Review Article

INFLUENCE OF DROUGHT STRESS ON CELL-MEMBRANE STABILITY, PROLINE, ACTIVE STOMATAL CLOSURE AND CHLOROPHYLLS

Alireza Sirusmehr[1], Mohammad Reza Vazirimehr[2*]
1. Department of Agriculture, Agriculture Faculty, University of Zabol, IR, Iran
2. PhD student, Department of Agriculture, Agriculture Faculty, University of Zabol, IR, Iran
Corresponding author: Mohammad Reza Vazirimehr

ABSTRACT

Drought stress is one of the most important environmental stresses affecting agricultural productivity worldwide and can result in considerable yield reductions. The physiological mechanisms involved in cellular and whole plant responses to water stress, therefore, generate considerable interest and are frequently reviewed. The classical pattern for plant responses to dry soil is based on hydraulic signalling including a decline in root water uptake and then water potential and turgor in the leaves and stomatal closure, decreased leaf elongation, and osmotic adjustment. Accumulation of higher proline concentration in crop plant under water deficit condition is highly associated with and drought tolerance genotypes depicts its concentration is much higher than drought sensitive genotypes. It has been found by many scientists that in saline stress soil proline are mainly accumulated in leaves of much higher halophytic plant. Hydro passive stomatal closure occurs when the water evaporation from the guard cells is too low to be balanced by water movement into these cells. The water content in the cells is then rapidly reduced to the extent where the osmotic pressure is reduced and the cells lose turgor pressure.

INTRODUCTION

Water stress

Water stress drives important losses in the crop market. Excess or deficit of water produces a cascade of physiological responses that ends-up in decreased production and reduced crop quality. Numerous factors are involved in plants responses to water stress. Several mechanisms that plants utilize to cope the effects of water stress are mediated by ethylene and abscisic acid (ABA). The independent effects of these molecules have been studied in different species. However, the interaction between these responses has not been specially analyzed. The interaction between ABA and ethylene in plants under water stress has been studied by different research groups. From these studies it has been concluded that these hormones interact between them, under stress conditions. Studies of endogenous ABA deficiency have shown that an important role of ABA is to limit ethylene production, and that this interaction is involved in the effects of ABA status on shoot and root growth (Sharp, 2002). This article is review and the aims are influence of drought stress on cell-membrane stability, proline, active Stomatal closure and Chlorophylls.

Root-shoot signaling

Plants can transduce positive and negative signals among roots and shoots to coordinate growth rate and behavior, and adapt to variable environments. When environmental stresses suppress root growth and change root distribution, shoot growth and functions may also be reduced as an effect of root-to-shoot signalling (Novák and Lipiec, 2012). The classical pattern for plant responses to dry soil is based on hydraulic signalling including a decline in root water uptake and then water potential and turgor in the leaves and stomatal closure, decreased leaf elongation, and osmotic adjustment (Clark et al., 2005). A number of plant hormones including abscisic acid (ABA), auxin, cytokinins, ethylene, gibberellins, and other factors (eg nitrogen, pH) have been shown to be involved in the regulation of physiological processes by acting as signal molecules under different environmental stresses (Dodd, 2005; Schachtman and Goodger, 2008). ABA has long been recognized as a major chemical root-to-shoot stress signal (Schachtman and Goodger, 2008). During soil drying, ABA is synthesized by the roots and transported in the xylemto the shoot,where it inhibits leaf expansion and induces stomatal closure before detectable changes in leaf water status and nutrient status (Dodd, 2005; Wang et al., 2000). Moreover, transcription factors and their target genes are engaged in mediating ABA perception and signaling and modulating stomatal movement (Abe et al., 2003). Limitation of stomata is often considered the first step to cope with drought by maintaining sufficient cell turgor to continue plant metabolism. In a

study of Wang et al. (2000) stomatal conductance and the transpiration rate under water stress conditions were lower under good than low fertility conditions. Also under the heat stress, soil fertility improved by application of some macronutrients like Kand Ca and micronutrients like B, Mn, and Se modified stomatal function and activated physiological and metabolic processes that helped in upholding high tissue water potential and increasing heat stress tolerance (Waraich et al., 2012). Biosynthesis of ABA is stimulated by decreased soil water content and plant turgor (Dodd, 2005; Vernieri et al., 2001). The effects of environmental stresses in the root zone on the shoot can be influenced by interaction between the chemical signals. For example, Yang et al. (2006) reported that the grain-filling rate in wheat is enhanced by an increase in the ratio of ABA to ethylene. Another study with wheat under water stress (Yang et al., 2003) suggested that ABA and cytokinins are involved in controlling plant senescence and enhanced carbon remobilization. While shoot responses resulting from root exposure to environmental stresses are frequently studied, little is known about how shoot-subjected stresses affect root growth (Novák and Lipiec, 2012). The results of Parsonsand Sunley (2001) indicate that N status in plants is likely to be most strongly sensed in the shoot and signals trans located to the roots may involve phloem-transported amino compounds or very low concentrations of specific signal molecule.

Proline

Proline is well known to occur extensively in higher crop plants and accumulates in higher concentration in response to different abiotic environmental stresses specially drought stress (Kavi-Kishore et al. 2005). Accumulation of higher proline concentration in crop plant under water deficit condition is highly associated with and drought tolerance genotypes depicts its concentration is much higher than drought sensitive genotypes. It has been found by many scientists that in saline stress soil proline are mainly accumulated in leaves of many higher halophytic plant (Briens & Larher 1982) but plants grown under drought stress showed much higher concentration of proline in leaves, shoots, in desiccating pollen and in root apical regions Lansac et al. 1996). Accumulation of higher concentration of proline permits plants to keep less amount of water potential which cause accumulation of osmolytes in osmoregulation process which enables the plant to take up water to perform growth and metabolic activities (Kumar et al. 2003). Under water deficit condition proline perform many functions like act as osmolyte contribute s in the maintenance of membrane and protein, scavenging free radicals. Moreover after the severe damage of stresses proline contents provide adequate reducing agents that assist in mitochondrial oxidative phosphorylation and production of adenosine triphosphate (ATP) for revival from damages of various stresses (Hare et al. 1998).The primary site of proline contents accumulation in response to drought stress in crop plant is cytosol (Ketchum et al. 1991).

Choice of Crops and Varieties

Crops do vary in their ability to tolerate drought and heat stresses. Plant growth and yield under water-limited conditions can be determined by genetic factors controlling resistance to drought and high temperature conditions and/or WUE (Blum, 2005; Rizza et al., 2004; Singh et al., 2010). Some crops/genotypes are more suitable than others to tolerate stress. In general, crop types and varieties that mature earlier perform better in drought-prone areas by escaping terminal drought as a result of early phonological stages such as flowering, which affects final crop yield (Singh et al., 2010). Moreover, crops and varieties with good stand establishment and canopy structure perform better in drought and heat prone areas through reduction in soil evaporation and heating (Sekhon et al., 2010). Plant tolerance to drought is enhanced by more extensive root systems (Rizza et al., 2004), including root hairs that help keeping root-soil contact in shrink soil due to drying (Gliñski and Lipiec, 1990; White and Kirkegaard, 2010). Additionally, greater hydraulic resistance of the root system related to smaller xylem vessels would increase drought tolerance of plants due to decreasing the rate of extraction of water from the soil without rapid decreasing the amount of available water. The number of seminal roots, root hair length, and an increase in the root hydraulic resistance that can be modified through breeding was indicated (Bengough et al., 2011), However, when crops are irrigated, extensive root systems using a large quantity of photosynthates are unnecessary. In a hydroponic experiment (unlimited water availability), Vysotskaya et al. (2004) showed that only one out of five wheat roots can maintain transpiration and stomatal conductivity at the same level as control plants with an intact root system. Therefore, different genotypes are required under irrigated and rain fed conditions or other farming practices. The effect of drought on crop growth is related to stress intensity and yield potential. Under moderate stress, varieties with high yield potential can be suitable whereas under severe stress varieties with high drought tolerance and low yield potential would be more beneficial (Panthuwan et al., 2002; Rizza et al., 2004). Plant tolerance to abiotic stresses can be improved using traditional and contemporary

molecular breeding protocols and transgenic approaches or genetic engineering (Mittler and Blumwald, 2010; Wahid and Close, 2007).

Cell-membrane stability (CMS)

Cell-membrane stability (CMS) is of vital important selection criteria of drought tolerant genotypes (Tripathy et al. 2000). It has been reported that under water stress cell membrane integrity and stability confers drought resistance (Bewley 1979). The water stress activates the reactive oxygen species which ultimately decreases membrane stability caused by lipid peroxidation (Menconi et al. 1995). Although many reports depicted lower lipid peroxidation and higher cell membrane stability (CMS) in drought tolerant wheat and maize genotypes (Pastori & Trippi 1992). It has been reported by Sairam & Saxena (2000) that higher level of accumulation of H_2O_2 under water stress leads to production of hydroxyl radicals, which cause lipid peroxidation and consequently cell membrane rupture. Damage caused by water deficit stress to cell membrane is negatively associated with increased activities of superoxide dismutase (SOD) and catalase (CAT) in drought susceptible and tolerant genotypes (Dhindsa & Matowe 1981). Under drought stress assembly of lower levels of H_2O_2 lead to lower damage of cell membrane in wheat drought tolerant genotypes. Cell membrane stability (CMS) under drought stress depicts the ability of plant tissues to prevent electrolytes leakage by keeping the cell membrane in safe mood (Sullivan 1971). Estimation of Cell membrane stability (CMS) via in vitro includes dehydration of leaf tissues by means of polyethylene glycol (PEG) and then assessment of electrolyte leakage from leaves. Leakage of various solutes, such as organic acids, amino acids, saccharides, phenolic compounds and hormones from revealed cell membrane stability (CMS) after subject to dehydration through polyethylene glycol has been reported (Leopold et al. 1981). CMS Values have immense significance in hybridization programs because these Values predict the drought tolerant varieties (Dhanda et al. 2004). Genotypes having lower CMS value are vulnerable to water deficit condition while the genotypes showing higher CMS values depicts drought tolerant behaviour. The genotypes having less than 50% values are tremendously susceptible to drought while genotypes with 71–80% values are considered to grow with full potential under water deficit. Farshadfar et al. (2011) noticed in investigation that under water deficit conditions cell membrane stability (CMS) depicted positively considerable relationship with tillers per plant, grain yield, but negative association 100 kernel weights (TGW).

Stomatal closure

Hydro passive stomatal closure occurs when the water evaporation from the guard cells is too low to be balanced by water movement into these cells. The water content in the cells is then rapidly reduced to the extent where the osmotic pressure is reduced and the cells lose turgor pressure and shrink (Luan, 2002). When this happens the guard cells are unable to maintain the shape and the stomatal pore is covered. Some studies have shown that passive stomatal closure is important in ferns and Lycopods, but not in Angiosperms and Gymnosperms (Franks and Farquhar, 2007; Brodribb and McAdam, 2011). This is because in Angiosperms and Gymnosperms the guard cells closely interact with their subsidiary cells. When the guard cells lose turgor pressure the subsidiary cells also lose turgor pressure and the force from the subsidiary cells pulls the guard cells apart, opening the stomata. This hydro passive opening is called the "wrong-way" response (Franks and Farquhar, 2007). In contrast the guard cells of ferns and Lycopods do not interact closely with their subsidiary cells.

Active stomatal closure

ABA as well as elevated levels of CO_2 activates signalling pathways leading to stomatal closure (Kim et al., 2010). ABA is produced in the roots and leaves during water stress and is transported to the guard cells. ABA is transported into the guard cells by ATP-binding cassette (ABC) transporters that are located in the plasma membrane (Kang et al., 2010). When the ABC transporters are knocked out the ABA uptake is lower, stomata remain more open during drought and the stress tolerance is decreased (Kang et al., 2010). The size of the stomatal opening is regulated by the turgor pressure and cell volume of the guard cells (Schroeder et al., 2001; Kim et al., 2010). Regulation of stomatal opening is linked to transport of ions and water through channel proteins across the plasma and vacuole membrane (Kim et al., 2010). ABA induces the production of reactive oxygen species (e.g. H_2O_2), which in turn acts as a trigger for NO production, inhibition of membrane proton pumps and Ca^{2+} influx across both the plasma and vacuole membranes. H^+-ATPases that are hyperpolarizing the plasma membranes must be inhibited to induce ABA mediated stomatal closure (Merlot et al., 2007). The increased Ca^{2+} levels activate slow and rapid type anion channels, generating an anion efflux from the cells. The anion efflux depolarizes the membrane, which in turn causes K^+ efflux through K^+out channels across both the vacuole and the plasma membrane. Simultaneously Ca^{2+} also inhibits K^+in

channels (Wasilewska et al., 2008). Malate is also converted to starch reducing the osmotic potential and turgor pressure further (Kim et al., 2010). The plasma membrane is thus depolarised, the turgor pressure and cell volume reduced and the stomata close (Kim et al., 2010).

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).

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). These data warrant concerted efforts on the either the induction of pigment synthesis or modification of pigment biosynthesis pathways for enhanced drought tolerance in plants.

Flowering and fertilization

For successful seed establishment, the pollen must remain viable and the stigma receptive, pollen tubes must grow properly and reach the ovules, double fertilization must be successful, and embryo and endosperm development should proceed normally. Some of these processes may be severely compromised by the unfavourable environmental conditions frequently encountered by cereals in the field. In cereals, pollen viability and germination is one of the most stress-sensitive of these processes (Saini & Aspinall 1982; Stone 2001). In maize, low kernel numbers can rarely be ascribed to pollen sterility under water stress (Westgate & Boyer 1986; Schoper et al. 1987); instead, the genotype dependent sensitivity of the pollen to high temperature could be observed (Schoper et al. 1987). Investigations by Barnabás (1985) showed that pollen grain viability in maize was closely and positively correlated with desiccation tolerance. In fact, maize pollen could sustain up to a limit of 80% water loss without detrimental changes in normal pollen functions. Close synchrony between pollen shed (anthesis) and silk emergence is required for high kernel set in maize and a negative relationship exists between final kernel number and the extent of the anthesis-silking interval(Westgate, Otegui&Andrade 2004).Anthesis and fertilization are particularly sensitive to drought in rice.Water stress during flowering may reduce the harvest index by as much as 60%, largely as a result of a reduction in grain set (Ekanayake, Steponkus & deDatta 1989; Garrity & O'Toole 1994). Among the events known to be drought-sensitive at flowering are panicle exsertion and anther dehiscence (O'Toole & Namuco 1983; Ekanayake, Steponkus & deDatta 1990).The failure of panicle exsertion alone accounts for approximately 25–30% of spikelet sterility because the unexserted spikelets cannot complete anthesis and shed pollen, even when development is otherwise normal (O'Toole&Namuco 1983). If an incomplete anther dehiscence occurred and only a few pollen grains could reach the stigma surface, the pollen grains appeared to cooperate rather than compete (Liu et al. 2006). Water deficiency, which

may also be caused by dry winds during or immediately prior to rice flowering, leads to a substantial reduction in seed set.This can be attributed to the fact that the panicle is unable to free itself completely from the flag leaf, while the spikelets dry out or do not open at anthesis. The anthers may shrivel up, so that insufficient pollen is available for fertilization. These reproductive abnormalities may prevent fertilization completely (Ekanayake,DeDatta&Steponkus 1993).Grain abortion at the early stages following fertilization also accounts for part of the reduction in grain number in rice (O'Toole&Namuco 1983). In maize, abortion is highly dependent on the timing of water stress: low water availability before pollination resulted in abortion even if sufficient water was available at the time of pollination (Westgate & Boyer 1986).

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