R-2381
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REVIEW ARTICLE Agricultural Reviews, Volume Issue : ()

Plant Metabolism during Water Deficit Stress: A Review

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10.18805/ag.R-2381

ABSTRACT

Water deficit stress is one of the chief abiotic stresses adversely affecting plant endurance leading serious effects on plant metabolism. Depending upon strength and duration of water deficit conditions, plants adjust a series of physiological, cellular and molecular mechanisms aiming a correct stress response. Some of the responses of plants to water stress include decreased growth and development and hence decrease in fresh biomass, decreased content of chlorophyll and hence the decreased rate of photosynthesis, decrease in leaf relative water content (RWC) and increased accumulation of osmolytes like proline, sucrose, soluble carbohydrates, *etc*. Several enzymes involved in carbohydrate metabolism seem to play a role in the multi-layered response of plants to water deficiency. Glycolysis is a central metabolic pathway that provide elasticity when production of energy for existence is confronted and is modulated to establish a novel homeostasis under stress conditions in plants. Evidence for the participation of glycolytic genes, proteins and enzymes in response to stress is established by the fact that their expression is deeply affected by exposure of plant tissues to environmental stresses such as drought. Keeping in mind the importance of glycolytic pathway during stress conditions in plants, the impact of the drought stress on plant glycolysis is the subject of current review. In addition, plant physiology and carbohydrate metabolism under drought stress are also discussed.

Key words: Glycolysis, Plant physiology, Sugar metabolism, Water deficit.

Plants encounter many abiotic stresses which severely affect their growth and ultimately the yield (Mei *et al.* 2018). The most detrimental one is certainly water-deficit, particularly given that environmental stresses as high temperature, freezing and salinity are also accompanied with or result in water deficit. Plants that receive inadequate water, experience water deficit stress. There is hardly a physiological process in plants which is not affected when the amount of water transpired exceeds the amount of water uptake which is caused by insufficient rainfall or decreased ground water level (Kapoor *et al.* 2020). The initial response to water-deficit is stomata closure to prevent tissue dehydration which results in reduced transpiration and a limited carbon dioxide uptake, consequently, the photosynthetic rate of plants decreases (Kumawat and Sharma, 2018). The declining photosynthetic activity negatively affects further vegetative growth. In the worst case, flowers and fruits may also be shed, negatively affecting the yield. Drought stress also causes decline in leaf water relations and membrane stability that results in membrane injury (Abid *et al.* 2018). In the present review, attempts have been made to comprehend the available literature on plant physiology and carbohydrate metabolism with special emphasis on plant glycolysis under water deficit stress.

Physiological responses elicited by water deficit stress

Plant growth

Since water is an essential element for plant growth, it is obvious that water deficit stress, depending on its severity and duration affects the growth and yield of the plant. Water loss causes lowering of the water potential in the cell and a corresponding decrease of cell turgor that has a direct impact on the rate of cell expansion and cell size, ultimately resulting in a reduction of plant growth (Lang *et al.* 2014; Abid *et al.* 2018; Prakash and Singh 2020). Water deficit reduces the number of leaves per plant and individual leaf size and leaf longevity (Bhargavi *et al.* 2017). Reduction in shoot growth, especially leaves is beneficial for the plant under drought stress as it reduces the surface area exposed for transpiration, hence minimizing water loss. Growth arrest can also be considered as a medium by which plants can preserve carbohydrates for sustained metabolism thus prolonging energy supply and faster recovery after stress relief. Decrease in leaf area index, leaf dry weight, shoot height and fresh and dry weight of root and shoot has been reported by many workers in different crop plants (Mohammadian *et al.* 2005; Yucel *et al.* 2010; Khanna *et al.* 2014a; Gheidary *et al.* 2017)

Chlorophyll content

Chlorophyll is one of the major components of photosynthesis and even a short-term water deficiency

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How to cite this article: Khanna, S.M. (2022). Plant Metabolism during Water Deficit Stress: A Review. Agricultural Reviews. DOI: 10.18805/ag.R-2381.

Submitted: 22-09-2021 **Accepted:** 02-03-2022 **Online:** 06-04-2022

changes the total contents of chlorophylls (Daoqian *et al.* 2016). As water deficit stress accelerates chlorophyll decomposition, chlorophyll content is one of the most commonly used metrics for the severity of drought stress (Efeoglu *et al.* 2009; Ying *et al.* 2015). Decreased chlorophyll level during drought stress has been reported in many plant species (Manivannan *et al.* 2007; Mafakheri *et al.* 2010; Khanna *et al.* 2014a). Maintaining lower chlorophyll content in drought stress conditions can help plants reduce photo-oxidative damage, which occurs when photosynthesis is inhibited and light excitation energy is in excess (Aranjuelo *et al.* 2011).

Water relations

Drought stress alters leaf water relations by decreasing leaf water potential and relative water content (RWC) but increasing osmotic adjustment (OA) (Abid *et al.* 2018). RWC is the appropriate measure of the plant water status in terms of the physiological consequences of cellular water deficit (Khanna *et al.* 2014a and b). It estimates the current water content of the sampled leaf tissue relative to the maximal water content it can hold at full turgidity. Decrease in RWC in response to drought stress has been noted in wide variety of plants (Yucel *et al.* 2010; Rahbarian *et al.* 2011).

Osmolyte accumulation

Under drought, plants accumulate different types of organic and inorganic solutes like proline, sucrose, soluble carbohydrates, glycine betaine in the cytosol to lower osmotic potential (Suprasanna *et al.* 2016; Ozturk *et al.* 2021). These solutes protect cellular structures and functions as well as maintain water balance and delay dehydrative damage by maintaining cell turgor and other physiological mechanisms under water-deficit conditions (Taiz and Zeiger, 2006). In addition, compatible solutes have some other functions in plants such as, protecting of enzymes, maintaining membrane structure and its integrity, stabilizing of protein conformation and scavenging of free oxygen radicals at low water potentials (Slama *et al.* 2015). In plants, sucrose is the usual osmoprotectant sugar (Pinheiro *et al.* 2001). Koster, (1991) suggested glass formation being a possible way for sugars shielding cellular structures. Liquids become supersaturated in the presence of sugars and enter the state of plastic solids rather than solutes crystallizing and disrupting membranes. Sugars have also been shown to directly protect membranes and proteins *in vitro*, possibly by replacing water molecules and altering physical properties through the formation of hydrogen bonds (Crowe *et al.* 1992).

Importance of sugar accumulation in plants during water deficit stress

In response to drought, plants accumulate a large amount of water-soluble carbohydrates such as glucose, fructose, sucrose, stachyose, mannitol and pinitol. Sugars protect cells during drought by two mechanisms (Leopold *et al.* 1994). First, the hydroxyl groups of sugars may substitute for water to maintain hydrophilic interactions in membranes and proteins during dehydration, thereby preventing protein denaturation. Secondly, sugars are a major contributing factor to vitrification, which is the formation of a biological glass in the cytoplasm of dehydrated cells. These intracellular glasses by virtue of their high viscosity, drastically reduce molecular movement, impede the diffusion of reactive compounds in the cell and may maintain the structural and functional integrity of macromolecules. The available reports (Table 1) stated that the content of soluble sugars and other carbohydrates in the leaves of various water stressed plants is altered and may act as metabolic signal in response to drought.

During stress, sugars not only function as osmoprotectants, but they are also considered important regulators of gene expression. Sugars act as key players in stress perception, signaling and are a regulatory hub for stress-mediated gene expression. The expression of stress responsive genes corresponding to enzymes of carbohydrate metabolism are down or upregulated by the sugar status of the cell, indicating the role of sugars during abiotic stresses (Seki *et al.* 2002; Price *et al.* 2004). Changes in expression of genes involved in carbohydrate metabolism during drought stress have been reported in many different studies (Bray, 2002; Chaves *et al.* 2002; Yamaguchi-Shinozaki and Shinozaki, 2006; Pan *et al.* 2016). Fluctuations in carbohydrate composition, genes and enzymes involved in carbohydrate metabolism are of particular importance because of their direct relationship with physiological processes such as photosynthesis, translocation and respiration.

Effect of water deficit stress on respiration

Respiratory pathway has a critical function in providing energy to the cell for the various metabolic activities. Environmental variables profoundly affect respiration. Despite its well-recognized importance, the regulation of respiration by drought at the plant physiological level is largely unknown, because of the apparent contradictions among different studies with either increased (Gratani *et al.* 2007; Slot *et al.* 2008) or decreased (Ribas-Carbo *et al.* 2005) or unaffected (Lawlor and Fock, 1977) rates of respiration. Reduced availability of the substrate to the mitochondria under conditions of low photosynthesis as well as inhibition of leaf growth may explain reduced respiration (Gimeno *et al.* 2010). However, an increased demand for respiratory ATP under severe water stress (to compensate for the lowered ATP production in the chloroplasts) may be required to support photosynthesis repair mechanisms, as suggested by Atkin and Macherel, (2009). De Vries *et al.* (1979) conducted studies in maize and wheat and observed that while respiration rate remained unaffected at low or moderate water stress, it decreased at severe water deficit stress. Flexas *et al.* (2005) attributed this controversy to three possible causes: (i) the use of different species, organs and techniques for respiration studies; (ii) the presence of

Table 1: Changes in carbohydrate metabolism in water stressed plants.

Carbohydrates changes	References
Increasing total carbohydrates	Cotton (Timpa *et al.* 1986, Parida *et al.* 2007)
Increasing total soluble sugars	Durum wheat (Kameli and Lösel 1996), nodulated alfalfa (Irigoyen *et al.* 1992), soybean (Liu *et al.* 2004) wheat (Abid *et al.* 2018)
Increasing sucrose	Alfalfa (Al-Suhaibani 1996), wheat (Drossopoulos *et al.* 1987), wilted bean (Stewart 1971), durum wheat (Kameli and Lösel 1993), *Cucumis sativus* L., *C. melo* L. (snake cucumber), *Cucurbita pepo* L., *Ecballium elaterium* (L.) A. Rich. (Akıncı and Lösel 2009), Soybean (Du *et al.* 2020).
Fructose, glucose accumulation	Durum wheat (Kameli and Lösel 1993), wheat (Abid *et al.* 2018)
Starch accumulation	Cotton (Ackerson and Hebert 1981)
Carbohydrate unchanged	*Artemisia tridentata* (Evans *et al.* 1992)
Sucrose and starch decreasing	Grapevine (Rodrigues *et al.* 1993)
Starch depletion	Wilted bean leaves (Stewart 1971), South African grasses (Schwab and Gaff 1986), cucumber (Akıncı and Lösel 2010), Soybean (Du *et al.* 2020)

complex interactions of respiration rates with other environmental factors and (iii) the presence of a threshold of water stress intensity in which a change in the response of respiration to water stress occurs.

Effect of water deficit stress on glycolysis

Glycolysis is a central metabolic pathway whose main function is to provide ATP, NADH and precursor metabolites for biomass production. In plants, glycolysis is organized as a network of reactions that provide elasticity when production of energy for survival is challenged. Evidence for the participation of glycolytic genes (Roche *et al.* 2007; Watkinson *et al.* 2008; Kim *et al.* 2009; Pan *et al.* 2016), proteins and enzymes (Xu and Huang, 2010a; Ford *et al.* 2011; Oliver *et al.* 2011, Khanna *et al.* 2014b; Khanna *et al.* 2016) in response to stress is established by the fact that their expression is deeply affected by exposure of plant tissues to environmental stresses such as drought. However, different workers quoted different and contrasting results. For instance, genes and proteins related to glycolytic pathway were either down regulated (Kim *et al.* 2009; Xu and Huang, 2010a), up regulated (Roche *et al.* 2007; Ford *et al.* 2011; Oliver *et al.* 2011) or remained unchanged (Watkinson *et al.* 2008, Khanna *et al.* 2016) under water deficit stress. Minhas and Grover, (1999) examined the changes in transcript levels of genes encoding various glycolytic enzymes in response to different abiotic stresses in rice. Selective alterations were noted with respect to triose phosphate isomerase induction in response to desiccation, salt and high temperature stresses, aldolase transcript in response to desiccation and salt stresses, glyceraldehyde-3-phosphate dehydrogenase (GAPDH) transcript in response to salt stress, enolase transcript in response to desiccation stress, glucose phosphate isomerase transcript in response to high temperature stress and pyruvate kinase transcript in response to salt stress. The gene probe corresponding to phosphoglycerate kinase showed no inducibility with respect to all the stresses tested in this work. Velasco *et al.* (1994) also found that dehydration and abscisic acid (ABA) increased mRNA levels and enzyme activity of cytosolic glyceraldehyde-3-phosphate dehydrogenase (GAPDH) in the resurrection plant *Craterostigma plantagineum*. Cytosolic GAPDH was also found to accumulate under dehydration in chickpea (Boominathan *et al.* 2004). However, Garg *et al.* (2010) and Khanna *et al.* (2014b) reported stability in gene expression of GAPDH for different stress series in chickpea. Gao *et al.* (2008) found downregulation of phosphoglycerate kinase (PGK) and NADP-GAPDH genes in chickpea in response to drought stress.

Several recent studies have dealt with protein expression changes in response to drought with the relatively limited number of studies reporting changes in glycolytic enzymes (Table 2). Phosphoglucomutase involved in glycolysis was decreased in leaves of *S. stapfianus* (Oliver *et al.* 2011) and *O. sativa* (Raorane *et al.* 2015) but increased in leaves of *C. lanatus* (Akashi *et al.* 2011), *O. sativa* (Pandey *et al.* 2010) and *M. paradisiaca* (Vanhove *et al.* 2012) in response to drought. Fructose-bisphosphate aldolase (FBPA), another glycolysis-related protein, was found to increase in response to drought in plants such as *O. sativa* (Pandey *et al.* 2010; Raorane *et al.* 2015), *S. stapfianus* (Oliver *et al.*, 2011) and *M. paradisiaca* (Vanhove *et al.* 2012). Besides, FBPA abundance was decreased in drought-sensitive cultivars of *M. domestica* (Zhou *et al.* 2015) and *P. pratensis* (Xu and Huang, 2010b) but was increased in tolerant cultivars. Glycolytic protein, triose-phosphate isomerase (TPI) was also found to be induced in maize (Riccardi *et al.* 1998), rice (Salekdeh *et al.* 2002) and wheat (Ford *et al.* 2011) in response to water stress, whereas a decrease in protein content of TPI was reported in water-stressed *Quercus ilex* plants (Echevarria-Zomeño *et al.* 2009).

From the above ongoing discussion, it could be inferred that genes, proteins and enzymes related to glycolysis are affected differently in different crops under water-deficit stress. The literature contains the contrasting information and the direction of change is also not uniform. The induction of glycolytic proteins/enzymes is thought to be essential for the activation of the entire energy-producing pathway to

Table 2: Summary of studies involving glycolytic enzymes under water-deficit stress.

Crop	Enzymes studied	Reference
Mosses	Desiccation did not affect the specific activities of NAD-GAPDH, PGK and phosphogluco isomerase (PGI) except reduction inNADP-GAPDH activity.	Stewart and Lee (1972)
Pigeonpea	Water stress had no effect on specific activities of PGI, NAD-GAPDH and PGK. However, specific activities of NADP-GAPDH aaldolase were reduced.	Singal *et al.* (1985)
Craterostigma plantagineum	Dehydration increased activity of cytosolic (NAD) GAPDH.	Velasco *et al.* (1994)
Sporobolus stapfianus and *Xerophyta viscosa*	Drying increased the activity of hexokinase.	Whittaker *et al.* (2001)
Mulberry	Water stress decreased the activities of NAD-GAPDH, NADP-GAPDH and PGK.	Thimmanaik *et al.* (2002)
Sporobolus stapfianus	Dehydration increased activities of hexokinase and enolase while phosphofructo kinase (PFK) activity increased only in drought tolerant cultivar and there was no change in activities of aldolase and PK under dehydration.	Whittaker *et al.* (2004)
Cicer arietinum	The activities and transcript levels of most of the glycolytic enzymes were not significantly affected, except the increased activity and transcript level of phoshoglycerate mutase (PGM) and decreased activities and transcript levels of PGK and NADP-GAPDH.	Khanna *et al.* (2014b; 2016)
Wheat	Drought did not affect the activity of PGM, PGI and PFK.	Shokat *et al.* (2020)

maintain homeostasis and activating stress defenses in stressed cells. It may be a mechanism by which plant cells prepare for a demand of ATP and NADH during recovery. On the other hand, the decline in the glycolytic proteins/enzymes is argued as a consequence of overall reduction in biochemical activities of the plant cells under water stress due to slow growth in shoots. Inhibition of glycolysis has also been suggested to be a mechanism for accumulating sugars as an energy source for recovery and fast growth once water is available (Echevarria-Zomeño *et al.* 2009). Such discrepancies can be attributed to specific features of different species and cultivars of crops on which stress is applied; different stages of plant growth and development; different degrees, length and method of imposing water stress; and other environmental conditions of the plants.

Molecular cloning of genes related to glycolytic pathway increases stress tolerance in transgenic plants

Several recent studies have demonstrated that overexpression of glycolytic genes/enzymes confers tolerance to several abiotic stresses. Transgenic yeast cells that overexpress the P.sajor-caju GAPC gene increased their tolerance to cold, salt, heat and drought stresses (Jeong *et al.* 2000). Moreover, the overexpression of GAPDH gene improved salt tolerance in transgenic potato plants (Jeong *et al.* 2001) and transgenic rice (Zhang *et al.* 2011; Lim *et al.* 2021). Zhang *et al.* (2011) also reported that the elevated stress tolerance of *Oryza sativa*-GAPC3-overexpressing plants coincided with the upregulation of several stress-responsive genes, including dehydration responsive element-binding protein (DREB2A), transcriptional inhibitory protein (Lip9) and catalase (catA). Several reports have described that the mRNA accumulation of fructose-1,6-bisphosphate aldolase (FBA) in plants increased in response to high salinity and the chloroplast FBA-overproduced tobacco could improve its salt-tolerance (Yamada *et al.* 2000; Zhang *et al.* 2003). Cloning and characterization of the cytosol FBA gene from *S. portulacastrum* roots showed that the SpFBA was involved in responding to abiotic stimuli such as seawater, NaCl, ABA and polyethylene glycol (PEG) and the SpFBA overproduction promoted the survival ability of the transgenic *Escherichia coli* (Fan *et al.* 2009). The transgenic potatoes with antisense of plastid aldolase gene displayed decreased enzymatic activities of photosynthetic pathway, including, phosphoribulokinase (PRK), sedoheptulose-1,7-biphosphatase (SBPase) and plastid fructose-1,6-bisphosphatase (FBPase) and very low starch synthesis, whereas sucrose synthesis was less strongly inhibited (Haake *et al.* 1998; 1999). Co-overexpression of the rice fructose-1,6-bisphosphate aldolase (FBA), spinach triosephosphate isomerase (TPI) and wheat FBPase genes could significantly improve the photosynthetic yield in transgenic cells via stimulating sedoheptulose-1,7-bisphosphatase (SBPase) activity and consequently accelerating the ribulose-1,5-bisphosphate (RuBP) regeneration rate (Ma *et al.* 2007). OsPGK is differentially regulated in contrasting genotypes of rice under salinity stress and its overexpression provides salinity tolerance to transgenic tobacco (Joshi *et al.* 2016).

CONCLUSION

From the above ongoing discussion, it could be concluded that water-deficit stress is one of the chief abiotic stresses affecting plant endurance leading to serious effects on cellular metabolism and is an important subject of study. Exposure of plants to drought causes substantial water loss within the plant and therefore causes a drop in its relative water content and leaf water potential. Plants accumulate different kinds of organic and inorganic solutes to lower osmotic potential thereby maintaining cell turgor. Drought stress also causes a change in the content of photosynthetic pigments adversely affecting the process of photosynthesis. Elucidation of biochemical, metabolic and molecular changes due to water deficit is an interesting area of research and one important aspect would be the identification and characterization of the carbohydrate metabolic pathway because changes in carbohydrate composition are in straight association with physiological processes such as photosynthesis, translocation and respiration. Respiratory pathway has significant role in providing energy to the cell for its diverse metabolic activities. Water stress has been reported to either decrease or maintain or increase the rate of respiration - the process which is divided into three major pathways: glycolysis, mitochondrial tricarboxylic acid cycle and mitochondrial electron transport. Glycolysis, a fermentative pathway of respiration, is the primary mode of sustained ATP production for meeting the energy demands of metabolic activities under stress conditions. The impact of water deficit on glycolytic pathway is still far from clear; with reports in the literature comprising contradictory observations. Despite the studies that have tried to understand the regulation of glycolysis, the role that this pathway plays in drought stressed plants is unknown due to inconsistencies in the reports. Therefore, further studies are needed to understand the mechanism modulating plant growth under stress.

Conflict of interest: None.

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