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RESEARCH PAPER

Influence of drought stress on photosynthetic, radical oxygen, respiration, assimilate partitioning, activities of enzymes, phytohormones and essential oils in crop plants

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Abstract

Water-deficit stresses occur in about 70% of arable land around the world and have been shown to have an effect on every aspect of plant growth. Drought is one of the most common environmental stresses that may limit agriculture production worldwide. Many crops have high water requirement and in most countries supplemental irrigation is necessary for successful crop production. Photosynthetic response to drought is a highly complex in plants. Water deficit inhibits photosynthesis by causing stomatal closure and metabolic damage. Stomata of the leaves that are slightly deficient in water opened more slowly in light and close more quickly in the dark. The activities of many enzymes are affected by drought conditions. For example, nitrate reductase activity has been shown to be highly sensitive to water stress, and a significant decrease in nitrate reductase activity was observed in many plant species under drought conditions. Drought stress also increases the levels of radical oxygen species (ROS) in plant cells, resulting in lipid peroxidation and protein damage.

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Introduction

Drought is one of the most common environmental stresses that may limit agriculture production worldwide. Many crops have high water requirement and in most countries supplemental irrigation is necessary for successful crop production. However, in many countries as a consequence of global climate change and environmental pollution, water use for agriculture is reduced. Drought in general is severely detrimental to the growth and yield of agricultural crops. Drought stress is not seriously detrimental to yield and can, in some instances, result in increased yield (Nautiyal *et al.*, 1999). Adequate supply of water is a prerequisite for optimum plant growth and satisfactory yield in every crop. Water-deficit stresses occur in about 70% of arable land around the world (LeHouerou, 1996) and have been shown to have an effect on every aspect of plant growth (Kramer, 1983). Of various abiotic factors, water scarcity adversely affects the crop productivity (Jones & Corlett, 1992). Generally, drought stress reduces growth (Levitt, 1980) and yield of various crops (Dhillon *et al.*, 1995) by decreasing chlorophyll pigments and photosynthetic rate (Asada, 1999), and stomatal conductance as well as transpiration rates (Lawlor, 1995). Drought stress reduces the nutrient uptake in plants (Baligar *et al.*, 2001).

Root system and drought stress

Maximized use of store soil water, increased biomass productivity per unit water use and highest of biomass productivity into economic yield under limited –water conditions are the ultimate goals of any drought research (Krishnamurthy *et al.*, 2007). Root traits associated with drought tolerance are important for drought resistant mechanisms of plant. Root characteristics such as root length density, rooting depth and root distribution have been established as constituting factor of drought resistance (Matsui & Singh, 2003). Rucker *et al.* (1995) reported that a large root system may improve a plants ability to continue growth during drought stress.

Growth and development

Plants growing under suboptimal water levels are associated with slow growth and, in severe cases, dieback of stems, such plants are more susceptible to disease and less tolerant of insect feeding (Wilson, 2009). In crops, water stress has been associated with reduced yields and possible crop failure. The effects of water stress however vary between plant species. As the plant undergoes water stress, the water pressure inside the leaves decreases and the plant wilts. The main consequence of moisture stress is decreased growth and development caused by reduced photosynthesis, a process in which plants combine water, carbon dioxide and light to make carbohydrates for energy. Chemical limitations due to reductions in critical photosynthetic components such as water can negatively impact plant growth. The ability to recognize early symptoms of water stress is crucial to maintaining the growth of plants; the most common symptom is wilting (Bauder, 2009).

Photosynthetic

Photosynthetic response to drought is a highly complex in plants. Water deficit inhibits photosynthesis by causing stomatal closure and metabolic damage. Stomata of the leaves that are slightly deficient in water opened more slowly in light and close more quickly in the dark (Nuruddin, 2001). Soil moisture stress reduces leaf water potential which in turn may reduce transpiration (Shibairo *et al.*, 1998). Kirnak *et al.* (2001) have found that water stress results in significant decreases in chlorophyll content, electrolyte leakage, leaf relative water content and vegetative growth; and plants grown under high water stress have less fruit yield and quality. Tomato plants tend to grow a denser root system at soil water potentials which are slightly less than field capacity (Nuruddin, 2001).

Respiration and Assimilate partitioning

It was reported by (Lawler and Cornic, 2002; Flexas *et al.*, 2005) that respiration is an equally important factor controlling productivity, unlike photosynthesis which is limited temporally (i.e., daytime hours) and spatially (i.e., to green biomass), respiration occurs continuously in every plant organ, particularly when photosynthesis is largely depressed due to water stress. Respiration is an essential metabolic process that generates Adenosine Tri- Phosphate (ATP) and several carbon skeletons - metabolites that are used in many synthetic processes essential for growth and maintenance of the cell homeostasis, including under water stress conditions (MacCabe *et al.*, 2000; Bartoli *et al.*, 2000). Several authors have found different results on the effect of water stress on respiration, ranging from decrease (Brix, 1962; Brown and Thomas, 1980; Palta and Nobel, 1989; Escalona *et al.*, 1999; Ghashghaie *et al.*, 2001; Haupt-Herting *et al.*, 2001) to stimulation (Upchurch *et al.*, 1955; Shearmann *et al.*, 1972; Zagdanska, 1995). Ghashghaie *et al.*, (2001), showed in sunflower (Helianthus annuus) that leaf respiration decreased at early stages of water stress and then increased even above control values at later stages. Water stress has been shown to affect the relationship between the carbon content in photosynthetic organs, such as leaves (source), and the carbon content in heterotrophic organs, such as seeds and roots (sink), indicating that the processes related to carbon partitioning are sensitive targets of this adverse environment (Cuellar-Ortiz *et al.*, 2008). Chaves *et al.*, (2002), stated that the ability of genotypes to partition stored vegetative biomass to reproductive organs to a larger extent determines sink establishment and economic yield under drought stress. Cuellar-Ortiz *et al.*, (2008), in their study showed that carbohydrate partitioning is affected by drought in common bean, and that the modulation of the partitioning towards seed filling has been a successful strategy in the development of drought-resistant cultivars. Setter, (1990), reported that during water stress photosynthate partitioning is altered to increase root/shoot ratio. Several authors (Pelleschi *et al.*, 1997; Pinheiro *et al.*, 2001; Yang *et al.*, 2001), have reported that under water deficit, there is a strong reduction in levels of inactive osmotically solutes (starch) and increase in active osmotically solutes (soluble sugars) and as a consequence the osmotic potential decreases, contributing to the maintenance of leaf water status. Rosales-Serna *et al.*, (2000, 2003), showed that drought resistant bean cultivar displayed a small reduction in harvest index under water stress and it was hypothesized that the cultivar was able to improve carbon partitioning into the pods as part of its drought adaptation mechanism.

Seedling

Seedlings are especially vulnerable to water stress and therefore seed germination and seedling recruitment are thought to be critical stages in the life cycle of many semi arid plants (Esler and Phillips, 1994). Availability of water greatly affects physiological processes which manifest in the structural details of plants and alter the timings of many vital processes (Agarwal *et al.*, 1986). Amongst many factors which run counter to the natural establishment, growth and development of plants in arid zones, soil moisture conditions perhaps play the most significant role. In these areas, where ensured irrigation is a limitation of agricultural crops, growing trees which are deep rooted and can meet their water requirements from the deeper horizons helps in overcoming drought conditions more easily (Gill *et al.*, 1993).Water stress may result in delayed and reduced seed germination or may prevent germination completely (Taylor *et al.*, 1982).

Activities of enzymes

The activities of many enzymes are affected by drought conditions. For example, nitrate reductase activity has been shown to be highly sensitive to water stress, and a significant decrease in nitrate reductase activity was observed in many plant species under drought conditions (Casadebaig *et al.*, 2008; Foyer *et al.*, 1998). Nitrate reductase activity is induced by nitrogen content in plant tissue, and is regulated at the transcriptional level by the availability of its' substrate, NO3 , and by glutamine, the end product of the nitrogen assimilation pathway (Downs *et al.*, 1993).

Changes in physiological and biochemical processes

Drought stress limits plants growth and fertility especially in arid and semi-arid regions (Erdem *et al.*, 2001; Yang *et al.*, 2009, Zaidi *et al.*, 2014). Plants by morphological, physiological and metabolic changes in all of their organs answer drought stress (Cellier *et al.*, 1998). Environmental factors and water deficit as the most important physiology and biochemistry aspects of plant can influence plants active substances (Petropoulos *et al.*, 2008). For optimum growth and yield, an adequate supply of water is needed. Water stresses have been shown to have an effect on every aspect of plant growth, causing anatomical and morphological alterations as well as changes in physiological and biochemical processes and functions of the plants (Hsiao, 1973; Turner and Kramer, 1980). Also, some morphological characters such as root length, tillering, spike number per m-2, grain number per spike, number of fertile tillers per plant, 1000 grain weight, peduncle length, spike weight, stem weight, awn length, grain weight per spike and affect wheat tolerance to the moisture shortage in the soil (Passioura, 1977; Levitt, 1980; Kramer, 1983; Jhonson *et al.*, 1983; Moustafa *et al.*, 1996; Plaut *et al.*, 2004; Blum, 2005).

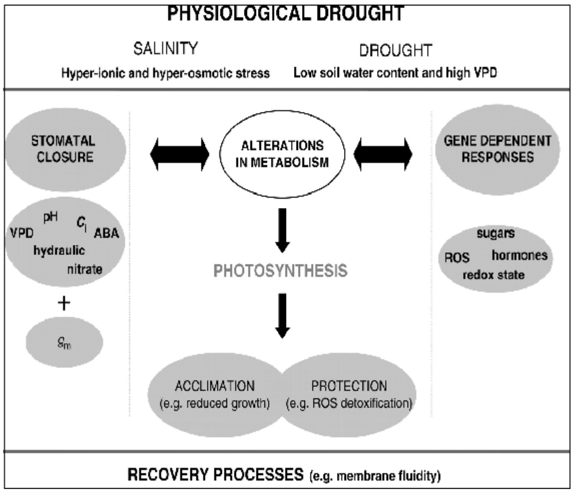

Fig. 1. Direct effects of drought and salinity on stomata and mesophyll (gm) conductance as well as on gene expression, resulting in alterations of photosynthetic metabolism and ultimately on plant acclimation.

Dehydration avoidance

Dehydration avoidance relates to the maintenance of high tissue water potential under varying soil water tension and consists of mechanisms that reduce water loss while maintaining water uptake. Reduction of water loss generally depends on stomatal control of transpiration while increased water uptake depends on a deep and prolific root system. The general risk thus under declining water status is increased root: shoot ratio as a result of altered assimilate partitioning with the result of reduced grain yield. Stomatal closure as a drought avoidance mechanism and is one of the first steps in a plant‘s adaptation to water deficit, allowing the water status to be maintained. Stomatal closure may reduce transpiration losses but reduces CO2 uptake (Ci) negatively affecting photosynthesis (Chaves, 1991, Flexas *et al.*, 2006).

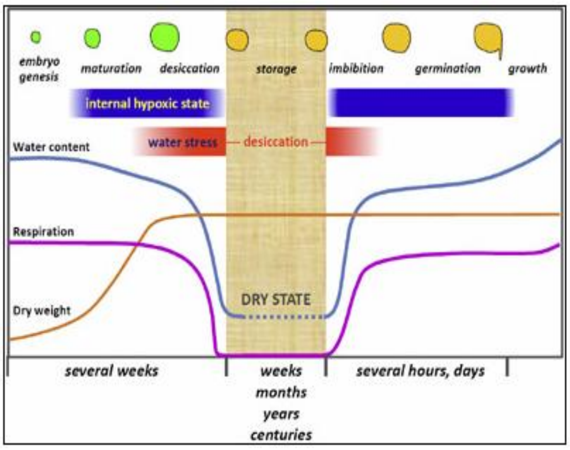

Fig. 2. Mitochondria are exposed to water stress, desiccation and hypoxic conditions in the course of seed development and germination. The scheme shows a typical timeline of seed development, storage and germination with changes in development of dry weight, water content and respiration. Mitochondria are exposed to severe water stress during late seed maturation, desiccation and imbibition. They also need to be functional at the onset of imbibition, and thus to retain sufficient integrity during storage in the dry state, which can last for long periods of time. In many species, mitochondria operating during seed maturation until late desiccation, as well as during seed imbibition and germination are likely to face internal hypoxic conditions, requiring a control of respiration to prevent anoxia.

Radical oxygen species (ROS) and superoxide dismutase (SOD)

Drought stress also increases the levels of radical oxygen species (ROS) in plant cells, resulting in lipid peroxidation and protein damage (Taylor *et al.*, 2004). Glutathione S-transferase (GST) is an essential enzyme which utilizes glutathione to catalyze glutathione- dependent detoxification reactions, reducing organic hydroperoxides and protecting protein sulfuric groups (Edwards *et al.*, 2005). Drought stress often leads to the accumulation of reactive oxygen species (ROS). ROS can act as second messengers involved in the stress signal transduction pathway, but excessive ROS production can cause oxidative stress to the photosynthetic apparatus and seriously impair the normal function of cells (Foyer *et al.* 1994, Smirnoff 1998, Niyogi 1999). In addition to proteolysis, ROS can damage lipids, terpenoids, carbohydrates and nucleic acids (Foyer and Noctor 2005, Moller *et al.* 2007). To keep the levels of active oxygen species under control, plants have evolved a series of antioxidative systems which are composed of metabolites such as ascorbate, glutathione, tocopherol, and enzymatic scavengers such as superoxide dismutase (SOD), peroxidase and catalase (Asada 1999). There are many cases that plants growing in hostile environments exhibit increased antioxidant enzyme activities to combat the deleterious effect of ROS (Duan *et al.* 2005, Jebara *et al.* 2005, Yin *et al.* 2005). The capabilityof scavenging ROS and reducing their damaging effects may correlate with the drought tolerance of plants (Tsugane *et al.* 1999).

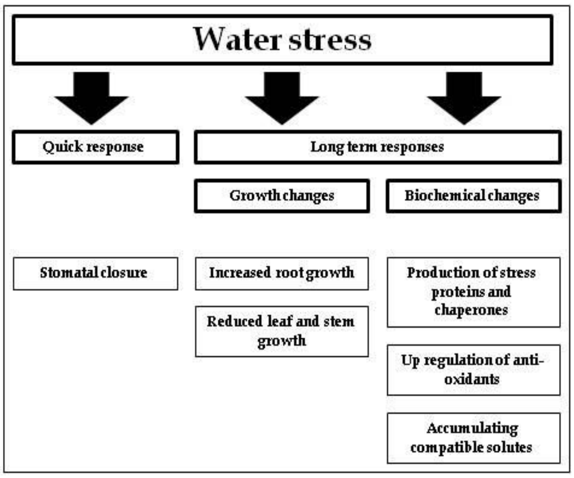

Fig. 3. Plant responses to water stress.

Osmotic adjustment

Osmotic adjustment is a mechanism to maintain water relations and sustains photosynthesis by maintaining leaf water content at reduced water potentials. Osmotic adjustment is accomplished with the accumulation of compatible solutes. Of these, proline is one amongst the most important cytosolutes and accumulates in plants during the adaptation to various types of environmental stress, such as drought, salinity, high temperature, nutrient deficiency, and exposure to heavy metals and high acidity (Oncel *et al.*, 2000). Of the two carotenoid content classes, carotenoids show multifarious roles in drought tolerance including light harvesting and protection from oxidative damage caused by drought. Thus, increased contents specifically of carotenoids are important for stress tolerance (Jaleel *et al.*, 2009).

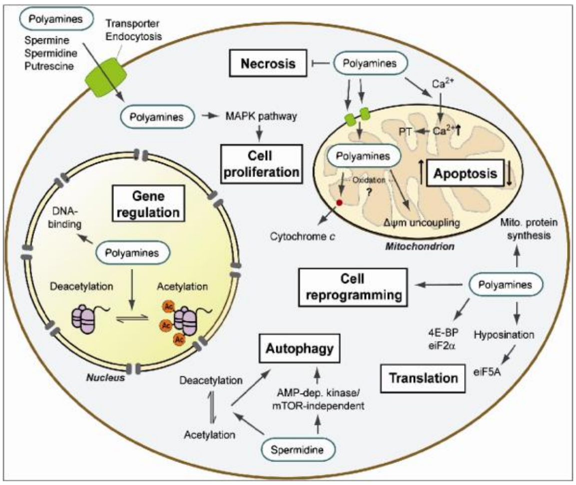

Fig. 4. Summary of the cellular mechanisms of action of polyamines. Upon entering the cell, polyamines exhibit various functions in the cytoplasm, nucleus and mitochondria. Polyamines are involved in the regulation of cell death and cell proliferation as well as in protein synthesis at the level of both gene expression and translation. Recent evidence also assigned polyamines functions in cell reprogramming and autophagy regulation. Thus, polyamines are involved in a broad array of processes and cellular responses that suggest a complex and important role in the control of cellular life and death. PT: permeability transition; Δψm: mitochondrial membrane potential.

Proline

Under various environmental stresses, high accumulation of proline is a characteristic feature of most plants (Rhodes *et al.*, 1999; Ozturk & Demir, 2002; Hsu *et al.*, 2003; Kavi-Kishore *et al.*, 2005). Its accumulation is generally correlated with stress tolerance because tolerant species accumulate more proline as compared to sensitive ones. For example, salt-tolerant alfalfa (Fougere *et al.*, 1991; Petrusa & Winicov, 1997) and drought tolerant wheat (Nayyar & Walia, 2003) accumulated higher amount of proline than the sensitive cultivars. Exogenous application of proline is known to induce abiotic stress tolerance in plants (Claussen, 2005; Ali *et al.*, 2007; Ashraf & Foolad, 2007), because proline may protect protein structure and membranes from damage, and reduce enzyme denaturation (Iyer & Caplan, 1998; Rajendrakumar *et al.*, 1994; Saradhi *et al.*, 1995; Smirnoff & Cumbes, 1989). It may also act as a regulatory or signaling molecule to activate a variety of responses (Maggio *et al.*, 2002). Its storage is also beneficial for plants as a source of nitrogen (Hare *et al.*, 1998). Ali *et al.*, (2007) found that exogenous application of proline enhances gas exchange attributes like net CO2 assimilation rate, transpiration rate and stomatal conductance. However, effect of proline is concentration dependent (Ashraf & Foolad, 2007). Exogenous application of proline in low concentration decreased the potassium efflux from the barley root under salt stress (Cuin & Shabala, 2005). In grasses, high nitrogen uptake due to high proline accumulation is also reported (Tanguiling *et al.*, 1987). Different osmotica can be applied exogenously to plants in three different ways i.e., through the rooting medium, as a foliar spray or pre-sowing seed treatment. Reports on the effects of foliar application of proline in alleviating the adverse effects of abiotic stresses can be deciphered from the literature (Claussen, 2005; Ali *et al.*, 2007; Ashraf & Foolad, 2007).

Water management

knowledge management is about applying the collective knowledge of the entire workforce to achieve specific organizational goals. It is about facilitating the process by which knowledge is created, shared and utilised. Though there is no way of neutralizing all negative impacts resulting from disasters such as droughts, efforts can be made in order to reduce their consequences. Knowledge on drought disaster management strategies, together with good practices and lessons learned can undoubtedly support this effort through well-informed mitigative measures and preparedness planning (Mohanty *et al.*, 2006). Knowledge on drought management strategies appears fragmented, emphasizing a perceived gap in information coordination and sharing (Mohanty *et al.*, 2006). The experiences, approaches and adopted modalities for drought management remain with individuals as tacit knowledge. Therefore the lack of effective information and knowledge sharing, and knowledge creation on drought management strategies can thereby be identified as one of major reasons behind the unsatisfactory performance levels of current drought management practices (Seneviratne *et al.*, 2010). Population growth and increased urbanization have increased competition for fresh water among agriculture, industry, and municipal water users (Lea-Cox and Ross, 2001). Therefore, water conservation and the improvement of irrigation efficiency are important in landscape water management (Nicolas *et al.*, 2008; Niu *et al.*, 2006).With watering restrictions, the effect of drought stress is exacerbated on plant establishment and survival, and selection of drought-tolerant plants becomes increasingly important for the development of sustainable landscapes.

Different irrigation levels

According to Abbaszadeh and his colleagues' study (Abbasazadeh *et al.*, 2009), different irrigation levels (100 (control), 80, 60, 40 and 20% of field capacity) significantly affected shoot yield, oil yield, oil percent, leaf yield, plant height, tiller number, stem diameter and yield of Melissa officinalis L. ($\alpha \leq 0.01$). The highest plant height and shoot yield were observed in control treatment. 40% of field capacity showed the highest oil yield. The highest oil percent and stem diameter belonged to 20% of field capacity treatment (Abbasazadeh *et al.*, 2009).

Water Use Efficiency (WUE)

The physiological parameter of crop WUE is important to describe the relationship between plant water use and dry matter production. With increased WUE, there is a greater biomass production per amount of water transpired and less amount of water needed for growth and development (Nemali and van Iersel, 2008). In several studies (Araus et al., 2002; McKay et al., 2003), it has been reasoned that plants having high WUE at low gS in response to drought stress are more drought-resistant. In a study on clover (Trifolium alexandrinum L.), increased instantaneous WUE resulting from lowered water loss was observed in plants under drought stress, which was induced by decreased transpiration rate and leaf area (Lazaridou and Koutroubas, 2004).

Drought tolerance

Drought tolerance is defined as relative yield of a genotype compared to other genotypes subjected to the same drought stress (Larcher, 2001). Improving the drought tolerance in cultivated species has been, for long time, a major objective for most of the plant breeding programs (Acevedo and Ceccarelli, 1989; Sánchez *et al.*, 1998). Intensive studies have been carried out in order to identify factors involved in drought tolerance, which can be used as criteria for selection (Acevedo and Ceccarelli, 1989; Blum, 1996) for example: the osmotic adjustment (OA) in wheat (Bajji *et al.*, 2001) and sorghum (Girma and Krieg, 1992), the water use efficiency (WUE) in barley (Acevedo and Ceccarelli, 1989) and wheat (Condon *et al.*, 2002) or the cellular wall elasticity (CWE) in soybean (Sinclair and Venables, 1983).

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).

Damages the cell membrane

Cell Membrane Thermo-stability (CMT) is the ability of a plant to resist cellular membrane modification as a result of environmental stress such as drought. Drought stress damages the cell membrane which leads to increased electrolyte leakage. The relative rate of this electrolyte leakage is used as a measure of the cell membrane stability. The electrolyte leakage is estimated by measuring the electrical conductivity of the medium in which the leaf sample is equilibrated. Cell membrane modification, which results in total dysfunction, is a major factor in plant environmental stress. The exact structural and functional modification caused by stress is not fully understood. However, the cellular membrane dysfunction due to stress is well expressed in its increased permeability for ions and electrolytes (Ruter, 1993). Chu-Yung *et al.*, (1985) and Espevig, *et al.*, (2012) suggested that increased solute leakage is attributed to the loss of membrane integrity through lipid phase transitions (principally, altered phospholipid and fatty acid composition) and to the effect on membrane bound transport proteins. These proteins play a role in preventing leakage.

Chlorophyll content

Severe drought stress also inhibits the photosynthesis of plants by causing changes in chlorophyll content, by affecting cholorophyll 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).

Polyamines

Polyamines (PAs) are essential to all cells, since mutants lacking the ability to synthesize polyamines are unable to grow and develop normally (Galston and Kaur-Sawhney, 1990). As polycations they bind readily to cellular polyanions such as DNA, RNA, phospholipids and acidic protein residues, affecting their synthesis and activity. They are also involved in the reproductive activity (flower initiation, fruit growth) (Galston *et al.*, 1997) and stress responses of plants (Bouchereau *et al.*, 1999). Their accumulation during a mild stress period functions as a type of hardening and results in better survival in the case of subsequent stress. The ability of PAs to reduce stress-induced injuries can be explained by their participation in the removal of reactive oxygen species (Guerrier *et al.*, 2000) and their involvement in the maintenance of turgor (Islam *et al.*, 2003) and photosyn thetic activity (Galston *et al.*, 1997). Polyamines can be synthesized in plants through both the ornithine decarboxylase and arginine (Arg) decarboxylase pathways, but the latter is much more important under stress situations (Tiburcio *et al.*, 1997; Cohen, 1998). The involvement of PAs in the response to drought stress was reported in several publications (Erdei *et al.*, 1996; Zhang *et al.*, 1996; Rajasekaran and Blake, 1999; Guerrier *et al.*, 2000).

Mannitolinduced osmotic stress increased the putrescine (Put), spermidine (Spd) and spermine (Spm) contents in wheat (Galiba et al., 1993). In a time course experiment a great increase in their level was detected after one week of drought (Kubis and Krzywanski, 1989). Similarly, osmotic stress induced a greater increase in Put and Spd contents in the tolerant species Lycopersicon pennellii than in the sensitive L. esculentum (Santa-Cruz et al., 1997). The withholding of water induced a greater increase in the Put synthesis (as shown by the greater activity of Arg decarboxylase and ornithine decarboxylase) in drought-tolerant sugarcane varieties than in sensitive ones (Zhang et al., 1996).

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).

Pigments synthesis

Water stress, among other changes, has the ability to reduce the tissue concentrations of chlorophylls and carotenoids (Havaux, 1998; Kiani *et al.*, 2008), primarily with the production of ROS in the thylakoids (Niyogi, 1999; Reddy *et al.*, 2004). However, reports dealing with the strategies to improve the pigments contents under water stress are entirely scarce. The available reports show that exogenous application of brassinolide, uniconazole and methyl jasmonate improved the drought tolerance with increased activities of SOD, CAT and APX, ABA and total improved carotenoid contents in maize (Li *et al.*, 1998), while methyl jasmonate brought about a threefold increase in the β-carotene synthesis as well as degradation of the cholorophyll contents in the epidermal peels (Pérez *et al.*, 1993). Likewise, an important role of tocopherols, lipid-soluble antioxidant in chloroplasts, has been envisioned in improved pigments contents under stress conditions in the photosynthetic organisms including tobacco (Tanaka *et al.*, 1999) and Arabidopsis thaliana and Synechocystis sp. PCC6803 (DellaPenna & Pogson, 2006).

Phytohormones

Some researchers have used PGRs for reducing or eradicating the negative effects of salinity (Kabar, 1987; Mutlu and Bozcuk, 2000). Phytohormones suggested playing important roles in stress responses and adaptation (Sharma *et al.*, 2005; Shaterian *et al.*, 2005). It is thought that the repressive effect of salinity on seed germination and plant growth could be related to a decline in endogenous levels of phytohormones (Zholkevich and Pustovoytova, 1993; Jackson, 1997; Debez *et al.*, 2001). Wang *et al.* (2001) clearly defined that ABA and JA will be increased in response to salinity, whereas indole-3-acetic acid (IAA) and salicylic acid (SA) are declined. For example, the exogenous application of PGRs, auxins (Khan *et al.*, 2004), gibberellins (Afzal *et al.*, 2005), cytokinins (Gul *et al.*, 2000) produces some benefit in alleviating the adverse effects of salt stress and also improves germination, growth, development and seed yields and yield quality (Egamberdieva, 2009). It has been reported that exogenous application of ABA reduces the release of ethylene and leaf abscission under salt stress in plants, probably by decreasing the accumulation of toxic Cl- ions in leaves (Gomez *et al.*, 2002).

Affecting drought on quality and quantity of essential oils

Farahani *et al*,(2009) indicated that drought stress motivated a significant reduction in all of growth parameters of Mentha piperita L and essential oil yield and percent. The highest values of menthol were obtained under 70 % yield capacity by using (GC-MS). The result of Rahbariana *et al*,(2010) showed that the water stress significantly decreased relative water content from 77.69% uder mild stress under severe stress. RWC increased as manure level increased. As stress was intensified, the electrolyte leakage increased, but it started to increase under severe stress. The manure treatment of 40 t/ha had the greatest electrolyte leakage (328.89 ds.m-1). The main components of the oil of Tagestes minuta L. were monoterpenes of which trans – cis tagetone together were 52.3%-64.2%. Drought significantly altered the content of some oil components. Drought stress is characterized by reduction of water content, diminished leaf water potential and turyor loss, closure of stomata and decrease in cell enlargement and growth. Severe water stress may result in the arrest of photosynthesis, disturbance of metabolism and finally the death of plant (Jaleel *et al.*, 2008a).

Water stress inhibits cell enlargement more than cell division. It reduces plant growth by affecting varios physiological and biochemical processes, such as photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism and growth promoters (Jaleel *et al.*, 2008a,b, Faroog *et al.*, 2008 and Hendawy and Khalil, 2005). Azizi *et al.*,(2008a) To compare the response of oregano (Origanum vulgare L.) populations to soil moisture regimes, a greenhouse experiment with three populations of oregano cultivated in Germany (O. vulgare var. creticum, O. vulgare ssp. hirtum, O. vulgare var. samothrake). The population of O. vulgare var. Samothrace showed a stable dry matter yield with higher essential oil content than the populations of O. vulgare var. creticum and O. vulgare ssp. hirtum. Water deficiency after beginning of blooming (folded flowers) can induce an increase in essential oil content and thus result in higher quality of oregano herbage and higher water use efficiency of oregano plants. The effects of water deficit on vegetative growth, fatty acids and essential oil yield and composition of Salvia officinalis aerial parts were investigatedby (Belaqziz *et al.*, 2009). Results showed important reductions of the different growth parameters. Drought decreased significantly the foliar fatty acid content and the double bond index (DBI) degree. A field experiment was evaluate the effect of drought stress on agromorphological characters (fresh flower weight, dried flower yield, shoot weight and root weight), oil content, oil composition and apigenin content of chamomile. Drought stress had four different levels of soil moisture depletion (30%, 50%, 70% and 90%). Analysis of variance showed that drought stress decreased plant height, flower yield, shoot weight and apigenin content but it had no significant effect on oil content or oil composition. Impacts of drought stress on growth indices were evaluated as well and the results indicated that plant managed to maintain potential for biomass production under the drought stress. Growth analysis results as well as phytochemical properties of this plant showed that despite decrease in agronomical traits, chamomile could be proposed as a moderate drought resistant medicinalplant with a reasonable performance (Baghalian *et al.*, 2011). Rajeswara (2002) the yield components, fatty acid, essential oil compositions and phenolic contents fruit essential oil composition and the total phenolic amounts as well as the antioxidant activities of cumin (Cuminum cyminum L.) seeds under drought. This plant is one of the most common aromatics in the Mediterranean kitchen. The results indicated that MWD improved the number of umbels per plant as well as the number of umbellets per umbel and the seed yield, in comparison to the control, but it decreased under severe water deficit (SWD). Fatty acid composition analysis indicated that petroselinic acid was the major fatty acid (55.9%) followed by palmitic (23.82%) and linoleic (12.40%) acids. Water deficit enhanced the palmitic acid percentage and affected the double bound index of the fatty acid pool and thus the oil quality. The essential oil yield was 1.64% based on the dry weight and increased by 1.40 folds under moderate water deficit (MWD). Nevertheless it decreased by 37.19% under SWD in comparison to the non-treated seeds. Drought results on the modification of the essential oil chemotype from γ-terpinene/phenyl-1,2 ethanediol in the control seeds to γ-terpinene/cuminaldehyde in stressed ones. Besides, total phenolic contents were higher in the treated seeds (MWD and SWD). Results suggest that water deficit treatment may regulate the production of bioactive compounds in cumin seeds, influencing their nutritional and industrial values. Besides, antioxidant activities of the extracts were determined by four different test systems, namely DPPH, β-carotene/linoleic acid chelating and reducing power assays and showed that treated seeds (MWD and SWD) exhibited the highest activity.

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