The Influence of Drought Stress on Stomatal Signaling, Rubisco, Heat Shock Proteins in Crop Plants

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Abstract The severity of drought is unpredictable as it depends on many factors such as occurrence and distribution of rainfall, evaporative demands and moisture storing capacity of soils. Investigations carried out in the past provide considerable insights into the mechanism of drought tolerance in plants at molecular level. The mechanism by which Rubisco may be down regulated in the light due to tight binding inhibitors could be pivotal for tolerance and recovery from stress and may be central to integrating the midday depression of photosynthesis. Additionally, enhanced rates of oxygenase activity and photorespiration maintain the ET rate in response to drought and are quantitatively much more important than the Mehler reaction. Stomatal activity, which is affected by environmental stresses, can influence CO_2 absorption and thus impact photosynthesis and plant growth. In response to a water deficit stress, ion- and water-transport systems across membranes function to control turgor pressure changes in guard cells and stimulate stomatal closure.

Keywords Photosynthetic enzymes, Root growth, Seed germination

Introduction

Faced with scarcity of water resources, drought is the single most critical threat to world food security. It was the catalyst of the great famines of the past. Because the world's water supply is limiting, future food demand for rapidly increasing population pressures is likely to further aggravate the effects of drought [1]. The severity of drought is unpredictable as it depends on many factors such as occurrence and distribution of rainfall, evaporative demands and moisture storing capacity of soils [2]. Investigations carried out in the past provide considerable insights into the mechanism of drought tolerance in plants at molecular level [3]. Three main mechanisms reduce crop yield by soil water deficit: (i) reduced canopy absorption of photosynthetically active radiation,(ii) decreased radiation-use efficiency and (iii) reduced harvest index [4]. This article is review and the aim and scope is influence of drought stress on stomatal signaling, rubisco, Heat shock proteins in crop plants.

Effect of Water Stress on Root Growth

A developed root system is constitutive feature in many environments. The roots help the plants to absorb water and minerals for their better use. Roots are also important component of drought tolerance at the various growth stages of plant [5]. The maximum accumulated water in the root zone depends on the anchorage of roots in the soil volume. Under the limited supply of water resource allocation pattern changes; root tissues gain more assimilates as compare to leaf tissues. If drought stress prevails at the early seedling stage the root-shoot changes [6] and commonly increases [7]. Investigation work showed that root weight enhance while shoot weight reduce with the application of water deficit stress [8]. It was found that drought reduced fresh and dry shoot and root weight by 40 and 58 %, respectively. Drought stress decreased the length and fresh weight of shoot in maize [9].

Rubisco

The mechanism by which Rubisco may be down regulated in the light due to tight binding inhibitors could be pivotal for tolerance and recovery from stress and may be central to integrating the midday depression of photosynthesis [10]. Additionally, enhanced rates of oxygenase activity and photorespiration maintain the ET rate in response to drought and are quantitatively much more important than the Mehler reaction [12]. Kanechi et al. [13] found a close relationship between Rubisco content and maximal O_2 evolution rate measured at high photosynthetic photon flux density (PPFD) during leaf dehydration. It was established that below -2.0 MPa inhibition of photosynthesis in two maize cvs is in part attributed to stomatal conductance but mostly to the decreased activities of carbonic anhydrase, phosphoenol pyruvate carboxylase and Rubisco [14]. As mentioned above, the primary site of limitation of maximal O_2 evolution rate, measured at high PPFD, seemed related to significantly reduced RuBP content, not to the amount of Chl or Rubisco. But as mentioned above, Rubisco is not a prime target of water deficit and is not limiting net CO_2 assimilation of leaves submitted to desiccation [15]. Decreased supply of CO_2 to Rubisco under both mild and severe water deficit is primarily responsible for the decrease in CO_2 fixation [16]. Specific proteins display particular structural features such as the highly conserved domain predicted to be involved in hydrophobic interaction leading to macromolecular stabilization [17]. The majority of new proteins belong to dehydrin-like proteins, which are abundantly induced during embryo maturation of many higher plants as well as in water stressed seedlings [18]. Dehydrins are synthesized by the cell in response to any environmental influence that has a dehydration component such as drought, salinity or extracellular freezing [19]. Dehydrins may stabilize macromolecules through detergent and chaperone like properties and may act synergistically with compatible solutes [17, 20]. The steady state levels of major PS2 proteins, including the Dl and D2 proteins in the PS2 reaction center, declined with increasing water deficit possibly as a result of increased degradation. The effects of WD on PS2 protein metabolism, especially on the reaction center proteins may account for the damage to PS2 photochemistry [21].

Seed germination

Seed germination and seedling growth traits are extremely important factors in determining yield [22]. Indicated that seed vigor index and plumule length are the most sensitive traits to drought stress. The rate of seed germination and the final germination percentage as well as amount of water absorption by seeds were considerably lowered with the rise of osmotic stress level at grain growth [23]. There are many studies such as the selecting plant species or the seed treatments that are helpful for alleviating the negative effect of drought stress on different plants [24].

Stomatal Signaling

Stomatal activity, which is affected by environmental stresses, can influence CO_2 absorption and thus impact photosynthesis and plant growth. In response to a water deficit stress, ion- and water-transport systems across membranes function to control turgor pressure changes in guard cells and stimulate stomatal closure. Endogenous ABA is rapidly produced during drought, triggering a cascade of physiological responses, including stomatal closure, which is regulated by a signal transduction network. 9-cis-epoxycarotenoid dioxygenase 3 (NCED3) in Arabidopsis catalyzes a key step in ABA biosynthesis, and NCED3 expression is rapidly induced by drought stress in a vascular tissue-specific manner ([25], Figure 1). Mutations in nced3 reduced, while the overexpression of NCED3 enhanced drought tolerance and/or increased WUE in several plant species [25, 26]. During drought stress, the accumulated ABA in the vascular tissue is transported to guard cells via passive diffusion in response to pH changes and by specific transporters. Two members of the membrane-localized ABC transporter family, ABCG25 and ABCG40, and one member from a nitrate transporter family, AIT1/NRT1.2/NPF4.6, have been independently isolated from Arabidopsis and reported as ABA transporters [27-28]. ABCG25 has a role in ABA export, whereas ABCG40 and AIT1 are involved in the import of ABA. ABA-induced stomatal closure and gene expression are reduced in the atabcg40 mutation, resulting in reduced drought tolerance [27].
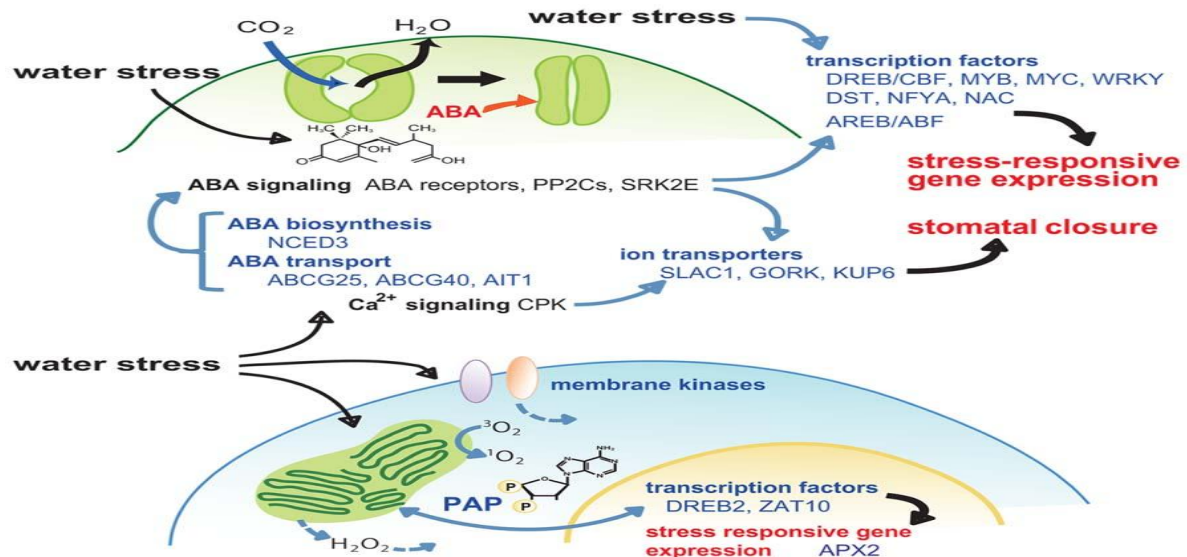
Figure 1: Model for the role of signaling factors in stomatal closure and retrograde signaling during water stress

Photosynthetic enzymes under water stress

The data on water stress induced regulation of the activity of photosynthetic enzymes other than Rubisco are scarce. Thimmanaik et al. [29] studied the activity of several photosynthetic enzymes under progressive water stress in two different cultivars of Morusalba. 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 polyethilenglycole, Rubisco activity significantly increased in young potato leaves, while decreased in mature leaves [30]. Similarly, some reports have shown strong drought-induced reductions of Rubisco activity per unit leaf area [31] and permg showed that the decrease of Rubisco activity in vivo was not connected with the protein content. It occurs because of CO_2 concentration decrease in the carboxylation center in consequence of the partly closing of stomata [32].

Nutrient Relations

Decreasing water availability under drought generally results in limited total nutrient uptake and their diminished tissue concentrations in crop plants. An important effect of water deficit is on the acquisition of nutrients by the root and their transport to shoots. Lowered absorption of the inorganic nutrients can result from interference in nutrient uptake and the unloading mechanism, and reduced transpirational flow [33]. However, plant species and genotypes of a species may vary in their response to mineral uptake under waterstress. In general, moisture stress induces an increase in N, a definitive decline in P and no definitive effects on K [33]. As nutrient and water requirements are closely related, fertilizer application is likely to increase the efficiency of crops in utilizing available water. This indicates a significant interaction between soil moisture deficits and nutrient acquisition. Studies show a positive response of crops to improved soil fertility under arid and semiarid conditions. Currently, it is evident that crop yields can be substantially improved by enhancing the plant nutrient efficiency under limited moisture supply [33].

Heat Shock Proteins

Heat shock proteins belong to a larger group of molecules called chaperones. They have a role in stabilizing other proteins' structure. Low-molecular-weight heat shock proteins are generally produced only in response to environmental stress, particularly high temperature [34]. But many heat shock proteins have been found to be induced by different stresses such as drought, anaerobic conditions and low temperatures [35]. They are reported to serve as molecular chaperones that participate in adenosine triphosphate-dependent protein unfolding or

assembly/disassembly reactions and prevent protein denaturation during stress [36]. Membrane-stabilizing proteins and late embryogenic abundant proteins are another important protein group responsible for conferring drought tolerance. These increase the water binding capacity by creating a protective environment for other proteins or structures, referred to as dehydrins. They also play a major role in the sequestration of ions that are concentrated during cellular dehydration [36]. These proteins help to protect the partner protein from degradation and proteinases that function to remove denatured and damaged proteins. Dehydrins, also known as a group of late embryogenesis abundant proteins, accumulate in response to both dehydration and low temperature [17].

References

[1]. Somerville C., Briscoe J. (2001) Genetic engineering and water, Science 292, 2217.

[2]. Wery J., Silim S.N., Knights E.J., Malhotra R.S., Cousin R. (1994) Screening techniques and sources and tolerance to extremes of moisture and air temperature in cool season food legumes, Euphytica 73, 73–83.

[3]. Hasegawa P.M., Bressan R.A., Zhu J.K., Bohnert H.J. (2000) Plant cellular and molecular responses to high salinity, Annu. Rev. Plant Phys. 51, 463–499.

[4]. Earl H., Davis R.F. (2003) Effect of drought stress on leaf and whole canopy radiation use efficiency and yield of maize, Agron. J. 95, 688–696.

[5]. Weerathaworn P, Soldati A, Stamp P. (1992a) Anatomy of seedling roots of tropical maize (Zea mays L.) cultivars at low water supply. Journal of Experimental Botany 43, 1015- 1021.

[6]. Nielson DC, Hinkle SE. (1996) Field evaluation of basal crop coefficients for corn based on growing degree days, growth stage, or time. Transactions of the ASAE 39, 97- 103.

[7]. Sharp RE, Davies WJ. (1989) - Regulation of growth and development of plants growing with a restricted supply of water. Plants under Stress, 71- 93.

[8]. Morizet T, Pollucsck M, Togola D. (1983) Drought tolerance in four maize varieties (Field Crops Abst.39: 306, 1986).

[9]. Thakur PS, Rai VK. (1984) Water stress effects on maize growth responses of two differentially drought sensitive maize cultivars during early stage of growth. Indian Journal of Ecology, 11:92-98.

[10]. Parry, M., Andraloje, P. J., Khan, S., Lea, P.J., A. Keys, (2002) Rubisco activity: effect of drought stress. Annals of Bot., 89, 833–639.

[11]. Haupt-Herting, S., H. P. Fock, (2002) Oxygen exchange in relation to carbon assimilation in water-stressed leaves during photosynthesis. Annals of Bot., 89, 851–859.

[12]. Noctor, G., Veljovic-Jovanovic, S., Driscoll, S., Novitskaya, L., C. H. Foyer, (2002) Drought and oxidative load in the leaves of C3 plants: a predominant role of photorespiration? Annals Bot., 89, 841–850.

[13]. Kanechi, M., Kunitomo, E., Inagaki, N., S. Maekawa, (1995) Water stress effects on ribulose- 1,5-bisphosphate carboxylase and its relationship to photosynthesis in sunflower leaves. In: Photosynthesis: from light to biosphere. Vol. IV, Ed. M. Mathis. Kluwer Acad. Publ., Dordrecht-Berlin-London, 597–600.

[14]. Prakash, K. R., V. S. Rao, (1996). The altered activities of carbonic-anhydrase, phosphoenol pyruvate-carboxylase and ribulose-bisphosphate carboxylase due to water-stress and after its relief. J. environ. Biol., 17, 39–42.

[15]. Holaday, A. S., Ritchie, S. W., H. T. Nguyen, (1992) Effect of water deficit on gas-exchange parameters and ribulose 1,5-bisphosphate carboxylase activation in wheat. Environ, exp. Bot., 32, 403–410.

[16]. Lal, A., Ku, M. S. B., G.E. Edwards, (1996) Analysis of inhibition of photosynthesis due to water-stress in the C3 species Hordeumvulgare and Viciafaba - electron-transport, CO_2 fixation and carboxylation capacity. Photosynth. Res., 49, 57–69.

[17]. Close, T. J., (1996) Dehydrins: emergence of a biochemical role of a family of plant dehydration proteins. Physiol. Plant., 97, 795–803.

[18]. Pelah, D., Altman, A., O. Shoseyov, (1997) Drought tolerance: a molecular perspective. In: Horticulture Biotechnology. In Vitro Culture and Breeding. Eds. Altman, A., M. Ziv. Acta Hort., 447, 439–445. ISHS.

[19]. Ingram, J., Bartels, D., 1996. The molecular basis of dehydration tolerance in plants. - Annu. Rev. Plant Physiol. Plant Mol. Biol., 47, 377–403.

[20]. Hoekstra, F., Golovina, E., J. Buitink, (2002) Mechanisms of plant desiccation tolerance. Trends in Plant Sci., 8(9), 431–438.

[21]. He, J.X., Wang, J., H.G. Liang, (1995) Effects of water-stress on photochemical function and protein-metabolism of photosystem-II in wheat leaves. Physiol. Plant., 93, 771–777.

[22]. Rauf M, Munir M, UI-Hassan M, Ahmed M, Afzai M. (2007) Performance of wheat genotypes under osmotic stress at germination and early seedling growth stage. Afri J Biotech 8: 971-975.

[23]. Heikal MM, Shaddad MA, Ahmed AM. (1981) Effect of water stress and gibberellic acid on germination of flax, sesame and onion seed. BiolPlantarum 24: 124-129.

[24]. Almansouri M, Kinet JM, Lutts S. (2001) Effect of salt and osmotic stresses on germination in durum wheat (Triticum durum Desf.). Plant Soil 231: 243-254.

[25]. Iuchi, S., Kobayashi, M., Taji, T., Naramoto, M., Seki, M., Kato, T., et al. (2001). Regulation of drought tolerance by gene manipulation of 9-cis-epoxycarotenoid dioxygenase, a key enzyme in abscisic acid biosynthesis in *Arabidopsis*. *Plant J.* 27, 325–333. doi: 10.1046/j.1365-313x.2001.01096.x

[26]. Tung, S. A., Smeeton, R., White, C. A., Black, C. R., Taylor, I. B., Hilton, H. W., et al. (2008). Over-expression of LeNCED1 in tomato (*Solanumly copersicum* L.) with the rbcS3C promoter allows recovery of lines that accumulate very high levels of abscisic acid and exhibit severe phenotypes. *Plant Cell Environ.* 31, 968–981. doi: 10.1111/j.1365-3040.2008.01812.x

[27]. Kang, J., Hwang, J. U., Lee, M., Kim, Y. Y., Assmann, S. M., Martinoia, E., et al. (2010). PDR-type ABC transporter mediates cellular uptake of the phytohormoneabscisic acid. *Proc. Natl. Acad. Sci. U.S.A.* 107, 2355–2360.doi: 10.1073/pnas.0909222107

[28]. Kuromori, T., Miyaji, T., Yabuuchi, H., Shimizu, H., Sugimoto, E., Kamiya, A., et al. (2010). ABC transporter AtABCG25 is involved in abscisic acid transport and responses. *Proc. Natl. Acad. Sci. U.S.A.* 107, 2361–2366.doi: 10.1073/pnas.0912516107

[29]. Thimmanaik S, Giridara KS, Jyothsna KG, Surnyanarayana N, Sudhakar C. (2002) Photosynthesis and the enzymes of photosynthetic carbon reduction cycle in mulberry during water stress and recovery. Photosynth. 40: 233-236

[30]. Bussis D, Kauder F, Heineke D. (1998) Acclimation of potato plants to polyethylene glycolinduced water deficit. J. Exp. Bot. 49: 1349-1360.

[31]. Maroco JP, Rodrigues ML, Lopes C, Chaves MM. (2002) Limitations to leaf photosynthesis in field-grown grapevine under drought-metabolicand modeling approaches. Func. Plant Biol. 29: 451- 459.

[32]. Flexas J, Ribas-Carbo MT, Bota J, Galmes J, Henkle M, Martinez-Canellas SF, Medrano H. (2006) Decreased Rubisco activity during waterstress is not induced by decreased relative water content but related to conditions of low stromal conductance and chloroplast CO_2 concentration. New Phytol. 172: 73-82.

[33]. Garg BK. (2003) Nutrient uptake and management under drought: nutrient-moisture interaction, Curr. Agric. 27, 1–8.

[34]. Wahid A. (2007) Physiological implications of metabolites biosynthesis in net assimilation and heat stress tolerance of sugarcane (*Saccharum officinarum*) sprouts, J. Plant Res. 120, 219–228.

[35]. Coca M.A., Almoguera C., Jordano J. (1994) Expression of sunflower low molecular weight heat shock proteins during embryogenesis and persistence after germination: localization and possible functional implications, Plant Mol. Biol. 25, 479–492.

[36]. Gorantla M., Babu P.R., Lachagari V.B.R., Reddy A.M.M., Wusirika R., Bennetzen J.L., Reddy A.R. (2006) Identification of stressresponsive genes in an indica rice (*Oryza sativa* L.) using ESTs generated from drought-stressed seedlings, J. Exp. Bot. 58, 253– 265.