P-ISSN: 2305-6622; E-ISSN: 2306-3599
International Journal of
Agriculture and Biosciences
www.ijagbio.com; editor@ijagbio.com

Review Article

Proteins Involved in the Molecular Mechanisms of Plant Photosynthesis under Drought Stress

Marouf Khalili* and Mohammad Reza Naghavi

Assistant Professors, Department of Agriculture, Payame Noor University, P. O. Box 19395-3697 Tehran, Iran
***Corresponding author:** makhalily@yahoo.com

Article History: Received: August 14, 2016 Revised: December 12, 2016 Accepted: December 23, 2016

ABSTRACT

Drought affects morphological, physiological, biochemical and molecular processes in plants resulting in growth inhibition, stomata closure with consecutive reduction of transpiration, decrease in chlorophyll content and inhibition of photosynthesis and protein changes. Important stages of photosynthesis are the light reactions of photosynthesis, Calvin cycle and starch biosynthesis that each of them have important molecular into self-processes. Recognize and study of these proteins and molecular are important for breeding programs. Proteomics is a potent tool for understanding basic processes in plant growth and development, as well as for examining changes in specific proteins in response to environmental fluctuations. By analyzing differentially expressed proteins under drought conditions we sought deeper knowledge, attempted to identify key protein-encoding genes that could be used as candidate marker protein and drought stress responsible proteins have been analyzed in plant. So, study and understanding of molecular pathway in plantcell such as these pathways into chloroplast and related to photosynthesis have a high importance.

Key words: Drought stress, Energy production, Molecular mechanism, Photosynthesis

INTRODUCTION

Drought is the most severe stress and the main cause of significant losses in growth, productivity of crop plants, and finally their yields (Ludlow and Muchow, 1990). Drought affects morphological, physiological, biochemical and molecular processes in plants resulting in growth inhibition, stomata closure with consecutive reduction of transpiration, decrease in chlorophyll content and inhibition of photosynthesis and protein changes (Lawlor and Cornic, 2002; Yordanov *et al*., 2003) to cope with osmotic changes in their tissues. Among the factors that contribute to this photosynthesis reduction, stomatal closure can be considered as a direct response to leaf water potential reduction induced by drought (Santos *et al*., 2004; Santos *et al*., 2006). During exposure to drought stress carbon metabolism and relations between sink and source organs are perturbed, as well as the metabolism of elements that are normally absorbed with water. Cellular responses include osmotic adjustment, regulation of water circulation (aquaporins), protection or degradation of proteins, and protection against oxidative stress (Kramer, 1980).So, when plants were subjected to drought stress, a number of physiological and morphological responses were observed and the magnitude of the response varies among species and between varieties within a crop species (Kramer, 1980). The response to drought was an increased level of a bscisic acid, the accumulation of unusual metabolites such as proline and polyamines, alterations in activity of certain enzymes and the induction of a specific set of genes (Skriver and Mundy, 1990). Drought stress is known to reduce photosynthetic rate and the extent of this decrease depends on osmotic adjustment and genotypic differences (Arnau *et al.*, 1997). On the other hands, Riccardi *et al.*, (2004) have demonstrated that plant response to water deficit shows some genetic variations. Water stress tolerance has been documented in almost all plants but its extent varies from species to species (Chaitanya *et al.*, 2003). Crop plants which can use water most efficiently and maintain acceptable yields are perspective regarding their tolerance. Drought tolerance is a complex trait where several characteristics influence plant success during vegetation period (Ingram and Bartels, 1996). It is achieved by modulation of gene expression and accumulation of specific protective proteins and metabolites (Reddy *et al.*, 2004; Zang and Komatsu, 2007). Proteomics is a potent tool for understanding basic processes in plant growth and

Cite This Article as: Khalili M, and MR Naghavi, 2017. Proteins involved in the molecular mechanisms of plant photosynthesis under drought stress. Inter J Agri Biosci, 6(1): 42-48. www.ijagbio.com

development, as well as for examining changes in specific proteins in response to environmental fluctuations. By analyzing differentially expressed proteins under drought conditions we sought deeper knowledge, attempted to identify key protein-encoding genes that could be used as candidate marker protein (Peng *et al.,* 2009). Using proteomics technique, drought stress responsible proteins have been analysed in plant (Ali and Komatsu, 2006). The results suggested that actin depolymerizing factor was one of the target proteins expressed in leaf blades, leaf sheaths and roots under drought stress but not under cold and salt stresses and/or abscisic acid treatment. The proteomics of drought stress acclimation has been done with the conclusion that proteins contributing to basic carbon metabolism were significantly increased (Fulda *et al.,* 2011). The leaf apoplast was examined as a compartment, which sensitively and differentially responds to drought and salinity with consequences for plant growth (Ramanjulu *et al.,* 1999). The more drought tolerant genotype had control stomata function to allow carbon fixation at stress thus improving water use efficiency and photosynthetic capacity (Yordanov *et al.,* 2000).

So, drought stress effect on the different part of plant cellular that recognize of molecular process into this steps is important for identification of types of proteins that are candidate to tolerant under drought stress. Generally, grouping of proteins in studies of proteomics that in present study was described according to importance of them follow.

The Light reactions of photosynthesis

Chloroplasts are organelles for photosynthesis. Chloroplasts also participate in the amino acid, vitamin, isoprenoid, and lipid biosynthesis, as well as reduction of nitrite and sulfate (vanWijk, 2000; Baginsky and Gruissem, 2004). A previous study has proposed that there are∼3000 proteins in mature chloroplasts that have specialized distributions and functions (Leister, 2003). Chlorophyll binding proteins are synthesized as precursor molecules in the cytoplasm and imported into the chloroplast where they are inserted in the thylakoid membranes (Bassi *et al.,* 1997). They have several functions including light harvesting, energy dissipation and pigment storage. As components of the light harvesting complexes in plants, the primary functions of chlorophyll a/b binding proteins is the absorption of light and the transfer of the excitation energy to the photochemical reaction centers (Bassi *et al.,* 1997; Ganeteg *et al.,* 2001). In some cases, plants are exposed to higher light intensities than used in photosynthesis. Therefore, to prevent photo inhibition and damage to the photosynthetic machinery, excess energy is then dissipated by these light-harvesting proteins. In addition, chlorophyll a/b binding proteins are believed to have a function in pigment storage (Bassi *et al.,* 1997). Hydrogen ions are also released in the process, creating a transmembrane chemiosmotic potential that is utilized by ATP syntheses during ATP synthesis Photolysis of water occurs in the oxygen-evolving complex (OEC) of Photosystem II (PSII) reaction centers (McEvoy and Brudvig, 2006; Sproviero *et al.,* 2007). The OEC is composed of four manganese ions, calcium and possibly chloride ions, which are bound to extrinsic proteins (McEvoy and Brudvig, 2006). Photosystem II OEC proteins are involved in retaining calcium and chloride ions, two inorganic cofactors for the water-splitting reaction (Ifuku *et al.,* 2005). The oxygen evolving enhancer protein is believed to have a dual function; (i) optimizing the manganese cluster during photolysis and (ii) protecting the reaction centre proteins from damage by oxygen radical formed in light (Heide *et al.,* 2004). In plants, this enzyme exists in two different forms; photosynthetic and heterotrophic forms, which are encoded for by different genes and may be associated with different metabolic pathways (Gummadova *et al.,* 2007). Ferrodoxin-NADP oxidoreduct as escatalyse the reversible electron transfers between one electron carrier systems (ferrodoxin) and the two-electron carrying NADP (H) (Thomas *et al.,* 2006). In chloroplasts, the main physiological function of this enzyme is to catalyze the final step of the photosynthetic electron transport, providing NADPH, which is then utilized in the carbon fixation step of the Calvin cycle (Arakaki *et al.,* 1997). Also, FNRs are involved in the photosynthetic machinery where electrons are transferred from ferredoxins or flavodoxins to NADPH and are also implicated in protection against ROS (Caruso *et al.,* 2008). In fact, isoforms of FNRs are assigned to a number of functions with differing catalytic properties (Moolna and Bowsher, 2010). In the Figure 1 general scheme of the light reactions of photosynthesis was showed.

As plants are exposed to a water deficit the absorbed light energy through the photosynthetic pigments exceeds its rate of consumption through the Calvin cycle (through decreases in proteins involved in the Calvin cycle), leading to photo-damage to the photosynthetic machinery, particularly the photosystem II (PSII) reaction center core proteins D1 and D2 (Aro *et al.,* 1993).Plants have evolved several mechanisms to avoid damage to the photosynthetic machinery such as antenna modulations; decreasing the size of antennae to reduce the amount of absorbed light (Eberhard *et al.,* 2008) is one mechanism that proteins in the antennae of the photosystems are the light-harvesting complex proteins (LHC).Other proteins changing within the photosynthesis machinery category are the extrinsic subunits of the PSII complex, known as oxygen-evolving complex (OEC) proteins, that are involved in the stabilization of the PSII complex (Ifuku *et al.,* 2008) and its impairment is proposed to be the rate limiting step in the photo-damage process to the PSII (Takahashi and Murata, 2008).On the other hands, HCF136, a protein that is essential for the repair and assembly of the PSII complex (Plucken *et al.,* 2002), decreased at under drought stress decreased (Ford *et al.,* 2011).

The Calvin cycle

Water deficiency leads to stomatal closure in leaves; thereby, decreasing the carbon dioxide flow into leaves and inducing the increased hydrolysis of starches and accumulation of sugars as well as the decreased output of photosynthetic products. All of these changes result in decreased photosynthesis (Lawlor and Cornic, 2002). During photosynthesis, light energy absorbed by the photosynthetic pigments in the chloroplasts is converted to chemical energy through the photosynthesis machinery

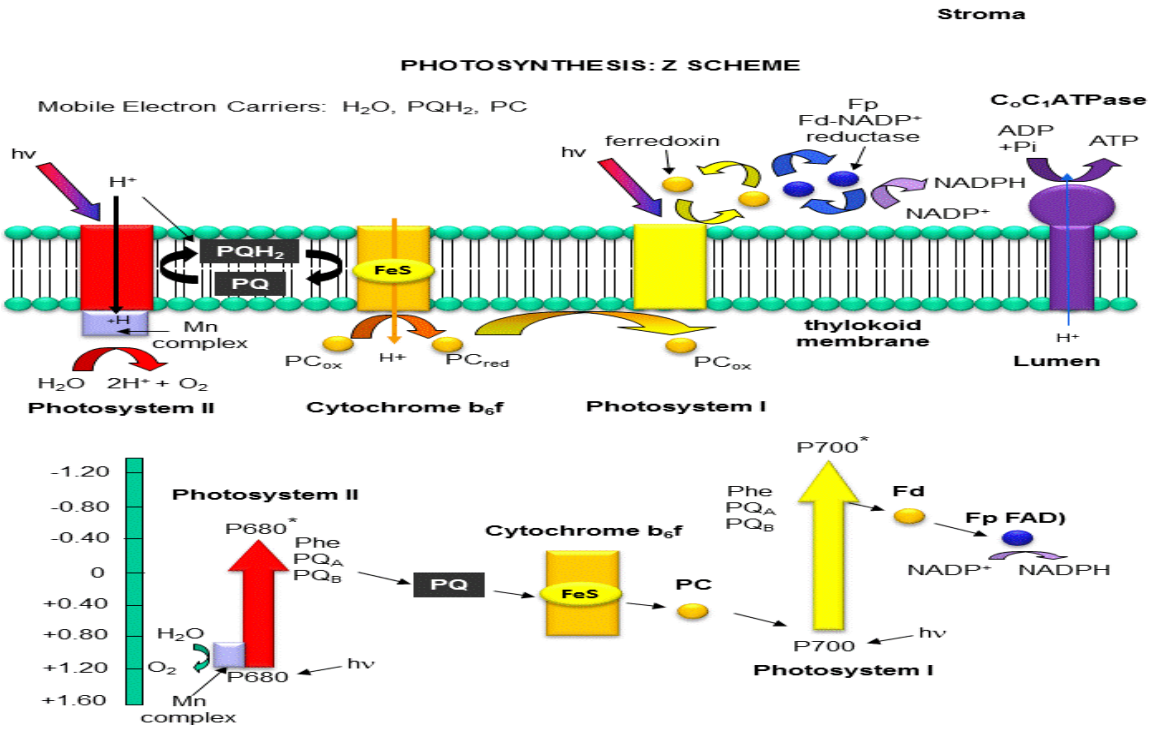

Fig. 1: Molecular process into the light reactions of photosynthesis.

with this chemical energy used for CO2 fixation in the Calvin cycle. Under a water deficit, the CO2 concentration in leaves decreases due to stomatal closure (Kaiser and Kappen, 1997) leading to a corresponding decrease in the activities of enzymes involved in Calvin cycle (Chaves et al., 2002). The Calvin cycle (also termed the reductive pentose phosphate pathway) is a metabolic pathway that produced pentose sugars (Heldt, 1997). The Calvin cycle, which consists of carboxylation, reduction and renewal phases, is the primary pathway of photosynthesis in plants. The cycle is characterized by three phases; the carboxylation, reduction and regeneration phases (Spreitzer and Salvucci, 2002). Rubisco, an enzyme involved to carbon dioxide fixation in photosynthesis, that a multimeric enzyme with two subunits; large (50-55 kDa) and small (12-18 kDa). Larg subunit of Rubisco has a catalytic subunit and small subunit is regulative (Andersson and Backlund, 2008). The key photosynthetic enzyme in plants is Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) which takes part in CO2 fixation and photorespiration (Bowes and Ogren, 1972). This enzyme is localized in the chloroplast stroma. Rubisco accounts for about 30-60% of the total soluble protein in plants. The enzyme constitutes a large pool of stored leaf nitrogen (20-30%) that can be quickly remobilized under stress and senescence (Kaiser *et al.*, 1987).

Generally, drought induces metabolic changes related to protein turnover (alterations in protein synthesis, maintaining the level of some proteins or protein degradation) (Bray, 1997). In accordance with Medrano *et al.*, (1997) the amount of Rubisco protein is slightly affected by moderate and even prolonged severe drought. Some data about a reduction in Rubisco amount in stressed plants also exist (Chaves *et al.*, 1991). Both the synthesis and assembly of Rubisco depend on two genomes. The RLS (Rubisco Large Subunit) are encoded by a single chloroplast gene whereas RSS (Rubisco Small Subunit) are encoded by a small family of nuclear genes (Musrati *et al.*, 1998). The correct folding of the RLS requires chaperonin system consisting of Rubisco binding protein (RBP) or cpn60 (the analog of GroL) and cochaperon in cpn10 (the analog of GroES). The Rubiscoholo enzyme assembly in chloroplast stroma is an ATP-dependent process (Kaiser *et al.*, 1987). Skriver and Mundy (1990) indicate that the level of cpn 60 is coordinated positively with that of Rubisco under normal conditions. Very limited data are available to date concerning the response of cpn 60 to stress conditions, especially to drought (Musrati *et al.*, 1998). Down regulation of Rubisco large subunit has been observed in drought stressed susceptible wheat lines (Demirevska *et al.*, 2009) showing its involvement in drought tolerance mechanism. Drought induced the decrease in rubisco binding protein content at the leaf level in alfalfa (Aranjuelo *et al.*, 2010). In maize leaves, the response to water deficit showed genetic variation. Some increased proteins were induced specifically in one of the two studied genotypes while others were significantly induced in both genotypes but to a different level or with different kinetics (Riccardi *et al.*, 2004). The activity of Rubisco is regulated by Rubisco activase protein (RA) that possesses ATPase activity (Kaiser *et al.*, 1987). The function of RA is to remove tightly bound sugar phosphates from the active centers of Rubisco. It is considered that RA protein is not a conventional enzyme and belongs to the ATPase family associated with various cellular activities (AAA^+ proteins), a class of chaperone-like proteins acting on other macromolecules and catalyzing mechanical processes, such as assembly, operation and disassembly of protein complexes (Martin and Smith, 1995). There are converse data about the abundance of RA under drought

conditions (Salekdeh *et al.*, 2002). RA protects chloroplast protein synthesis from drought stress as a chaperone. Chaperons like RBP and RA might associate to each other by protein-protein interactions facilitating directly Rubisco assembly and activation or promoting different processes (Ramanjulu *et al.*,1999). Inhibitory effects of environmental stresses on photosynthetic machinery of plants are well established; among these stresses drought is of particular importance (Nogues and Baker, 2000; Flexas and Medrano, 2002). Although RuBis CO, a central enzyme in the photosynthetic machinery, would be expected to be down-regulated due to the inhibition of photosynthesis in response to drought stress, previous studies showed contradictory results. Some researchers reported its up-regulation (Caruso *et al.*, 2008; Ge *et al.*, 2012), whereas others found down-regulation (Gao *et al.*, 2011) or even both (Guo *et al.*, 2012) in response to abiotic stresses such as drought and salinity.

In response to drought, closure of stomata to reduce water loss simultaneously leads to reduction in CO2 assimilation. At low CO2 to O2 ratios RuBisCO, the key enzyme of the Calvin cycle, switches to its oxygenase activity a process known as photorespiration (Nogues and Baker, 2000; Wingler *et al.*, 2000). As a result, an up-regulation in RuBisCO levels may also indicate an increase in the photorespiration rate which may be the case for the drought sensitive genotype (Salekdeh *et al.*, 2002; Ge *et al.*, 2012). Although this energy depleting process is generally considered as damaging to plants, photorespiration may prevent over reduction and, thus, photo-inhibition of photosystem II, thereby protecting the photosynthetic electron transport chain (Wingler *et al.*, 2000).

Based on the primary product of carbon fixation, plants are classified as C3 and C4 species. Oxaloacetate (a four-carbon compound) and 3-phosphoglycerate (a three-carbon compound) are the primary products of carbon assimilation in the C4 and C3 plants, respectively. Functionally, RuBisCO proteins catalyse carbon fixation (carboxylation) reactions in the Calvin cycle of photosynthetic plants. In this process, ribulose 1,5-bisphosphate (RuBP), a 5-carbon compound serves as an acceptor molecule for CO2 to form an unstable 6-carbon compound. The 6-carbon intermediate compound immediately breaks down, forming two molecules of 3-phosphoglycerate (3PGA) (Tabita *et al.*, 2007; Andersson and Backlund, 2008). The end product of this carboxylation reaction, 3PGA, is phosphorylated by ATP to form 1,3-biphosphoglycerate and ADP. This reaction in catalysed by a cytosolic 3-phosphoglycerate kinase. GAPDH plays a key role in reducing glycerate 3-phosphate into glyceraldehyde-3-phosphate. The latter is not only a photosynthetic product but also the substrate of ribulose 5-phosphate. The above reaction is one of the two that occur in the second phase (reduction phase) of the Calvin cycle (Macdonald and Buchanan, 1997). In the third phase, RuBP molecules are regenerated to allow the first carbon fixation step to occur. The regeneration phase is characterized by a series of enzymatic reactions that convert triose phosphate to RuBP (Macdonald and Buchanan, 1997). Together with others, these two enzymes catalyze reactions, which ultimately result in the formation of ribulose-5-phosphate. The ribulose-5-phosphate is then phosphorylated to form RuBP by phosphoribulokinase. To complete the cycle, RuBP is then used as a substrate by RuBisCo in the first phase of carbon fixation. Some of the triose phosphate produced in the Calvin cycle is used for sucrose and starch biosynthesis (Raines, 2003; Tamoi *et al.*, 2005). Fructose-1,6-bisphosphatase, which catalyzes fructose-1,6-diphosphate to fructose-6- phosphate, plays an important regulatory role in the Calvin cycle and the transportation of photosynthetic intermediates (Kiddle *et al.*, 1999). In the Calvin cycle, transketolase catalyzes glycerate 3-

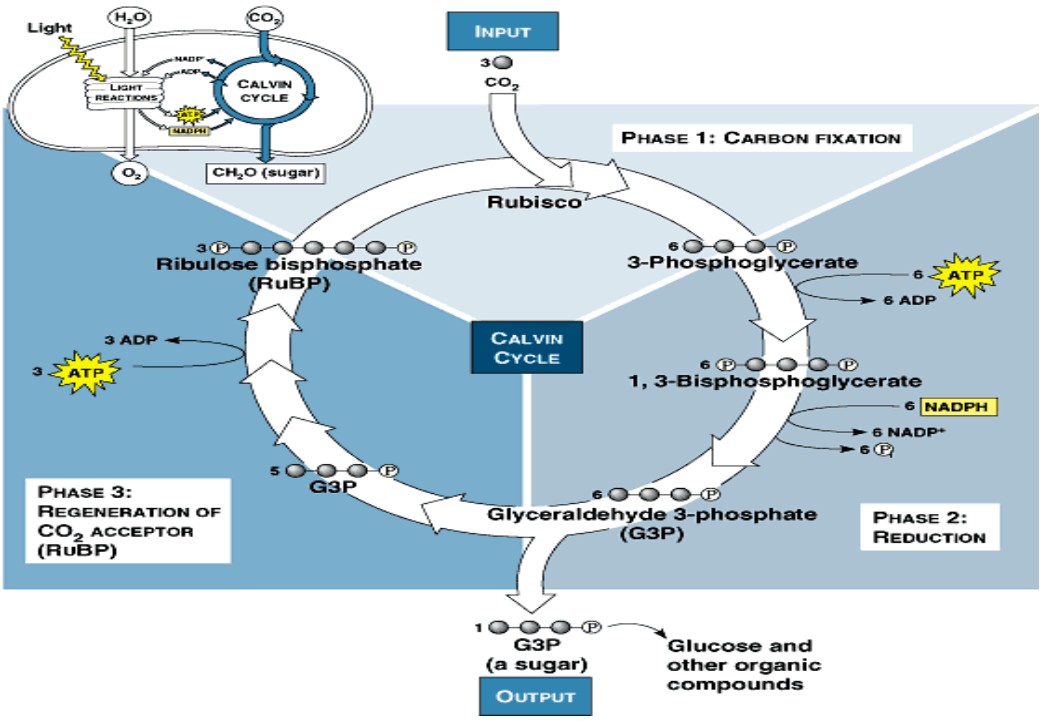

Fig. 2: Molecular process into the Calvin cycle of photosynthesis

phosphate and fructose-6-phosphate into xylose-5-phosphate and erythrose-4 in ribulose-1,5-bisphosphate carboxylase/oxygenase in hydrogen peroxide-stressed young rice leaves. Triosephosphate isomerase, an enzyme involved in isomerisation of dihydroxyacetone phosphate and D-glyceraldehyde-3-P has been reported to be down regulated under drought stress in wheat (Xue *et al.*, 2008). In the Figure 2 general scheme of Calvin cycle of photosynthesis have showed.

Starch biosynthesis

Starch is an important storage polysaccharide in plants, providing an energy source for various metabolic processes (Kruger, 1997). Starch synthesis involves three enzymes; adenosine diphosphate glucose pyrophosphatase (AGPase), a starch synthase and a branching enzyme (Guan and Keeling, 1998). Plant AGPases are tetrameric in structure, being composed of two different subunits, which are products of different genes. The small and large subunits have a subunit MW range of 50-54 kDa and 51-60 kDa respectively (Preiss, 1997). AGPasescatalyse the formation of ADP-glucose and inorganic pyrophosphate from ATP and glucose-1-phosphate (Boehlein *et al.*, 2005). The end product of this reaction, ADP glucose is a precursor for starch synthesis (Tetlow *et al.*, 2003). Starch synthase then transfers the glucose from ADP-glucose to the non-reducing end of a growing acceptor chain thus elongating the α-1,4glucan chains. In the third step, the starch branching enzyme then cleaves an elongated α-1,4 glucan chain simultaneously transferring it to an acceptor chain to form!-1,6 linkages (Guan and Keeling, 1998).

Malate/oxaloacetate shuttling system

Plant cells are known to contain multiple isoforms of MDHs, which differ in co-enzyme specificity, subcellular localization and biological function (Minarik *et al.*, 2002; Ding and Ma, 2004). In plants, five different classes of MDHs are present; (i) chloroplast NADP-dependent MDH; (ii) mitochondrial NAD-dependent MDH; (iii) micro body NAD-dependent MDH; (iv) chloroplast NAD-dependent MDH and (v) cytosolic NAD dependent MDH (Ding and Ma, 2004). These enzymes occur as homodimers, with subunit MW ranging between 32-37 kDa for the NAD-dependent MDH and 42-43 for the NADP dependent MDHs (Ding and Ma, 2004). Generally, MDHs catalyse the interconversion of oxaloacetate and malate using the NAD/NADP coenzyme system (Minarik *et al.*, 2002). So, Malate dehydrogenase is an important enzyme of cellular metabolism and it catalyzes the conversion of oxaloacetate and malate (Musrati *et al.*, 1998). However, different isoforms in different subcellular locations are thought to have different functions. For example, the chloroplastic NADP-dependent MDH forms part of a malate valve system (Scheibe, 2004), which converts excess NADPH into malate and transports in from the chloroplast into the cytosol (Fridlyand *et al.*, 1998). Therefore, it is highly probable that the chloroplastic NADP-dependent MDH identified in this study might have a function in balancing reducing equivalents between the cytosol and the chloroplast stroma. In C4 plants such as sorghum and maize, this chloroplastic NADP134 dependent MDH isoform may have an additional role in the synthesis of malate, which is transported into the chloroplast of bundle sheath cells and takes part in carbon fixation (Ding and Ma, 2004). On the other hand, cytoplasmic NAD-dependent MDH isoforms are less well characterized with limited structural and functional information being known. Nevertheless, a cytoplasmic NAD-dependent MDHs was isolated from wheat (TaMDH). (Ding and Ma, 2004). Since the cytoplasmic NAD-dependent MDH isoforms were shown to be present in different plants tissues (Ding and Ma, 2004), they are proposed to have housekeeping functions in plant metabolism. However, their actual physiological functions and mechanism of action are yet to be elucidated.

Conclusion

Photosynthesis have different stages that each of them involved with different molecular and proteins. Proteomics help to us for the recognize of candidate proteins that have important role between tolerant and susceptible genotype. So, study and understanding of molecular pathway in cell plant such as these pathways into chloroplast and related to photosynthesis have high importance.

REFERENCES

Ali GM and S Komatsu, 2006. Proteome analysis of rice leaf sheath during drought stress. J Proteome Res, 5: 396-403.

Andersson I and A Backlund, 2008. Structure and function of Rubisco. Plant Physiol Biochem, 46: 275-291.

Aranjuelo I, G Molero, G Erice, JC Avice and S Nogues, 2010. Plant physiology and proteomics reveals the leaf response of drought in alfalfa (*Medicago sativa* L.). J Exp Bot, 62:111-123.

Aro EM, I Virgin and B Andersson, 1993.Photoinhibition of photosystem-II–inactivation, protein damage and turnover.BiochemBiophysActa, 1143: 113-134.

Baginsky S and W Gruissem, 2004. Chloroplast proteomics: potentials and challenges. J Exp Bot, 55: 1213-1220.

Boehlein SK, AK Sewell, J Cross, JD Stewart and LC Hannah, 2005. Purification and characterization of adenosine diphosphate glucosepyrophosphorylase from maize/potato mosaics. Plant Physiol, 138: 1552-1562.

Bowes G and WL Ogren, 1972.Oxygen inhibition and other properties of soybean ribulose 1, 5-diphosphate carboxylase. J Biol Chem, 247: 2171-2176.

Caruso G, C Cavaliere, C Guarino, R Gubbiotti, P Foglia and A Lagana, 2008. Identification of changes in *Triticum durum* L. leaf proteome in response to salt stress by two-dimensional electrophoresis and MALDI-TOF mass spectrometry. Analytical Bioanalytical Chem, 391: 381-390.

Chaitanya KV, D Sundar, PP Jutur and Reddy A Ramachandra, 2003. Water stress effects on photosynthesis in different mulberry cultivars. Plant Growth Regul, 40: 75-80.

Chaves MM, 1991. Effect of water deficits on carbon assimilation. J Exp Bot, 42: 1-16.

Chaves MM, Pereira JS, Maroco J, ML Rodrigues, CPP Ricardo and ML Osorio, 2002. How plants cope with water stress in the field? Photosynthesis and growth. Anal Bot Water Stress, 89: 907-916.

Demirevska K, D Zasheva, R Dimitrov, L Simova-Stoilova, M Stamenova and U Feller, 2009. Drought stress effects on Rubisco in wheat: changes in the Rubisco large subunit. Acta Physiol Plant, 31: 1129-1138.

Ding Y and QH Ma, 2004. Characterization of a cytosolic malate dehydrogenase cDNA which encodes an isozyme toward oxaloacetate reduction in wheat.Biochimie, 86: 509-518.

Eberhard S, G Finazzi and FA Wollman, 2008.The dynamics of photosynthesis. Ann Rev Genet, 42: 463-515.

Flexas J and H Medrano, 2002. Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited. Ann Bot, 89: 183-189.

Ford KL, A Cassin and A Bacic, 2011. Quantitative proteomic analysis of wheat cultivars with differing drought stress tolerance. Plant Sci, 2: 1-11.

Fridlyand LE, JE Backhausen and R Scheibe, 1998. Flux control of the malatevalve in leaf cells. Arch Biochem Biophys, 349: 290-298.

Fulda S, S Mikkat, H Stegmann and R Horn, 2011. Physiology and proteomics of drought stress acclimation in sunflower (*Helianthus annus* L.). Plant Biol, 13: 632-642.

Ganeteg U, A Strand, P Gustafsson and S Jansson, 2001. The properties of the chlorophyll a/b-binding proteins Lhca2 and Lhca3 studied *in vivo* using antisense inhibition. Plant Physiol, 127: 150-158.

Heide H, HM Kalisz and H Follmann, 2004. The oxygen evolving enhancer protein 1 (OEE) of photo system II in green algae exhibits thioredoxin activity. J Plant Physiol, 161: 139-149.

Gao L, X Yan, X Li, G Guo, Y Hu, W Ma and Y Yan, 2011. Proteome analysis of wheat leaf under salt stress by two-dimensional difference gel electrophoresis (2D-DIGE). Phytochem, 72: 1180-1191.

Ge P, C Ma, S Wang, L Gao, X Li, G Guo, W Ma and Y Yan, 2012.Comparative proteomic analysis of grain development in two spring wheat varieties under drought stress. Analytical and Bioanalytical Chemistry, 402:1297-1313.

Guan HP and PL Keeling, 1998. Starch Biosynthesis: Understanding the functions and interactions of multiple isoenzymes of starch synthase and branching enzyme.Trends Glycosci Glycotechnol, 10: 307-319.

Gummadova JO, GJ Fletcher, A Moolna, GT Hanke, T Hase and CG Bowsher, 2007. Expression of multiple forms of ferredoxin $NADP^+$oxidoreductase in wheat leaves. J Exp Bot, 58: 3971-3985.

Guo G, P Ge, C Ma, X Li, D Lv, S Wang, W Ma and Y Yan, 2012. Comparative proteomic analysis of salt response proteins in seedling roots of two wheat varieties. J Proteomics, 75: 1867-1885.

Ifuku K, S Ishihara, R Shimamoto, K Ido and F Sato, 2008.Structure, function and evolution of the PsbP protein family in higher plants. Photosynthesis Res, 98: 427-437.

Ifuku K, T Nakatsu, R Shimamoto, Y Yamamoto, S Ishihara, H Kato and F Sato, 2005.Structure and function of the PsbP protein of photosystem II from higher plants. Photosynthesis Res, 84: 251-255.

Ingram J and D Bartels, 1996.The molecular basis of dehydration tolerance in plants. Annual Review of Plant Physiol Plant Mol Biol, 47: 377-403.

Kaiser WM, 1987. Effects of water deficit on photosynthetic capacity. Physiol Plant, 71:142-9.

Kellogg EA and ND Juliano, 1997.The structure and function of RuBisCo and their implications for systematic studies. American J Bot, 84: 413-428.

Kiddle G, R Bennett, A Hick and R Walls grove, 1999. C-S lyase activities in leaves of crucifers and non-crucifers, and the characterization of three classes of C-S lyase activities from oilseed rape (*Brassica napus*L.). Plant, Cell Environ, 22: 433-445.

Kramer PJ, 1980.Drought stress and the origin of adaptations. In: Turner NC, Kramer PJ. (eds.) Adaptation of plants to water and high temperature stress. Wiley, New York, pp: 7-20.

Kruger NJ, 1997.Carbohydrate synthesis and degradation. In: Dennis DT Turpin, DH, Lefebvre DD, Layzell DB. (eds.), Plant Metabolism (2nd ed.), Essex: Addison Wesley Longman, pp: 83-104.

Lawlor D and G Cornic, 2002.Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant, Cell Environ, 25: 275-94.

Leister D, 2003. Chloroplastre search in the genomicage. Trends Genetics, 19: 47-56.

Ludlow MM and RC Muchow, 1990. A critical evaluation of traits for improving crop yields in water-limited environments. Adv Agron, 43: 107-153.

Macdonald FD and BB Buchanan, 1997.The reductive pentose phosphate pathway and its regulation. In: Dennis DT, Turpin DH, Lefebvre DD, Layzell DB (eds.), Plant Metabolism (2nd ed.). Essex: Addison Wesley Longman, pp: 299-313.

Martin C and AM Smith, 1995. Starch biosynthesis. Plant Cell, 7: 971-985.

McEvoy JP and GW Brudvig, 2006.Water-splitting chemistry of photosystem II. Chemical Reviews, 106: 4455-4483.

Moolna A and CG Bowsher, 2010.The physiological importance of photosynthetic ferredoxin NADP oxidoreductase (FNR) iso forms in wheat. J Exp Bot, 6110: 2669-2681.

Musrati RA, M Kollarova, N Mernik and D Mikulasova, 1998. Malate dehydrogenase: distribution, function and properties. General Physiology and Biophysics, 17: 193-210.

Nogues S and NR Baker, 2000. Effects of drought on photosynthesis in Mediterranean plants grown under enhanced UV-B radiation. J Exp Bot, 51: 1309-1317.

Peng Z, M Wang, F Li, H Lv, C Li and G Xia, 2009.A proteomic study of the response to salinity and drought stress in an introgression strain of bread wheat.Mol Cellular Proteomics, 8: 2676-86.

Plucken H, B Muller, D Grohmann, P Westhoff and LA Eichacker, 2002. The HCF136 protein is essential for assembly of the photo system II reaction center in *Arabidopsis thaliana*. FEBS Letters, 532: 85-90.

Preiss J, 1997. Modulation of starch synthesis. In: Foyer CH, Quick WP. (eds.), A molecular Approach to Primary Metabolism in Higher plants. London: Taylor and Francis Publishers, pp: 81-104.

Raines CA, 2003. The Calvin cycle revisited. Photo synthesis Res, 75: 1-10.

Ramanjulu S, W Kaiser, KJ Dietz, 1999. Salt and drought stress differentially affect the accumulation of extracellular proteins in barley, Zeitschriftfür Natur for schung C-A J Biosci, 54: 337-347.

Reddy AR, KV Chaitanya and M Vivekanandan, 2004. Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J Plant Physiol, 161: 1189-1202.

Riccardi F, P Gazeau, MP Jacquemot, D Vincent and M Zivy, 2004.Deciphering genetic variation of proteome responses to water deficit in maize leaves. Plant Physiol Biochem, 42: 1003-1011.

Salekdeh GH, J Siopongco, LJ Wade, B Ghareyazie and J Bennett, 2002. Proteomic analysis of rice leaves during drought stress and recovery. Proteomics, 2: 1131-1145.

Santos, MG, RV Ribeiro, RF Oliveira, EC Machado and C Pimentel, 2006.The role of inorganic phosphate on photosynthesis recovery of common bean after a mild drought deficit. Plant Sci Clare, 170: 659-64.

Santos MG, RV Ribeiro, RF Oliveira and C Pimentel, 2004. Gas exchange and yield response to foliar phosphorus application in *Phaseolus vulgaris* L. under drought stress. Brazilian J Plant Physiol Londrina, 16:171-9.

Scheibe R, 2004. Malate valves to balance cellular energy supply. Physiologia Plantarum, 120: 21-26.

Skriver K and J Mundy, 1990.Gene expression in response to a bscisic acid and osmotic stress. Plant Cell, 2:503-512.

Spreitzer RJ and ME Salvucci, 2002.Rubisco: structure, regulatory interactions, and possibilities for a better enzyme. Ann Rev Plant Biol, 53:449-475.

Sproviero EM, JA Gascon, JP McEvoy, GW Brudvig and VS Batista, 2007.Quantum mechanics/molecular mechanics structural models of theoxygen-evolving complex of photo system II. Cur Opinion Structural Biol, 17: 173-180.

Tabita FR, TE Hanson, H Li, S Satagopan, J Singh and S Chan, 2007.Function, structure, and evolution of the RubisCO-like proteins and their RubisCO homologs. Microbiol Mol Biol Rev, 71: 576-599.

Takahashi S and N Murata, 2008. How do environmental stresses accelerate photo inhibition? Trends Plant Sci, 13: 178-182.

Tamoi M, M Nagaoka, Y Yabuta and S Shigeoka, 2005.Carbon metabolism in the Calvin cycle. Plant Biotechnol, 22: 355-360.

Tetlow IJ, EJ Davies, KA Vardy, CG Bowsher, MM Burrell and MJ Emes, 2003.Subcellular localization of AD Pglucosepyrophosphorylase in developing wheat endosperm and analysis of the properties of a plastidial isoform. J Exp Bot, 54: 715-725.

Thomas JC, B Ughy, B Lagoutte and G Ajlani, 2006. A second isoform of the ferredoxin: NADP oxidoreductase generated by an in-frame initiation oftranslation. Proceeding of National Academy of Science USA, 103: 18368-18373.

VanWijk JK, 2000. Proteomics of the chloroplast: experimentation and prediction. Trends Plant Sci, 5: 420-425.

Wingler A, PJ Lea, WP Quick and RC Leegood, 2000. Photorespiration: metabolic pathways and their role in stress protection. Philosophical Transactions of the Royal Society B: Biol, 355: 1517-1529.

Xue G-P, CL Mcintyre, D Glassop and R Shorter, 2008.Use of expression analysis to dissect alterations in carbohydrate metabolism in wheat leaves during drought stress. Plant Mol Biol, 67: 197-214.

Yordanov I, V Velikova and T Tsonev, 2000.Plant responses to drought, acclimation and stress tolerance. Photosynthetica, 38: 171-186

Yordanov I, V Velikova and T Tsonev, 2003. Plant responses to drought and stress tolerance. Bulgarian J Plant Physiol, Special Issue, 3: 187-206.

Zang X and S Komatsu, 2007.A proteomic approach for identifying osmotic-stress-related proteins in rice. Phytochem, 68: 426-437.