Influence of drought stress on assimilation of carbon, activity of photosynthetic enzymes, heat shock proteins, antioxidants, proline accumulation and protein contents in crop plants

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Abstract

Drought stress is one of the most important abiotic stress factors which are generally accompanied by heat stress in dry season. Drought is perceived as the most significant environmental stress in agriculture worldwide, and improving yield under drought is therefore a major goal of plant breeding. The data on water stress induced regulation of the activity of photosynthetic enzymes other than rubisco are scarce. Recently, most researchers have agreed that the stomatal closure is the main determinant for decreased photosynthesis under mild and moderate stress. Severe drought stress also inhibits the photosynthesis of plants by causing changes in chlorophyll content, by affecting chlorophyll components and by damaging the photosynthetic apparatus. Water availability mostly affects accumulation of some organic compatible solutes such as sugars, betaines and proline which adjusts the intercellular osmotic potential is also early reaction of plants to water stress.

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Introduction
Water is essential at every stage of plant growth and agricultural productivity is solely dependent upon water and it is essential at every stage of plant growth, from seed germination to plant maturation (Turner, 1991). Drought stress is one of the most important abiotic stress factors which are generally accompanied by heat stress in dry season (Dash and Mohanty, 2001). Water deficit stress due to drought, salinity or extremes in temperature is the main limiting factors for plant growth and productivity resulting in large economic losses in many regions of the world (Borsani et al., 2001). Plants respond to water stress through a number of biochemical, physiological and developmental changes (Pattanagul, 1999. Shinozaki, 1997). Drought is perceived as the most significant environmental stress in agriculture worldwide, and improving yield under drought is therefore a major goal of plant breeding (Cattivelli et al., 2008). With a projected increase in drought with climate change, the breeding for drought-tolerant crops is even more emphasised (Witcombe et al., 2008). In addition to drought, temperature-induced stress causes variability in wheat yields (Semenov and Shewry, 2011; Asseng et al., 2011), corn and soybean (Schlenker and Roberts, 2009) and other crops (e.g. Tashiro and Wardlaw, 1989; Prasad et al., 2000; Challinor et al., 2005). Drought and heat stress often occur simultaneously, but they can have very different effects on various physiological, growth, developmental and yield forming processes (Rizhytsky et al., 2004; Boote et al., 2005). The majority of indices have been developed to determine long-term (months) drought or excess rain and are less suitable for short-term effects (weeks). Examples are the Drought Severity Index (PDSI; Palmer, 1965), the Reconnaissance Drought Index (RDI; Tsakiris et al., 2007) and Standardised Precipitation Index (SPI; McKee et al., 1993).

Deficit irrigation
Deficit irrigation was proposed long time ago as a technique that irrigates the entire root zone with less evapotranspiration and leads to reduce the irrigation water use with maintaining farmers’ net profits (Hoffman et al., 1990). The decline in water availability for irrigation and the positive results obtained in some fruit tree crops have renewed the interest in developing information on deficit irrigation for a variety of crops (FAO Report, 2002; Dorji et al., 2005 and Ferreres and Soriano, 2007).

Assimilation of carbon
Assimilation of carbon by plants incurs water costs. According to Boyer (1982) the ratio of carbon fixation to water loss (water use efficiency) is critical to plant survival, crop yield and vegetation dynamics. At a leaf level, water use efficiency can be defined as a ratio of photosynthetic rate to transpiration rate or to leaf conductance for water vapour (WUEi - intrinsic water use efficiency) (Escalona et al., 1999).

Activity of photosynthetic enzymes
The data on water stress induced regulation of the activity of photosynthetic enzymes other than Rubisco are scarce. Thimmanaik et al (2002) studied the activity of several photosynthetic enzymes under progressive water stress in two different cultivars of Morus alba. Unlike Rubisco, which is highly stable and resistant to water stress, the activity of some enzymes involved in the regeneration of ribulose-1,5-bisphosphate (RuBP) are progressively impaired from very early stages of water stress. Thus, these results present the possibility that some enzymes involved in the regeneration of RuBP could play a key regulatory role in photosynthesis under water stress. During water stress induced by polyethilen glycole, Rubisco activity significantly increased in young potato leaves, while decreased in mature leaves (Bussis et al., 1998). But NADP-GAPDH and PRK activities have been decreased and this change became faster in the course of drought. While decreased Rubisco activity may not be the cause of photosynthetic reduction during water stress, its down-regulation may still be important because it could preclude a rapid recovery upon rewatering (Ennahli and Earl, 2005). Similarly, some reports have shown strong drought-induced reductions of Rubisco activity per unit leaf area (Maroco et al., 2002) and per mg showed that the decrease of Rubisco activity in vivo was not connected.
with the protein content. It occurs because of CO2 concentration decrease in the carboxylation center in consequence of the partly closing of stomata (Flexas et al., 2006). But it is known, that enzyme regulation occurs not only in transcription, but also in posttranscriptional level. Activities of the tested enzymes are regulated by light as well as by the concentration of photosynthetic metabolites (Raines, 2006). Reductions of more than 50% in the levels of NADP-GAPDH, FBP, PRK, and plastid aldolase were also needed before photosynthetic capacity was affected (Stitt and Schulze, 1994).

Photosynthesis
The question as to whether drought mainly limits photosynthesis through stomatal closure or metabolic impairments has not been finally answered (Cornic, 2000; Flexas et al., 2004). The relative part of stomatal limitation of photosynthesis depends on stress severity. Recently, most researchers have agreed that the stomatal closure is the main determinant for decreased photosynthesis under mild and moderate stress. Changes in photosynthetic reactions are considered as a prevailing factor which led to photosynthesis depression under severe water stress (Yordanov et al., 2003). According to Chaves et al. (2003) discrepancies in results concerning the contribution of stomatal and non-stomatal factors in photosynthesis inhibition may be explained by differences in the rate of imposition and severity of stress, developmental stage and plant condition, species studied and superimposition of other stresses.

Biochemical and physiological changes
Usually, water deficit stress has detrimental effects on many processes in plants, which include reducing photosynthesis, accumulation of dry matter, stomatal exchanges, and protein synthesis that affect their growth stages (Larcher, 2003; Ohashi et al., 2006). Generally, plants respond to water deficit stress through developmental, biochemical and physiological changes and the type of the observed response depends on several factors such as stress intensity (SI), stress duration and genotype (Moradshahi et al., 2004). Many physiological processes associated with crop growth and development is reported to be influenced by water deficits (Turner and Begg 1978; Bousha et al., 2009). Previous research has shown various physiological and biochemical changes in durum wheat plants (Ykhlef et al., 2011) when drought stressed, such as the regulation of stomatal aperture, osmotic pressure of cells, and protein synthesis (Lu et al., 1994; Cheng, 1995).

Heat shock proteins (Hsps)
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).

Irrigation methods and management
Irrigation methods and management are of importance to soil water status, and thus, to plant water status. Inappropriate irrigation could result in water stress. Drip irrigation provides more efficient water use for crops than furrow irrigation because drip irrigation applies frequent small amounts of water to the root zone and reduces adverse effects of cyclic over irrigated and water stress commonly caused by furrow irrigation. Many studies and reports have addressed that yield and quality of hop (Humulus Lupulus L.), potato (Solanum tuberosum) tuber, tomato, cotton, and cantaloupe could be
improved with drip irrigation (Bernstein and Francois, 1973; Sammis, 1980; Wample and Farrar, 1983; Wood, 1988). Reports about the effect of irrigation on chile pepper yields are few (Wierenga and Hendrickx, 1985).

Antioxidation strategies

Drought stress is accompanied by the formation of ROS such as O2, H2O2, and OH (Moran et al. 1994; Mittler 2002), which damage membranes and macromolecules. Plants have developed several antioxidation strategies to scavenge these toxic compounds. Enhancement of antioxidant defense in plants can thus increase tolerance to different stress factors. Antioxidants (ROS scavengers) include enzymes such as catalase, superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase, as well as non-enzyme molecules such as ascorbate, glutathione, carotenoids, and anthocyanins. Additional compounds, such as osmolytes, proteins can also function as ROS scavengers (Bowler et al. 1992; Noctor and Foyer 1998). The antioxidant defenses appear to provide crucial protection against oxidative damage in cellular membranes and organelles in plants grown under unfavorable conditions (Al-Ghamdi, 2009; Kocsy et al., 1996). Plant cells synthesize a variety of antioxidants to cope with ROS produced under normal and stress conditions (Noctor and Foyer, 1998).

Environmental stresses exert their effects on plant growth and development indirectly through formation of ROS (Arora et al., 2002). The antioxidant defenses appear to provide crucial protection against oxidative damage in cellular membranes and organelles in plants grown under unfavorable conditions (Kocsy et al., 1996). Cellular antioxidative defense system, which keeps ROS under control and functions as a reductant for many free radicals, minimizes the damage caused by oxidative stress (Al-Ghamdi, 2009; Noctor and Foyer, 1998). Plants possess a complex antioxidant system, which consists of ascorbic acid, glutathione and enzymes that protect the plant against oxidative damage induced by environmental stresses. ASC (ascorbate), a ubiquitous soluble antioxidant in photosynthetic organisms, is the most important reducing substrate for H2O2 detoxification (Chen et al., 2007). An antioxidant system consists of low molecular weight antioxidants such as ascorbate, glutathione, α-tocopherol and carotenoids, as well as several enzymes such as SOD (superoxide dismutase), CAT (catalase), POD (peroxidase), APX (ascorbate peroxidase), and GR (glutathione reductase) (Feng et al., 2004). SOD is a group of metalloenzymes that catalyse the disproportionation of O2` (superoxide) to H2O2 and O2. Thus, SOD constitutes the first line of defense against O2` derived oxidative stress in the plant cell. Cellular H2O2 is detoxified by CAT and in chloroplasts by ascorbate-glutathione cycle with its key enzymes APX and GR (Arora et al., 2002). Enhanced activities of antioxidants are associated with resistance to environmental stresses. In sunflower seedlings, it was reported that there was an induction of defense enzyme activities and an increase in glutathione content when plants reached a moderate level of water deficit stress. Wheat plants subjected to water stress showed that ascorbate-glutathione cycle allowed the plants to maintain H2O2 at the control level, despite a greater capacity of the thylakoid membranes to leak electrons towards O2 (Szechynska et al., 2007; Loschiavo et al., 1989; Vergara et al., 1990).

Stomata control

Stomata control gas exchange between the interior of a leaf and the atmosphere. Therefore they mainly contribute to the ability of plants to control their water relations and to gain carbon (Hetherington and Woodward, 2003).

It has been shown that environmental signals such as light intensity, carbon dioxide concentration and water availability may affect stomatal development by modifying their size and frequency (Knapp et al., 1994; Naupajal et al., 1994; Dyki et al., 1998). The ability of a plant to live under stress has been shown to be related to stomatal density and size, since these were found to be related to the plant gas exchange.
Therefore, it is possible that variations in stomatal characteristics may influence plant growth and productivity (Kundu and Tigerstedt, 1998).

Fig. 1. Plant survival against on abiotic stress.

Chlorophyll content
Severe drought stress also inhibits the photosynthesis of plants by causing changes in chlorophyll content, by affecting chlorophyll components and by damaging the photosynthetic apparatus (IturbeOrmaetxe et al., 1998). Ommen et al. (1999) reported that leaf chlorophyll content decreases as a result of drought stress. Drought stress caused a large decline in the chlorophyll a content, the chlorophyll b content, and the total chlorophyll content in all sunflower varieties investigated (Manivannan et al., 2007). The decrease in chlorophyll under drought stress is mainly the result of damage to chloroplasts caused by active oxygen species (Smirnoff 1995). The decrease in chlorophyll under stress condition can be attributed to the sensitivity of this pigment to increasing environmental stresses, especially to salinity and drought, which has been reported by several researchers (Mekliche et al., 2003; Younis et al., 2000); many studies indicated that stay-green is associated with improved yield and transpiration efficiency under water-limited conditions in sorghum, maize and wheat (Borrell et al. 2000; Verma et al. 2004). The results are agreement with Nyachiro et al. (2001), who described a significant decrease of chlorophyll a and b caused by water deficit in six Triticum aestivum cultivars. Decreased or unchanged chlorophyll level during drought stress has been reported in other species, depending on the duration and severity of drought (Kpyoarissis et al., 1995). A decrease of total chlorophyll with drought stress implies a lowered capacity for light harvesting. Since the production of reactive oxygen species is mainly driven by excess energy absorption in the photosynthetic apparatus, this might be avoided by degrading the absorbing pigments (Herbinger et al., 2002).

Drought tolerance
Drought tolerance consist the ability of crop against the growth and production under water deficit conditions. A long term drought stress effects on plant metabolic reactions associates with, plant growth stage, water storage capacity of soil and physiological aspects of plant. Drought tolerance in crop plants is different from wild plants. In practice, planting of crop encounter severe water deficit, it dies or seriously loses yield while in wild plants their surviving under this conditions but no yield loss, is taken into consideration. However, water deficit has always been considered as a main problem and is of great importance, so has taken into account as one of the breeding factors (Talebi, 2009). Nowadays many physiological, biochemical and molecular biology studies on the mechanisms of drought tolerance of agriculturally important crops have been performed (Simova-Stoilova et al., 2006).

Fig. 2. Some physiological and biochemical perturbations in plants caused by fluctuations in abiotic environments.

Plant breeding programs
Achieving a genetic increase in yield under these environments has been recognized to be a difficult
challenge for plant breeders while progress in yield grain has been much higher in favorable environments (Richards et al., 2002). Improving drought resistance is, therefore, a major objective in plant breeding programs for reined agriculture in these regions. Knowledge of genetic behavior and type of gene action controlling target traits is a basic principle for designing an appropriate breeding procedure for the purpose of genetic improvement. Hence, the success of any selection or hybridization breeding program for developing drought-tolerant varieties depends on precise estimates of genetic variation components for traits of interest consisting of additive, dominant and non-allelic interaction effects (Farshadfar et al., 2011; Nouri et al., 2011). In plant breeding program, several characters are simultaneously considered that make it feasible to approximate the genetic divergence by using multivariate techniques. These multivariate techniques include principal component and cluster analysis which have analogous efficacy to establish the most suitable cross combinations (Amjad-Ali et al., 2011).

**C4 concentrating mechanism**

Some controlled environment studies of well watered plants suggest that growth at elevated [CO2] can directly impact C4 photosynthesis by a number of mechanisms (for review, see Ghannoum et al., 2000). As examples, intercellular [CO2] (ci) below the saturation point of the photosynthetic intercellular CO2 response curve has been reported under ambient [CO2], allowing direct stimulation of photosynthesis under elevated [CO2] (Wong, 1979; Watling and Press, 1997; Ziska and Bunce, 1997). Bundle sheath leakiness increased under elevated [CO2], reducing the initial slope and CO2-saturated photosynthetic rate of the curve in sorghum (Sorghum bicolor; Watling et al., 2000). In developing Flaviae trinervia leaves, 10% of CO2 fixation occurred directly in the bundle sheath, without involvement of the C4 concentrating mechanism, allowing the possibility that elevated [CO2] could directly stimulate photosynthesis (Moore et al., 1986). Some immature C4 leaves have C3-like photosynthesis and are therefore more sensitive to enhanced photosynthesis under elevated [CO2] (Dai et al., 1995; Ziska et al., 1999). Enzymes of both the C4 cycle and Calvin cycle in maize were consistently lower under elevated [CO2], with malate dehydrogenase (237%) and glyceraldehyde-3-phosphate dehydrogenase activities (229%) declining to the greatest extent in young leaves (Maroco et al., 1999).

**Protein contents**

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). According to ROSE (1988) water stress decreased protein contents in plants. The results of present investigations were inconsistent with the finding, which implies that soluble protein did not contribute to osmotic adjustment. The increase in proline content due to drought stress was more severe at flowering stage than at the vegetative stage. The proline content depends on plant age, leaf age, leaf position or leaf part (Chiang and Dandekar, 1995). Under vegetative stage, drought stress increased proline content about tenfold, this increasing roles as an osmotic compatible and adjust osmotic potential which resulted in drought stress avoidance in chickpea. Prolin accumulation is believed to play adaptive roles in plant stress tolerance (Verbruggen and Hermans 2008). Accumulation of proline has been advocated as a parameter of selection for stress tolerance (Yancy et al., 1982. Jaleel et al., 2007).

**Fig. 4.** Visual aspect of shoot in Phaseolus vulgaris plants exposed to drought by four days.

**Water use efficiency (WUE)** Limited of irrigation means that the soil water deficit is controlled at certain stages of crop growth, a practice that has become more important in recent years in areas where water resources are limited. Water use efficiency (WUE) is defined here as the ratio between grain yield and total evapotranspiration during the growing season. Studies on the effects of limited irrigation show that crop yield can be largely maintained and product quality can sometimes be improved while substantially reducing irrigation volume (Li 1982; Shan 1983; Fapohunda et al. 1984; Sharma et al. 1986; Singh et al. 1991; Zhang et al. 1999). Aggarwal et al. (1986) reported that WUE decreased with increasing evapotranspiration, whereas Musick et al. (1994) found that WUE did not change with seasonal evapotranspiration. Under limited irrigation, reductions in grain yield due to restricted water availability depend on the degree, duration and timing of the imposed soil moisture deficit. The impact of soil moisture deficit on crop yield depends on the particular phenological stage of the crop, and the most sensitive stage can vary regionally (Singh et al. 1991).

**Fig. 5.** The basic ROS cycle. This cycle modulates the cellular levels of ROS during normal metabolism. Some of the key ROS scavenging enzymes of plants, ascorbate peroxidase(APX), and catalase(CAT) are indicated.

**Oxidative stress and proline accumulation** Water availability mostly affects accumulation of some organic compatible solutes such as sugars, betaines and proline which adjusts the intercellular osmotic potential is also early reaction of plants to water stress. Sairam and Saxena (2000) reported that oxidative stress which caused metabolic damage in water stress, increases lipid per oxidation, resulting in greater membrane injury and pigment bleaching.
Zlatev and Stoyanov (2005) suggested that proline accumulation of plants could be only useful as a possible drought injury sensor instead of its role in stress tolerance mechanism. Vendruscolo et al. (2007) found that proline is involved in tolerance mechanisms against oxidative stress and this was the main strategy of plants to avoid detrimental effects of water stress.

**Stomatal conductance**

Plants grown under drought condition have a lower stomatal conductance in order to conserve water. Consequently, CO₂ fixation is reduced and photosynthetic rate decreases, resulting in less assimilate production for growth and yield of plants. Diffusive resistance of the stomata to CO₂ entry probably is the main factor limiting photosynthesis under drought (Boyer, 1970). Certainly under mild or moderate drought stress stomatal closure (causing reduced leaf internal CO₂ concentration (CI)) is the major reason for reduced rates of leaf photosynthetic (Chaves, 1991; Cornic, 2000; Flexas et al., 2004). Varieties significantly differed in photosynthetic activities, but these differences could only be expressed under the control conditions. In many experiments it has been shown that A decreases when gs decreases (e.g., Tenhunen et al., 1987; Nilsen and Orcutt, 1996). Chaves and Oliviera (2004) concluded that gs only affect A at severe drought stress. The decrease in photosynthesis in drought stressed plants can be attributed both to stomatal (stomatal closure)
and non-stomatal (impairments of metabolic processes) factors. Under control treatment, the yield of cultivars followed the same trend of A, under this condition ‘Bivaniej’ showed highest A and seed yield. At present most researchers agree that the stomatal closure and the resulting CO2 deficit in the chloroplasts is the main cause of decreased photosynthesis under mild and moderate stresses (Flexas and Medrano, 2002). However, some authors claim that impaired ATP is a likely explanation for decreased photosynthesis under water stress (Lawlor, 2002; Tang et al., 2002).

Fig. 8. Water vapor moves out and carbon dioxide move into the leaf through the stomata.

Plants anatomy, morphology and physiology
Water stress may affect on the plants anatomy, morphology, physiology and biochemistry and influence on almost all of their growth and development aspects. Plants respond to drought through morphologic, physiologic and metabolic changes in all theirs organs (Heidary et al, 2007). Drought stress, by disturbing the equilibrium relations between water and plant and the structure of cell biologic membrane m creates basic disorder in rice growth and decreases the performance. Most crops particularly during flowering phase to seed development are sensitive to water shortage stress. Even plants cultivating in dry and semidry regions are influenced by drought stress (Mitra, 2001). Plants survival and production power of crops is greatly influenced by water accessibility and decreased due to decrease of this vital factor (Ozhur et al., 2009).

Time–domain reflectometry (TDR)
New methods such as time–domain reflectometry (TDR) are now available for use; however, these methods are limited because of difficulties in conducting field operations when multiple cables are installed in large fields for long periods. Moreover, measuring multiple depths within the soil profile requires installation of multiple TDR probes at a location. This procedure makes water content profiling impractical for monitoring soil water available over the depth of the soil profile at a large number of locations within a field. Sadler et al. (2000) used TDR probes at eight sites in their field to investigate water use and stress. Their results demonstrated the need for within–season observations of crop water use and stress to augment interpretation of site–specific yield maps. Nijbroek (1999) used conventional TDR probes in an irrigated soybean field in Georgia to estimate drained upper limit values based on nighttime drainage rates measured at 2–hour intervals. Their system required a long cable from the probes to the cable tester, so data collection was limited to certain areas in the field.

Fig. 9. Leaf rolling in corn.

Sensitive to water stress
It has been observed that vegetative and reproductive growth in trees is differentially sensitive to water stress. Additionally, reproductive growth is differentially sensitive to water stress at different times of the season. It has been reported that mild water stress applied during the intermediate developmental period of slow fruit growth has no effect on crop yields but reduces vegetative growth in peach (Mitchell and Chalmers 1982) and pear (Mitchell et al. 1984). However, the final period of very rapid fruit growth has been reported to be
relatively sensitive to water stress in peach (Li et al. 1989, Crisosto et al. 1994), apple (Lotter et al. 1985) and Asian pear (Caspari et al. 1994). Deficit irrigation (DI) and partial root drying (PRD) are water-saving irrigation strategies (Kang and Zhang, 2004). DI irrigates the entire root zone with an amount of water less than the potential evapotranspiration (ETfull) and the minor stress that develops has minimal effects on the yield (English et al., 1990). DI has proved successfully with a number of crops; however it has been difficult to manage in potatoes (Lynch et al., 1995). PRD involves alternate watering to each side of the plant root system, by which it allows the plant to explore rootsourced ABA signaling to regulate plant growth and water use thereby increasing WUE (Dry et al., 2000). PRD has been found to be promising in several crops (Kang and Zhang, 2004). However, until now PRD has not been studied in potatoes. It is suggested that plants under PRD performed better than under DI when the same amount of water was applied. Davies and Hartung (2004) proposed that PRD could stimulate root growth and maintain a constant ABA signaling to regulate shoot physiology; whereas plants under DI, some of the roots in dry soils for long period may die and signaling may diminish and shoot water deficits may occur.

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