Biological Forum – An International Journal **7**(1): 1732-1738(2015)

ISSN No. (Print): 0975-1130
ISSN No. (Online): 2249-3239

Influence of drought stress on some characteristics of plants

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(Received 27 April, 2015, Accepted 27 June, 2015)
(Published by Research Trend, Website: www.researchtrend.net)

ABSTRACT: Drought is one of the most severe limitations on the yield of crops. This stress induces various biochemical and physiological responses in plants as a survival mechanism. In general, drought is responsible for several metabolic processes of plants, with photosynthetic apparatus. Drought 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. Drought stress produced changes in the ratio of chlorophyll 'a' and 'b' and carotenoids. A reduction in chlorophyll content was reported in drought stress. The production of reactive oxygen species is a common phenomenon in plants under drought stress. These reactive oxygen species (ROS) generations led to lipid peroxidation, protein degradation and nucleic acid damages. HSPs, or molecular chaperones, are structurally diverse, but they all share the property of binding other proteins that are in non-native structural states, facilitating many structural processes such as folding, targeting and degradation.

Key words: ROS, Photosynthesis, Antioxidant enzymes, Proline, Hsps

INTRODUCTION

A. Stress

Stress is an altered physiological condition caused by factors that tend to disrupt the equilibrium. Strain is any physical and chemical change produced by a stress (Gaspar *et al.*, 2002). The term stress is used with various meanings, the physiological definition and appropriate term as responses in different situations. The flexibility of normal metabolism allows the response initiation to the environmental changes, which fluctuate regularly and are predictable over daily and seasonal cycles. Thus every deviation of a factor from its optimum does not necessarily result in stress. Stress being a constraint or highly unpredictable fluctuations imposed on regular metabolic patterns cause injury, disease or aberrant physiology. Plants are frequently exposed to many stresses such as drought, low temperature, salt, flooding, heat, oxidative stress and heavy metal toxicity, while growing in nature (Gaspar *et al.*, 2002).This article is review and the aim is influence of drought stress on some characteristics of plants.

B. Drought

Drought is one of the most severe limitations on the yield of crops. This stress induces various biochemical and physiological responses in plants as a survival mechanism (Tas and Tas, 2007). In general, drought is responsible for several metabolic processes of plants, with photosynthetic apparatus (Nayyar and Gupta, 2006). 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).

C. Deficit irrigation

Deficit irrigation is a watering strategy that can be applied by different types of irrigation system methods. The correct application of deficit irrigation requires thorough understanding of the yield response to water and the economic impact of reductions in harvesting (English,1990).

In regions where water resources are restrictive it can be more profitable for a farmer to maximize crop water productivity instead of maximizing the harvest per unit of land (Fereres and Soriano, 2007). The saved irrigation water can be used for other purposes or to irrigate extra units of land Deficit irrigation is sometimes referred to incomplete supplemental or regulated deficit irrigation (Kipkorir *et al.,* 2007).

D. Influence of drought stress on morphological characteristics

It has been established that drought stress is a very important limiting factor at the initial phase of plant growth and establishment. It affects both elongation and expansion growth (Anjum *et al.,* 2003a; Bhatt & Srinivasa Rao, 2005; Kusaka *et al.,* 2005; Shao *et al.,* 2008). Among the crops, rice as a submerged crop, is probably more susceptible to drought stress than most other plant species. In soybean, the stem length was decreased under water deficit conditions (Specht *et al.,* 2001). The plant height was reduced up to 25% in water stressed citrus seedlings (Wu *et al.,* 2008). Stem length was significantly affected under water stress in potato (Heuer & Nadler, 1995), Abelmoschus esculentus (Sankar *et al.,* 2007 & 08); Vigna unguiculata (Manivannan *et al.,* 2007a); soybean (Zhang *et al.,* 2004) and parsley (Petroselinum crispum) (Petropoulos *et al.,* 2008). Water stress greatly suppresses cell expansion and cell growth due to the low turgor pressure. Osmotic regulation can enable the maintenance of cell turgor for survival or to assist plant growth under severe drought conditions in pearl millet (Shao *et al.,* 2008). The reduction in plant height was associated with a decline in the cell enlargement and more leaf senescence in A. esculentus under water stress (Bhatt & Srinivasa Rao, 2005). Development of optimal leaf area is important to photosynthesis and dry matter yield. Water deficit stress mostly reduced leaf growth and in turn the leaf areas in many species of plant like Populus (Wullschleger *et al.,* 2005), soybean (Zhang *et al.,* 2004) and many other species (Farooq *et al.,* 2009). Significant inter-specific differences between two sympatric Populus species were found in total number of leaves, total leaf area and total leaf biomass under drought stress (Wullschleger *et al.,* 2005). The leaf growth was more sensitive to water stress in wheat than in maize (Sacks *et al.,* 1997); Vigna unguiculata (Manivannan *et al.,* 2007a) and sunflower (Manivannan *et al.,* 2007b & 2008).

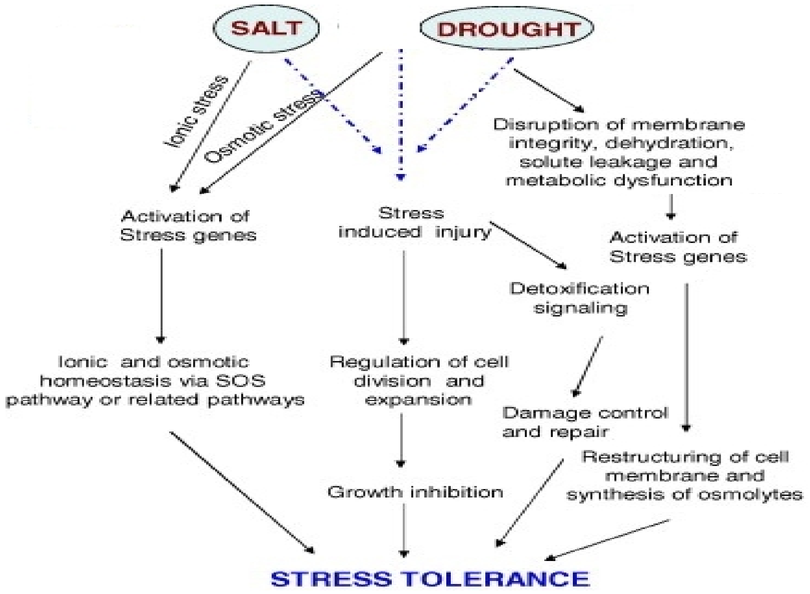
E. Photosynthesis

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.

F. Chlorophylls

Drought stress produced changes in the ratio of chlorophyll 'a' and 'b' and carotenoids (Anjum *et al.,* 2003b; Farooq *et al.,* 2009). A reduction in chlorophyll content was reported in drought stressed cotton (Massacci *et al.,* 2008) and Catharanthus roseus (Jaleel *et al.,* 2008a-d). The chlorophyll content decreased to a significant level at higher water deficits in sunflower plants (Kiani *et al.,* 2008) and in Vaccinium myrtillus (Tahkokorpi *et al.,* 2007). The foliar photosynthetic rate of higher plants is known to decrease as the relative water content and leaf water potential decreases (Lawlor & Cornic, 2002). However, the debate continues as, whether drought mainly limits photosynthesis through stomatal closure or through metabolic impairment (Lawson *et al.,* 2003; Anjum *et al.,* 2003b). Both stomatal and non-stomatal limitation was generally accepted to be the main determinant of reduced photosynthesis under drought stress (Farooq *et al.,* 2009).

The limitation of photosynthesis under drought through metabolic impairment is more complex phenomenon than stomatal limitation and mainly it is through reduced photosynthetic pigment contents in sunflower (Reddy *et al.,* 2004). Chlorophyll b content increased in two lines of okra, whereas chlorophyll a remained unaffected resulting in a significant reduction in Chl a: b ratio in both cultivars under water limiting regimes (Estill *et al.*, 1991; Ashraf *et al.*, 1994).



G. 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 produces through dismutation of O_2^{-} catalyzed by SOD.

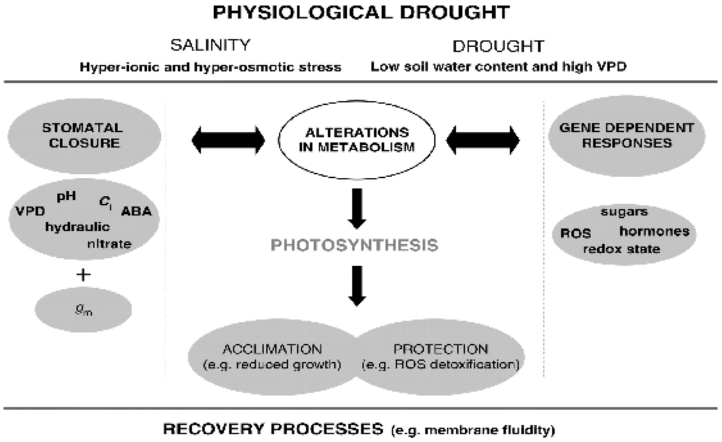


Fig 1. Direct effects of drought and salinity on stomata and mesophyll (gm) conductance as well as on gene expression, resulting in alterations of photosynthetic metabolism and ultimately on plant acclimation.

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. 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.

H. Reactive Oxygen Species (ROS)

Understanding the biochemical and physiological basis of water stress tolerance in plants is vital to select and breed plants for improving crop water stress tolerance (Chaves *et al.* 2003). The production of reactive oxygen species is a common phenomenon in plants under drought stress. These reactive oxygen species (ROS) generations led to lipid peroxidation (Sreeni-Nivasuhu *et al.* 1999, Chen *et al.* 2000), protein degradation (Jiang and Zhang 2001) and nucleic acid damages (Hagar et al. 1996). Water stress leads to the formation of Reactive Oxygen Species (ROS), which are extremely harmful to the plants. Generation of ROS also leads to lipid peroxidation (Chen *et al.* 2000). During water stress, there is considerable potential for increased accumulation of superoxide and hydrogen peroxide resulting from the increased rate of O_2 photoreduction in chloroplasts (Robinson and Bunce, 2000). Mechanisms of ROS detoxification exist in all plants (Mundree *et al.,* 2002). One of the defense mechanisms against different stresses is the antioxidant enzymes production. Plants to prevent or alleviate injuries from ROS have evolved an antioxidant defense system that includes nonenzymatic compounds, like ascorbate, glutathione, tocopherol, carotenoids, flavonoids and enzymes such as SOD, CAT, POX, APOX, GR and PPO (Gratao *et al.,* 2005). Changes of antioxidants reflect the impact of environmental stresses on plant metabolism (Herbinger *et al.,* 2002). The level of response depends on the species, the development and the metabolic status of the plant, as well as the duration and intensity of the stress. In addition, the degree of damage by ROS depends on the balance between the product of ROS and its removal by this antioxidant scavenging mechanism (Azooz and Al-Fredan, 2009). On the other hand, it has been reported that membrane of plant cells are subject to rapid damage with increase in water stress. This leakage of membrane is caused by an uncontrolled enhancement of free radical, which cause lipid peroxidation. Damage to fatly acids of membrane could produce small hydrocarbon fragments including Malondialdehyde (MDA).

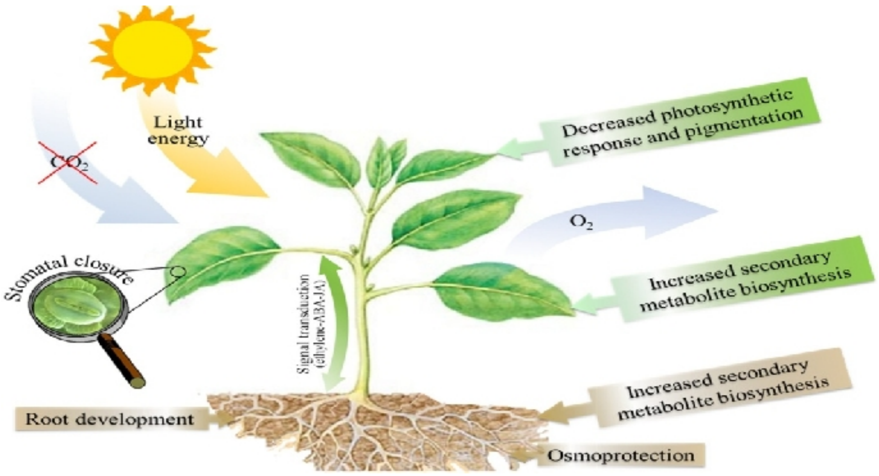


Fig. 2. Plant global response to cope with water deficit, high temperature and salinity.

I. ABA accumulates

It is known that the phytohormone abscisic acid (ABA) is a key component of the signalling system integrating the adaptive response of the plant to stressful conditions including water deficits and high temperature (Finkelstein *et al.,* 2002). In early drought stress experiments, it was found that ABA accumulates under water deficits (Mizrahi *et al.,* 1971; Boussiba *et al.,* 1975). Many genes that are expressed after ABA application are also expressed under drought stress (Bray, 1997; Bray, 2002; Chaves *et al.,* 2003; Yamaguchi-Shinozaki and Shinozaki, 2006) suggesting that ABA acts as a signaling molecule under drought stress conditions. Later microarray experiments, showed that there were genes that are up-regulated by drought stress but not after ABA application (Ishitani *et al.,* 1997; Shinozaki and Yamaguchi-Shinozaki, 1997; Zhu *et al.,* 2002) suggesting the existence of ABA alternative signaling pathways. ABA also signals stomatal closure in guard cells by ion efflux (Schroeder *et al.,* 2001; Israelsson *et al.,* 2006).

Recent studies have shown that phospholipase D alpha-1 mediates this response (Mishra *et al.*, 2006). ABA is also associated with decreased shoot growth during drought stress, although there is speculation that this is due to ABA interaction with ethylene, resulting in reduced shoot and root growth (Sharp and LeNoble, 2002; LeNoble *et al.*, 2004).

J. Heat shock proteins (Hsps)

HSPs, or molecular chaperones, are structurally diverse, but they all share the property of binding other proteins that are in non-native structural states, facilitating many structural processes such as folding, targeting and degradation. They are called heat shock proteins because the proteins were first discovered in abundance after heat stress. Chen and Wang, 2003; Zhu and Zhang, 2003; Xie *et al.*, 2005 founded that the synthesis of some original proteins (namely stress-induced proteins) may be induced or up regulated to adjust osmotic potential of cells in order to keep a certain turgor and thus to ensure the normal proceeding of physiological processes such as cell growth, stomatal opening and photosynthesis it can concluded that to cope with environmental stress, plants activate a large set of genes leading to the accumulation of specific stress-associated proteins (Vierling 1991; Ingram and Bartels 1996; Bohnert and Sheveleva 1998; Thomashow 1999; Hoekstra *et al.* 2001). Heat-shock proteins (Hsps) and late embryogenesis abundant (LEA)-type proteins are two major types of stress-induced proteins that accumulate upon water, salinity, and extreme temperature stress. They have been shown to play a role in cellular protection during the stress (Bakalova *et al.* 2008 ; Thomashow 1998).

K. Proline

Plants can partly protect themselves against mild drought stress by accumulating osmolytes. Proline is one of the most common compatible osmolytes in drought stressed plants. For example, the proline content increased under drought stress in pea (Sanchez *et al.*, 1998; Alexieva *et al.*, 2001). Proline accumulation can also be observed with other stresses such as high temperature and under starvation (Sairam *et al.*, 2002). Proline metabolism in plants, however, has mainly been studied in response to osmotic stress (Verbruggen and Hermans 2008). Proline does not interfere with normal biochemical reactions but allows the plants to survive under stress (Stewart, 1981). The accumulation of proline in plant tissues is also a clear marker for environmental stress, particularly in plants under drought stress (Routley, 1966). Proline accumulation may also be part of the stress signal influencing adaptive responses (Maggio *et al.* 2002).

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