panneerselvam R (2008). Differential responses in water use efficiency in two varieties of *Catharanthus roseus* under drought stress. *Comp. Rend. Biol.*, 331: 42-47.
- Kamara AY, Menkir A, Badu-apraku B, Ibikunle O (2003). The influence of drought stress on growth, yield and yield components of selected maize genotypes. *J. Agric. Sci.*, 141: 43-50.
- Kaiser WM, Kaiser G, Schöner S, Neimann S (1981). Photosynthesis under osmotic stress. Differential recovery of photosynthetic activities of stroma enzymes, intact chloroplasts and leaf slices after exposure to high solute concentrations. *Planta*, 153: 430-435.
- Khan MB, Hussain N, Iqbal M (2001). Effect of water stress on growth and yield components of maize variety YHS 202. *J. Res. (Science)*, 12: 15-18.
- Kyparissis A, Petropoulou Y, Manetas Y (1995). Summer survival of leaves in a soft-leaved shrub (*Phlomis fruticosa* L., Labiatae) under Mediterranean field conditions: avoidance of photoinhibitory damage through decreased chlorophyll contents. *J. Exp. Bot.*, 46: 1825-1831.
- Manivannan P, Jaleel CA, Kishorekumar A, Sankar B, Somasundaram R, Sridharan R, Panneerselvam R (2007a). Changes in antioxidant metabolism of *Vigna unguiculata* L. Walp. by propiconazole under water deficit stress. *Colloids Surf B: Biointerf.*, 57: 69-74.
- Manivannan P, Jaleel CA, Sankar B, Kishorekumar A, Somasundaram R, Alagu Lakshmanan GM, Panneerselvam R (2007b). Growth, biochemical modifications and proline metabolism in *Helianthus annuus* L. as induced by drought stress. *Colloids Surf. B: Biointerf.*, 59: 141-149.
- Menconi M, Sgherri CLM, Pinzino C, Navari-Izzo F (1995). Activated oxygen production and detoxification in wheat plants subjected to a water deficit programme. *J. Exp. Bot.*, 46: 1123-1130.
- Mittler R (2002). Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.*, 7: 405-410.
- Moller IM, Jensen PE, Hansson A (2007). Oxidative modifications to cellular components in plants. *Annu. Rev. Plant Biol.*, 58: 459-481.
- Moran JF, Becana M, Iturbe-Ormaetxe I, Frechilla S, Klucas RV, Aparicio-Tejo P (1994). Drought induces oxidative stress in pea plants. *Planta*, 194: 346-352.
- Munns R, King RW (1988). Abscisic acid is not the only stomatal inhibitor in the transpiration stream of wheat plants. *Plant Physiol.*, 88: 703-708.
- Nayyar H, Walia DP (2003). Water stress induced proline accumulation in contrasting wheat genotypes as affected by calcium and abscisic acid. *Biol. Plant.*, 46: 275-279.
- Nayyar H, Gupta D (2006). Differential sensitivity of C₃ and C₄ plants to water deficit stress: association with oxidative stress and antioxidants. *Environ. Exp. Bot.* 58: 106-113.
- Nam NH, Subbarao GV, Chauhan YS, Johansen C (1998). Importance of canopy attributes in determining dry matter accumulation of pigeon pea under contrasting moisture regimes. *Crop Sci.*, 38: 955-961.
- Nonami H (1998). Plant water relations and control of cell elongation at low water potentials. *J. Plant Res.*, 111: 373-382.
- Praba ML, Cairns JE, Babu RC, Lafitte HR (2009). Identification of physiological traits underlying cultivar differences in drought tolerance in rice and wheat. *J. Agron. Crop Sci.*, 195: 30-46.
- Rhodes D, Samaras Y (1994). Genetic control of osmoregulation in plants. In cellular and molecular physiology of cell volume regulation. Strange, K. Boca Raton: CRC Press, pp. 347-361.
- Rucker KS, Kvien CK, Holbrook CC, Hook JE (1995). Identification of peanut genotypes with improved drought avoidance traits. *Peanut Sci.*, 24: 14-18.
- Sacks MM, Silk WK, Burman P (1997). Effect of water stress on cortical cell division rates within the apical meristem of primary roots of maize. *Plant Physiol.*, 114: 519-527.
- Samarah NH, Alqudah AM, Amayreh JA, McAndrews GM (2009). The effect of late-terminal drought stress on yield components of four barley cultivars. *J. Agron. Crop Sci.*, 195: 427-441.
- Schachtman DP, Shin R (2007). Nutrient sensing and signaling: NPKS. *Annu. Rev. Plant Biol.*, 58: 47-69.
- Shao HB, Chu LY, Jaleel CA, Manivannan P, Panneerselvam R, Shao MA (2009). Understanding water deficit stress-induced changes in the basic metabolism of higher plants-biotechnologically and sustainably improving agriculture and the environment in arid regions of the globe. *Crit. Rev. Biotechnol.*, 29: 131-151.
- Sharma P, Dubey RS (2005). Drought induces oxidative stress and enhances the activities of antioxidant enzyme in growing rice seedling. *Plant Growth Regul.*, 46: 209-221.

- Shigeoka S, Ishikawa T, Tamoi M, Miyagawa Y, Takeda T, Yabuta Y, Yoshimura K (2002). Regulation and function of ascorbate peroxidase isoenzymes. *J. Exp. Bot.*, 53: 1305-1319.
- Siddique MRB, Hamid A, Islam MS (2001). Drought stress effects on water relations of wheat. *Bot. Bull. Acad. Sin.*, 41: 35-39.
- Szabados L, Savoure´ A (2009). Proline: a multifunctional amino acid. *Trends Plant Sci.*, 15: 89-97.
- Wu Y, Cosgrove DJ (2000). Adaptation of roots to low water potentials by changes in cell wall extensibility and cell wall proteins. *J. Exp. Bot.*, 51: 1543-1553.
- Yang F, Xu X, Xiao X, Li C (2009). Responses to drought stress in two poplar species originating from different altitudes. *Biol. Plant.*, 53: 511-516.
- Yang F, Miao LF (2010). Adaptive responses to progressive drought stress in two poplar species originating from different altitudes. *Silva Fennica*, 44: 23-37.
- Yadav RS, Hash CT, Bidinger FR, Devos KM, Howarth CJ (2004). Genomic regions associated with grain yield and aspects of post flowering drought tolerance in pearl millet across environments and tester background. *Euphytica*, 136: 265-277.
- Zhao TJ, Sun S, Liu Y, Liu JM, Liu Q, Yan YB, Zhou HM (2006). Regulating the drought-responsive element (DRE)-mediated signaling pathway by synergic functions of trans-active and transinactive DRE binding factors in *Brassica napus*. *J. Biol. Chem.*, 281: 10752-10759.
- Zhang J, Kirkham MB (1996). Antioxidant response to drought in sunflower and sorghum seedlings. *New Phytol.*, 132: 361-373.