

ROLE OF SUGARS, AMINO ACIDS AND ORGANIC ACIDS IN IMPROVING PLANT ABIOTIC STRESS TOLERANCE

NAEEM KHAN^{1*}, SHAHID ALI², PEIMAN ZANDI³, ASIF MEHMOOD⁴, SHARIAT ULLAH⁵, MUHAMMAD IKRAM⁶, ISMAIL⁴, MOHAMMAD ADNAN SHAHID⁷ AND MD ALI BABAR⁸

¹Department of Plant Sciences Quaid-i-Azam University Islamabad, Pakistan

²Plant Epigenetic and Development Northeast Forestry University Harbin, China

³Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing, China

⁴Institute of Biological Sciences, Sarhad University of Science and Information Technology, Peshawar

⁵Department of Botany, University of Malakand Chakdara, Dir Lower, Pakistan

⁶Department of Botany, Hazara University, Mansehra, Pakistan

⁷Horticulture Science Department University of Florida, USA

⁸Agronomy Department, University of Florida, USA

*Corresponding author email: naeemkhan@bs.qau.edu.pk; naeemkhan001@gmail.com

Abstract

Plant growth and development are affected by many environmental factors. Among them, abiotic factors such as drought and salinity are more destructive; and responsible for worldwide crop losses. These stresses are also responsible for several biochemical and physiological changes in the plants. During metabolomic profiling, it was confirmed that sugars, amino acids and amines are accumulated in different plant species under abiotic stress condition. In most plant species, sugars are considered as the major contributing factor in osmotic adjustment. Soluble sugars are very important in various metabolic events, work as a signal to regulate different gene expression that are involved in photosynthesis, osmolyte synthesis and sucrose metabolism. It was suggested that the accretion of amino acids helps in stress tolerance of plants; through contributing in detoxification of reactive oxygen species, regulation of pH and osmotic adjustments. Among all organic acids, especially succinic, malic and galacturonic acids increase the plant response to long-term drought stress. Amphoteric quaternary amines such as glycine betaine regulate water balance between a plant cell and the environment by stabilizing macromolecular structure and activity. Metabolomic analysis of sugars, amino acids and organic acids is an important tool to correlate the metabolic changes with plant responses. This review aims to explore how sugars, amino acids and organic acids assist plants under severe environmental conditions and alleviate the adverse effects of abiotic stresses.

Key words: Abiotic stresses, Soluble sugars, Amino acids, Metabolomics.

Abbreviations: GB- Glycine betaine, ROS- Reactive oxygen species, QTL-Quantitative trait locus, GABA-Gamma-amino butyric acid, LC-HRMS- Liquid chromatography-high-resolution mass spectrometry, NMR-Nuclear magnetic resonance, Spm-Spermine, SPD-Spermidine, Put-Putrescine

Introduction

Abiotic stresses such as drought, heat and salinity, significantly reduce the production of crop plants if present alone or in combination. Selection of stress tolerant varieties is vital to cope with these challenges in agriculture. Substantial data are available for dissecting plant responses to environmental stresses, but the connections between diverse stresses have been far less inspected (Khan *et al.*, 2018a; Suzuki *et al.*, 2014). The appearance of a specific metabolite is greatly affected by genotypic and environmental interactions. Although the synthesis of metabolites is under the control of genes, its onset is triggered at development stages and/or by environmental factors, particularly soil type, temperature, light, composts, humidity, and insecticides (Dorais *et al.*, 2008; Ali *et al.*, 2016).

Plants react differently to various abiotic stimuli; but, changes in primary metabolism are the commonest response. It includes modifications in the levels of amino acids, sugars/sugar alcohols and tricarboxylic acid cycle intermediates; exhibiting common characters in abiotic stress responses. Plants also show alterations in the level of secondary metabolites when exposed to abiotic stresses; but, these alterations vary according to species

and to stress type (Khan *et al.*, 2018b). The involvement of genomic analysis with metabolomics for phenotype calculation is typically interesting in crop breeding; as the environmental factors strongly influence the selection based on genetic markers (Summer *et al.*, 2003). The previous investigation on *Thellungiella* accessions proved that polyamines and sugars are of help in adaptation to extremely cold temperatures (Colinet *et al.*, 2012).

Plant metabolites associated with abiotic stress tolerance such as sorbitol, fructan, trehalose, polyols mannitol, dimethyl-sulfoniopropionate and proline that help as osmolytes and osmoprotectant under harsh environments (Khan *et al.*, 2018a). Plants produce epicuticular waxes, which protect plant cells from the different pathogenic attacks; and help under drought stress to regulate water loss from the aerial part. Many small molecules like anthocyanins, glutathione, ascorbic acid and tocopherols secure the plant by scavenging active oxygen species during oxidative stress. The biosynthesis of lignin, phytoalexins and phenylpropanoid pathway are also accountable for plant stress defense. Various phytohormones also produced under stress conditions act as signaling molecules and activate the systematic defense system in plants (Shulaev, 2008).

Role of sugar in abiotic stress tolerance: Soluble sugars are involved in many biological processes and structural constituents of the cell and act as a metabolic resource (Ahmad *et al.*, 2016). Soluble sugars are an important component of the signaling pathway, which interconnects the stress pathways that form a complex network and control metabolic responses of plants (Jang & Sheen, 1997). Soluble sugars may assist in stress and may act directly as negative signals or modify the cell reactive pathways to induce the stress response signals and increase plant resistance to stress (Rosa *et al.*, 2009). The concentration of soluble sugars is generally augmented by high salt concentration, flooding and low temperature. Soluble sugars have different actions, which depend on plant species and intensity of stress (Blumwald *et al.*, 2000). The concentration of sugars is also affected by the type of abiotic stress and due to fluctuations in CO₂ assimilation (Close, 1997). The current research confirmed that the accumulation of soluble sugars and other osmolytes significantly improve plant tolerance to external harsh conditions (Shi *et al.*, 2000). In some cases, it was noticed that increases in solutes content have surprising harmful effects on plant growth and expansion. It was noticed that the accumulation of solutes through genetic engineering is not a direct solution to abiotic stress but important to combine sugar metabolic pathways to build the source-sink relationship in the whole plant body and to extend the stress tolerance to the whole plant.

Soluble sugars act as a primary messenger to control gene expression and enzymatic activities that are implicated with development and metabolism (Quintero *et al.*, 2002; Uozumi *et al.*, 2000). Soluble sugars also regulate the gene expression in sugar exporting and importing tissue and could be used as vital sources of energy (Rus *et al.*, 2001). It was confirmed that the deposition of many sugars, for example, fructan, trehalose, galactinol and sugar alcohols such as mannitol and D-inositol play key role in the water stress tolerance (Taji *et al.*, 2002; Seki *et al.*, 2007; Wang *et al.*, 2003). In *Arabidopsis thaliana*, the transgene galactinol synthase (*AtGols2*) induces more drought susceptibility due to an increase of galactinol and raffinose. In a transgenic plant with overexpression of DREB1A/C-repeat binding factor 3 (CBF3) increase the resistance to drought and cold stress due to more galactinol and raffinose content as compared to wild-type plants (Avonce *et al.*, 2004; Valliyodan *et al.*, 2006). This suggests the osmoprotective role of galactinol and raffinose under drought stress. Non-reducing disaccharide trehaloses assist in abiotic stress in partial revival in plants, invertebrates, fungi and bacteria. The scientists introduced the trehalose genes into plants and increased plant resistance to drought stress without any change in morphological or physiological effects (Abebe *et al.*, 2003). Fructans formed from the oligo- and polyfructoses also play a critical role in drought stress tolerance; it also helps to form a protective membrane from adverse effects of water lacking environment (Hinch *et al.*, 2006; Sheveleva *et al.*, 1997). Mannitol a sugar alcohol also helps in imparting drought stress tolerance in many plants species. The transgenic wheat variety containing mannitol-1-phosphate dehydrogenase

gene of *E. coli* improved plant growth and enhanced the salinity and drought stress tolerance (Abebe *et al.*, 2003). Sugar alcohol D-ononitol thought to form membranes and decrease the adverse effects of free hydroxyl radicals. The introduction of myo-inositol O-methyltransferase gene of *Mesembryanthemum crystallinum* and over-expression of D-ononitol improve salt and drought stress tolerance in transgenic tobacco plants (Wang *et al.*, 2003; Borsani *et al.*, 2005). Abiotic stresses also change the leaf carbohydrates and metabolic content and this might help as a signal due to which the plants respond to harsh environmental conditions (Fig. 2) (Jang & Sheen 1997; Chaves, 1991). Previously it has been reported that under stress condition the invertase activities was enhanced by glucose and fructose in the drought-affected plant's leaves (Pinheiro *et al.*, 2001; Trouverie *et al.*, 2003, Ali *et al.*, 2018). There is also a strong link between sugar accumulation and phytohormone content. Glucose and ABA regulate different signaling mechanism during plant growth and the elevated level of ABA and glucose stop the plant growth under drought condition; but, in lower concentration, it behaves as an antagonistic and promotes plant growth. These compounds appear as osmoprotectant rather than acting in osmotic adjustments (Shabala & Lew, 2002). Mannitol is the most common sugar alcohol in nature that is involved in stabilizing Reactive Oxygen Species (ROS) and help in maintaining the molecular confirmation of enzymes (Shen *et al.*, 1997). The macromolecules and osmolytes form hydrogen bonds under water deficit condition and avert the intermolecular hydrogen bond formation, which damages the protein confirmation for forever. The non-reducing disaccharides such as trehaloses play a very positive role to stabilize the macromolecules and membranes structure during drought stress. Photosynthesis rate is enhancing under overexpression of trhaloses due to the protection of PSII against the photo-oxidation (Garg *et al.*, 2002).

Glucose and fructose are hexoses that cause a massive alternation in sugars as compared to the cyclitol and scyllo-inositol. Morgan (1984) has recognized effects of the water stress on the balance of sugars and starch. Glucose helps directly in the osmotic adjustment in different species such as Oak Pine, and Poplar, but the cyclitols primarily help to protect and stabilize the DNA structure under drought stress (Gebre *et al.*, 1994; Epron & Dreyer, 1996; Ottow *et al.*, 2005). Sucrose and hexoses have dual functions by regulating expression of stress-related genes. The sugars also coordinate the regulation of growth and stress-related genes through HXK-dependent and independent pathways (Rosa *et al.*, 2009). It has been identified in several plants species that the soluble sugars content is increased under drought stress condition; but, the starch content decrease (Kameli & Losel, 1993; Chaves *et al.*, 2009). It was noted that starch breakdown from chloroplast increases the content of soluble sugars, for example, sucrose fructose and glucose, it was also revealed that the maximum amount of galactose was present in *Arabidopsis*, potato and in rice under water stress

(Rizhsky *et al.*, 2004; Morsy *et al.*, 2007). The enhancement of galactose is associated with the biosynthesis of osmoprotectants. Other sugars are also amplified under drought stress condition such as mannose, xylose, and maltose. The maltose helps to increase the defensive effect on the cell membranes and maintained the cell function normally during osmotic treatment reported by Ferrando & Spiess (2001). The other soluble sugar such as xylose act as a precursor for the hemicelluloses of the cell wall, in different plant species such as tobacco culture cell and durum wheat the water induced the build-up of hemicelluloses (Seifert, 2004). Role of sugars in protein stabilization has also been studied in detail (Crow *et al.*, 1987; Yancey, 2005). Many researchers analyzed that trehalose form hydrogen bonds with polar residues protein molecules (Figueroa *et al.*, 2016) (Fig. 1). Hydrogen bonds between the phosphate group of phospholipids and the hydroxyl group of trehalose assessments the vacillations in the infrared spectrum during dehydration. The scientists used the Cation Eu^{3+} that form ionic bonds to the phosphate of phospholipids, through this the sucrose maybe display between the phosphate sites and dry membranes (Texier *et al.*, 2005). The author also suggested that addition of Eu^{3+} decreased the upkeep of liposomes by sucrose during freeze-drying condition; it's showed the sensible binding of sucrose and Eu^{3+} to the phosphate site of phospholipids.

Soluble sugars produced under stress environment can act as signaling molecules, work in connotation with plant growth regulator, the sugar form, and demonstrate a complex network in plants (Chaves & Oliveira, 2004; Rolland *et al.*, 2006). The soluble sugar content increase under drought stress as compared to the starch content but, under the severe condition, the sugar content also decrease. These fluctuations of sugar content bring change in the gene expression and proteomic patterns, especially in photosynthetic metabolism. It is also accepted that under high sugar content the genes involved in the photosynthesis activates become decline, whereas those intricate in the sink activities are persuaded such as gene intricate in the dilapidation of carbohydrates, polysaccharides, lipids, and proteins (Chaves *et al.*, 2009). In fact, there is no expensive drought specific study regarding the metabolomics. However, several studies showed the role of sugar and their correlation with different enzyme during the water stress environment (Boyer & Westgate, 2004; Sami *et al.*, 2016). During drought condition, the plant starts to emergent gain in the early stage as compared to the normal growing plants especially in maize, but the grain is not full filled and infertile. This is due to the restrictive factor invertase in the emerging kernel of maize under drought condition. The QTL designed for invertase activity express mapping near *Ivr2*, an inverse-encoding gene. In young maize plants, the colocalization between the ADP-glucose pyrophosphorylase and sucrose-p synthase also exist (Pelleschi *et al.*, 2006). These studies demonstrated how different metabolites and protein interact with one and other under stress

conditions. It also provides the information related to the new metabolomic analysis and help in the discovery of new stress resistance system that would be fruitful for understanding stress-engineering mechanisms in plants (Khan *et al.*, 2017).

Role of Amino acids in plant responses to stress:

Amino acids are imitated as precursors of proteins and other organic compounds like nucleic acids that show an active role in plant reactions to many stresses. They can act as regulatory and signaling molecules (Dondoni *et al.*, 2006). Proline is an important amino acid that plays crucial roles in plant during abiotic stress responses. The content of proline increases in plants under diverse environmental stresses (Anjum *et al.*, 2011; Gill & Tuteja, 2010; Hayat *et al.*, 2012). Proline acting as an osmoprotective was first studied in microorganisms like bacteria; where a causal connotation between proline accretion and salt tolerance has been confirmed (Csonka & Hanson, 1991).

Similarly, a close connection in the enhancement of proline and water deficient tolerance in barley was reported previously (Lewin *et al.*, 1972). Drought tolerant plant species collect many folds higher free proline as compared to susceptible species (Khan *et al.*, 2018a). The positive effect of proline has been noted on enzymes and membrane integrity mediating osmotic adjustments under stress (Kishor *et al.*, 2005). Some studies also revealed that the proline enhancement under stress condition is a product, not a response to harsh environment; although many researchers have specified a positive relationship between accumulation of proline and plant stress (Ashraf & Foolad, 2007). Kumar & Sharma (1989) found that augmented proline increased K content and improved the effect of salt on the growth of *Vigna radiata* cultures. Proline reduces the damaging effects of nascent oxygen and hydroxyl radicals on Photosystem II located in the thylakoid membranes (Nishiyama *et al.*, 2004). In transgenic tobacco plants the over-expression of proline by *P5Cs* decrease the free radicals content under stress condition (Siripornadulsil *et al.*, 2002).

Amino acids are also known for their role in the inhibition of protein aggregation and M4 lactate dehydrogenase stabilization throughout during excessive temperatures (Szabados *et al.*, 2010). During osmotic, heavy metal stress it also helps to protect the nitrate reductase and during arsenate environments it can stabilize the protease and ribonuclease (Sharma & Dubey, 2005; Mishra & Dubey, 2006). Prior treatment of amino acids can ease the Hg^{2+} toxicity in rice because of its ROS scavenging activity (Gautam *et al.*, 2010, Ali & Linan, 2019). It was confirmed earlier that amino acids also affect the flowering under stress condition. Tanaka *et al.*, (1997) found that amino acids; asparagin, glutamic acid, alanine, aspartic acid, glycine, and serine endorsed flowering whereas, cysteine, threoinine and phenylalanine repressed flowering in *Lemma pausicostata*. The exogenous application of amino acids on plants controls membrane permeability and ion uptake; thus enabling plants to withstand severe stress (El-Tayeb, 2005). Besides this, different amino acids play various roles in plants *e.g.*, acting as an osmolyte, alter enzyme activity, modulate stomatal opening, regulate ion transport and detoxify heavy metals (Torres & Dangl, 2005).

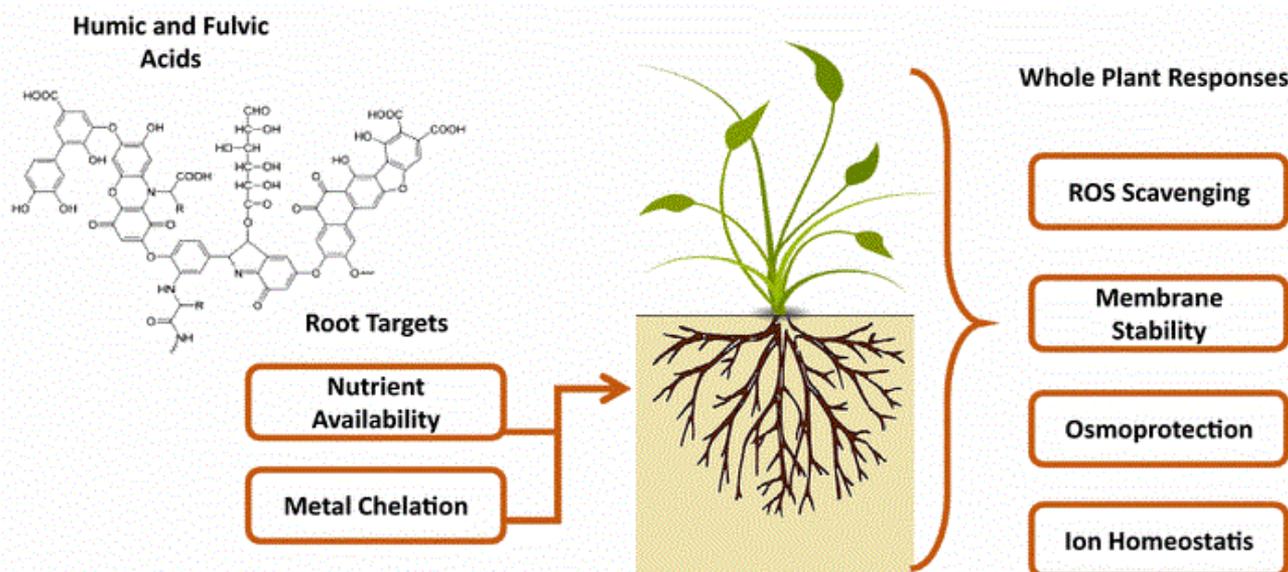


Fig. 1. Key mechanism of stress avoidance targeted by humic acid and fulvic acid (Van Oosten *et al.*, 2017).

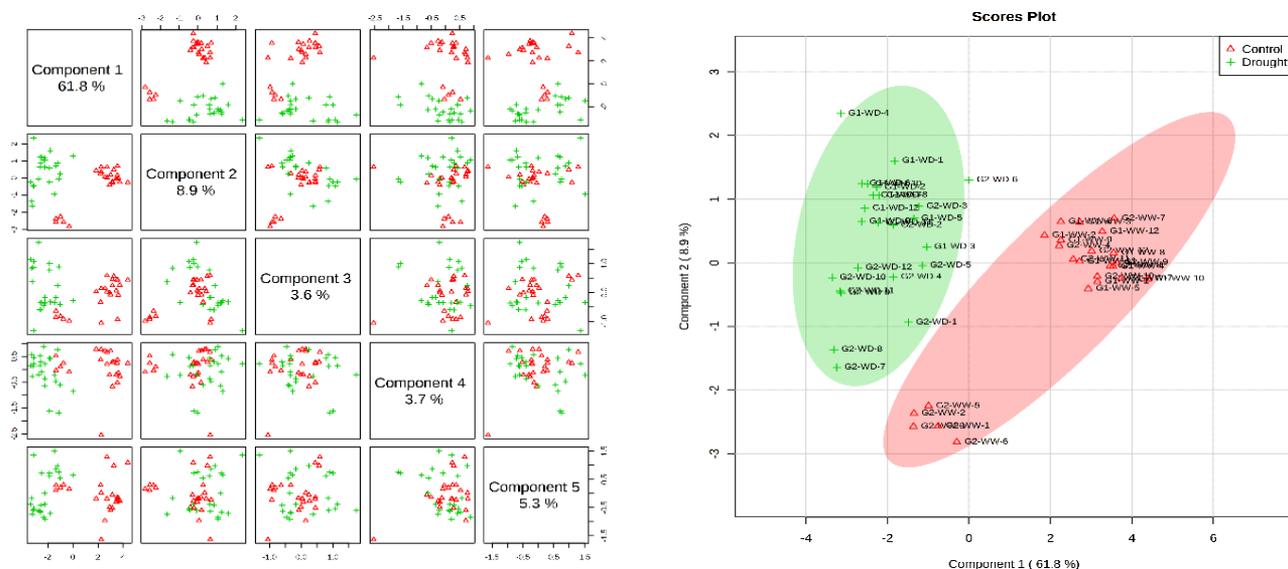


Fig. 2. Partial least square discriminant analysis (PLS-DA) and 2D Scores loading plot for the Chickpea Punjab Noor-2009 (G1) and 93127 (G2) under control (well-watered) and drought treatments at 2 time points (14 and 25 days). Samples at control and drought treatments did not overlap with each other indicating an altered state of metabolite levels in the chickpea leaves. G1, sensitive variety; G2, tolerant variety (Khan *et al.*, 2018a).

Du & Wang (2012) analyzed the polar compounds mine by using the GC-MS techniques from the hybrid Bermuda leaves under short-term (6 d) well watered condition and long-term (18 d) drought condition. The organic content showed non-significant change such as sugars and sugar alcohols during short-term stress; however, a decline in the content of amino acids (*e.g.* serine, GABA, and isoleucine) was noted. They also noted a significant augment in the content of other 11 amino acids *i.e.* proline, methionine, serine, asparagine, phenylalanine, aspartic acid, GABA, glycine, 5-hydroxynorvaline, threonine, and valine significantly improved during long-term stress. There is a close connection with the ion of GABA shunt deficiencies and with the accumulation of reactive oxygen species (Fait *et al.*, 2005). In *Arabidopsis* and pea plants, the reduction of

isoleucine content was denoted under water stress environments (Charlton *et al.*, 2008). The expression level of protein analogue decreases with serine protease activity in drought-tolerant *P. vulgaris* variety during water stress, suggesting serine protease allied in defense mechanism in early drought-induced senescence (Hieng *et al.*, 2004). Among amino acids, alanine, lysine and isoleucine contents significantly reduced whereas, tyrosine content did not change. The amino acid content also helps in stress tolerant, through regulating the intracellular pH, osmotic adjustment, and detoxification of ROS (Rizhsky *et al.*, 2004).

Warth *et al.*, (2015) found that amino acids, which were visibly plentiful in DON-treated wheat, have been interrelated with diverse plant resistance mechanisms. The three important amino acids such as tryptophan,

phenylalanine, and tyrosine all are produced in shikimate pathways. Phenylalanine, tryptophane, and tyrosine are considered the three central molecules in plant metabolism (Galili & Hoefgen, 2002). The shikimate pathway plays a fundamental role in plant reproduction, development, pest-defense, and environmental stresses (Maeda & Dudareva, 2012). In plants, the biosynthetic pathway of these aromatic amino acids serves as precursor for the synthesis of plant hormones, viz. auxin and salicylates and for aromatic secondary metabolites including indole-acetate, lipid precursor, and lignin which plays a critical role is stress tolerance (Suguiyama *et al.*, 2014). Witt *et al.*, (2012) reported an increased level of tryptophan and phenylalanine in corn under drought condition. Maize plants under high temperature stress showed increases in metabolites such as tryptophan, serine, threonine, beta-alanine, proline, glutamate, myo-inositol, and urea (Obata *et al.*, 2015). The increased level of proline and tryptophan was evident in both the sensitive and the tolerant varieties of chickpea when plants were exposed to drought condition (Khan *et al.*, 2018a). In addition, of acting as alternate source for energy under stress conditions, L-tryptophan had been demonstrated to play roles in transportation of ions, opening of stomata, reducing reactive oxygen species (ROS) and act as an osmolyte (Rai, 2002). Before the use of LC-HRMS techniques, the phenylalanine was termed as FHB resistance related metabolite (Gunnaiah *et al.*, 2012). It was discovered by using NMR techniques that the level of threonine valine, isoleucine, leucine, proline and homoserine as well as myo-inositol, c-aminobutyrate and malate were elevated in the field condition; but the level of isoleucine and leucine is no increased under greenhouse condition in the same pea plant (Charlton *et al.*, 2008). By using LC-MS methods the researcher analyzed the elevated level of proline, caffeate, malate and p-coumarate in maize xylem sap. However, the condensation of ferulate was observed under water stress condition (Alvarez *et al.*, 2008). The link between the stress level and the modification in metabolite profile was inspected in a different level of drought stress conditions in *Lotus japonicus* species. All the changes were programmatic in the concentration of polyols, sugars and organic acid (Sanchez *et al.*, 2011).

Organic acids: The drought tolerance in plant species is attended through a change in the content of different organic compounds because of environmental stress condition. The comparative organic content significantly depends upon the specific metabolites in the given condition such as the succinic acid, malic acid, and galacturonic acid displayed the utmost surges in response to long-term drought stress among all organic acids. Gao *et al.*, (2012) reported that under long-term drought stress, the level of malic acid elevated two folds as compared to the well-watered condition. The malic acid increased the drought tolerance was found in different plant species such as spear grass, cotton and tropical grasses (Cutler *et al.*, 1977; Ford & Wilson, 1981; Umezawa *et al.*, 2006). In potato genotypes, the overexpression of galacturonic acid reductase increases the ascorbic acid and enhanced the water stress tolerance (Conclin, 2001). In hybrid Bermuda

grass under the oxidative stress, the galacturonic acid level rises in the leaves suggesting that galacturonic acids have a vital role in oxidative damage under drought stress. Steuer *et al.*, (2007) reported that succinate is an important constituent of the citric acid cycle, and help in energy production through respiration. In alfalfa, the elevated level of succinic acid in nodules was found under severe water stress condition (Naya *et al.*, 2007). During the long-term water stress, the deterioration in the content of organic acid was analyzed which including methylmalonic acid, citric acid, glyceric acid and isocitric acid, which declined by 36%, 49%, 55%, and 49% respectively in comparison to the control. Sassi *et al.*, (2010) reported reduction in the level of organic acids, in the leaves of bean sensitive genotypes on exposure to stress. It has been reported that major cereal phenolics are linked to Grandrieu rye, Dicktoo barely, Bajka oat and winter wheat varieties. In all these cereals, the concentration of caffeic acid was elevated (14-23%) as compared to the previous study that was below 1% (Kim *et al.*, 2006; Shewry *et al.*, 2010; Zieliński & Kozłowska, 2000).

Similarly, in wheat, oat and barley the content of ferulic acid elevated from 20-33%, the elevation is more prominent in two rye varieties. According to these results, the authors concluded that in grains mostly the caffeic and ferulic acid present in a conjugated form which can cleave by alkaline hydrolysis. In earlier metabolomics studies showed that the most common phenolic acid was ferulic sinapinic and 3, 5 dihydroxybenzoic acid, although, in the present study ferulic, caffeic acid and sinapinic is more abundant phenolic acid. In rye the concentration of fumaric and 2, hydroxycyclohexacarboxylic acid is higher, but in barely the maximum concentration of malic and ketogultaric acid was recorded (Kuldao *et al.*, 2008).

Polyamines: Polyamines are polycations, required for plant growth and play a vital role in abiotic stress condition in higher plants. The important polyamines such as spermine (Spm), soermidine (SPD) and putrescine (Put) are commonly present in all organisms. In *Arabidopsis thaliana*, the expression of Put is under the control of arginine decarboxylase gene (*ADC2*) in water and salt stress condition (Urano *et al.*, 2003). In transgenic rice, the over-expression of *ADC* gene showed more drought tolerance due to the elevated level of polyamines. The accumulation of spermidine through overexpression of spermidine synthase of *Cucurbita ficifolia* increased many stresses resistance in transgenic *Arabidopsis* plants such as water and salt stresses (Kasukabe *et al.*, 2004; Capell *et al.*, 2004). It was reported that spermidine regulates the expression of genes that are involved in drought stress tolerance and spermidine act as signaling molecules. All these studies indicated that polyamines play dynamic roles during water stress conditions (Seki *et al.*, 2007). Glycine betaine (GB) is important quaternary amine; during drought condition, these amines kept the water balance between the plant cell and the environments and alleviating the structure and activities of macromolecule (Ashraf & Foolad, 2007). The scientist distinguished the plants according to the synthesis of glycine betaine, some plants such as barley and spinach produce and accumulate maximum amount of glycine betaine in their chloroplast, while other plants do

not synthesize this compounds such as *Arabidopsis thaliana* and tobacco. Transgenic *Arabidopsis*, the genes of cyanobacteria such as glycine sarcosine methyltransferase (ApGSMT) and dimethylglycine methyltransferase (ApDMT) enhanced the tolerance of drought, salt and low-temperatures stresses (Sakamoto & Murata, 2002).

Different types of polyamines are accumulated in different plant species under salinity stress condition, the action of their major metabolic enzyme was explored in *Brassica* species under stress condition (Mo *et al.*, 2002). It was confirmed that extended stress caused only a trivial change in the polyamine production and the action of ornithine and arginine decarboxylase and polyamine oxidase; but, under short-term stress, increase in the production of enzyme activities and polyamines level were noted. Some studies showed that the enhanced and accumulation of polyamines is linked with the salt stress and salt sensitive species. In rice and tomato, salt tolerance species the accumulation of polyamines and variation in polyamines content have been reported in response to diverse stress conditions (Ashraf & Harries, 2004; Krishnamurthy & Bhagwat, 1989).

Conclusion

Drought stress alters the overall plant morphology and cell content. However, plant metabolites play a key role in the adjustment and the regulation of various developmental processes through signaling and response to different abiotic stresses. This study indicated that the leaves of control and stressed plants have distinct mechanisms to regulate the accumulation of different metabolites that provides a better idea to understand the responsive mechanisms of plants during different biotic and abiotic stress conditions. During metabolomic profiling, it was confirmed that sugars, amino acids and amines accumulated in different plant species under drought stress condition. The levels of proline, tryptophan, leucine, isoleucine, and valine amplified in plant leaves under stress condition and organic acid had positive correlation to water scarcity. The crosstalk between plant metabolites and abiotic stresses has positive impacts on the induction of plant growth in a sustainable manner that also enhance drought tolerance and immunity.

References

- Abebe, T., A.C. Guenzi, B. Martin and J.C. Cushman. 2003. Tolerance of mannitol-accumulating transgenic wheat to water stress and salinity. *Plant Physiol.*, 131(4): 1748-1755.
- Ahmad, P., A.A. Abdel Latef, A. Hashem, E.F. Abd_Allah, S. Gucel and L.S. Tran. 2006. Nitric oxide mitigates salt stress by regulating levels of osmolytes and antioxidant enzymes in chickpea. *Front. Plant Sci.*, 31(7): 347.
- Ali, S., N. Khan F. Nouroz, S. Erum, W. Nasim and M.A. Shahid. 2018. *In vitro* effects of GA3 on morphogenesis of CIP potato explants and acclimatization of plantlets in field *In Vitro Cell. Dev. Biol.*, 54: 104.
- Ali, S., S. Erum, F. Nouroz, N. Khan, A. Mehmood, S.H.A. Shah, A. Raheem and A. Muhammad. 2016. *In vitro* conservation of exotic potato genotypes through different incubated temperatures, aerophilic and micro-aerophilic conditions. *Int. J. Biodiv. Conserv.*, 8(7): 147-152.
- Ali, S. and X. Linan. 2019. Plant growth promoting and stress mitigating abilities of soil born microorganisms. *Recent Pat Food Nutr Agric.*, 10: 1. <https://doi.org/10.2174/2212798410666190515115548>
- Alvarez, S., E.L. Marsh, S.G. Schroeder and D.P. Schachtman. 2008. Metabolomic and proteomic changes in the xylem sap of maize under drought. *Plant Cell Environ.*, 31(3): 325-340.
- Anjum, S.A., X.Y. Xie, L.C. Wang, M.F. Saleem, C. Man and W. Lei. 2011. Morphological, physiological and biochemical responses of plants to drought stress. *Afr. J. Agri. Res.*, 6(9): 2026-2032.
- Ashraf, M.F. and M. Foolad. 2007. Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environ. Exp. Bot.*, 59(2): 206-216.
- Ashraf, M.P. and P.J. Harris. 2004. Potential biochemical indicators of salinity tolerance in plants. *Plant Sci.*, 166(1): 3-16.
- Avonce, N., B. Leyman, J.O. Mascorro-Gallardo, P. Van Dijk, J.M. Thevelein and G. Iturriaga. 2004. The *Arabidopsis* trehalose-6-P synthase AtTPS1 gene is a regulator of glucose, abscisic acid, and stress signaling. *Plant Physiol.*, 136(3): 3649-3659.
- Blumwald, E., G.S. Aharon and M.P. Apse. 2000. Sodium transport in plant cells. *Biochim Biophys Acta (BBA)-Biomemb.*, 465(1-2): 140-51.
- Borsani, O., J. Zhu, P.E. Verslues, R. Sunkar and J.K. Zhu. 2005. Endogenous siRNAs derived from a pair of natural cis-antisense transcripts regulate salt tolerance in *Arabidopsis*. *Cell*, 123(7): 1279-91.
- Boyer, J.S. and M.E. Westgate. 2004. Grain yields with limited water. *J. Exp. Bot.*, 55(407): 2385-2394.
- Capell, T., L. Bassie and P. Christou. 2004. Modulation of the polyamine biosynthetic pathway in transgenic rice confers tolerance to drought stress. *Proc. Nat. Acad. Sci.*, 101(26): 9909-9914.
- Charlton, A.J., J.A. Donarski, M. Harrison, S.A. Jones, J. Godward, S. Oehlschlager, J.L. Arques, M. Ambrose, C. Chinoy, P.M. Mullineaux and C. Domoney. 2008. Responses of the pea (*Pisum sativum* L.) leaf metabolome to drought stress assessed by nuclear magnetic resonance spectroscopy. *Metabolomics*, 4(4): 312.
- Chaves, M.M. and M.M. Oliveira. 2004. Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. *J. Exp. Bot.*, 55(407): 2365-2384.
- Chaves, M.M. 1991. Effects of water deficits on carbon assimilation. *J. Exp. Bot.*, 42(1): 1-6.
- Chaves, M.M., J. Flexas and C. Pinheiro. 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann. Bot.*, 103(4): 551-560.
- Close, T.J. 1997. Dehydrins: a commonality in the response of plants to dehydration and low temperature. *Physiol Plant.*, 100(2): 291-296.
- Colinet, H., V. Larvor, M. Laparie and D. Renault. 2012. Exploring the plastic response to cold acclimation through metabolomics. *Fun. Ecol.*, 26(3): 711-722.
- Conklin, P.L. 2001. Recent advances in the role and biosynthesis of ascorbic acid in plants. *Plant Cell Environ.*, 24(4): 383-394.
- Crowe, J.H., L.M. Crowe, J.F. Carpenter and C.A. Wistrom. 1987. Stabilization of dry phospholipid bilayers and proteins by sugars. *Biochem. J.*, 15: 242(1): 1.
- Csonka, L.N. and A.D. Hanson. 1991. Prokaryotic osmoregulation: genetics and physiology. *Ann. Rev. Microb.*, 45(1): 569-606.
- Cutler, J.M. and D.W. Rains. 1978. Effects of water stress and hardening on the internal water relations and osmotic constituents of cotton leaves. *Physiol Plant.*, 42(2): 261-268.

- Dondoni, A. and A. Massi. 2006. Design and synthesis of new classes of heterocyclic c-glycoconjugates and carbon-linked sugar and heterocyclic amino acids by asymmetric multicomponent reactions (AMCRs). *Acc. Chem. Res.*, 39(7): 451-463.
- Dorais, M., D.L. Ehret and A.P. Papadopoulos. 2008. Tomato (*Solanum lycopersicum*) health components: from the seed to the consumer. *Phytochem. Rev.*, 7(2):231.
- Du, J., J. Qi, D. Wang and Z. Tang. 2012. Facile synthesis of Au@TiO₂ core-shell hollow spheres for dye-sensitized solar cells with remarkably improved efficiency. *Energy Environ. Sci.*, 5(5): 6914-6918.
- El-Tayeb, M.A. 2005. Response of barley grains to the interactive effect of salinity and salicylic acid. *Plant Growth Regul.*, 45(3): 215-224.
- Epron, D. and E. Dreyer. 1996. Starch and soluble carbohydrates in leaves of water-stressed oak saplings. *In Ann. Des. Sci. Forest.*, 53: 2-3. 263-268.
- Fait, A., A. Yellin and H. Fromm. 2005. GABA shunt deficiencies and accumulation of reactive oxygen intermediates: insight from Arabidopsis mutants. *FEBS Lett.*, 579(2): 415-420.
- Ferrando, M. and W.E. Spiess. 2001. Cellular response of plant tissue during the osmotic treatment with sucrose, maltose, and trehalose solutions. *J. Food Engin.*, 49(2-3): 115-127.
- Figueroa, C.M., R. Feil, H. Ishihara, M. Watanabe, K. Kölling, U. Krause, M. Höhne, B. Encke, W.C. Plaxton, S.C. Zeeman and Z. Li. 2016. Trehalose 6-phosphate coordinates organic and amino acid metabolism with carbon availability. *Plant J.*, 85(3): 410-423.
- Ford, C.W. and J.R. Wilson. 1981. Changes in levels of solutes during osmotic adjustment to water stress in leaves of four tropical pasture species. *Fun. Plant Biol.*, 8(1): 77-91.
- Galili, G. and R. Höfgen. 2002. Metabolic engineering of amino acids and storage proteins in plants. *Metab. Eng.*, 4(1): 3-11.
- Gao, Q.H., C.S. Wu, M. Wang, B.N. Xu and L.J. Du. 2012. Effect of drying of jujubes (*Ziziphus jujuba* Mill.) on the contents of sugars, organic acids, α -tocopherol, β -carotene, and phenolic compounds. *J. Agri. Food Chem.*, 60(38): 9642-9648.
- Garg, A.K., J.K. Kim, T.G. Owens, A.P. Ranwala, Y. Do Choi, L.V. Kochian and R.J. Wu. 2002. Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. *Proc. Nat. Acad. Sci.*, 99(25): 15898-15903.
- Gautam, M., R.S. Sengar, R. Chaudhary, K. Sengar and S. Garg. 2010. Possible cause of inhibition of seed germination in two rice cultivars by heavy metals Pb²⁺ and Hg²⁺. *Toxicol. Environ. Chem.*, 92(6): 1111-1119.
- Gebre, G.M., M.R. Kuhns and J.R. Brandle. 1994. Organic solute accumulation and dehydration tolerance in three water-stressed *Populus deltoides* clones. *Tree Physiol.*, 14(6): 575-587.
- Gill, S.S. and N. Tuteja. 2012. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.*, 48(12): 909-930.
- Gunnaiah, R., A.C. Kushalappa, R. Duggavathi, S. Fox and D.J. Somers. 2012. Integrated metabolite-proteomic approach to decipher the mechanisms by which wheat QTL (Fhb1) contributes to resistance against *Fusarium graminearum*. *PLoS One.*, 7(7): e40695.
- Hayat, S., Q. Hayat, M.N. Alyemeni, A.S. Wani, J. Pichtel and A. Ahmad. 2012. Role of proline under changing environments: A review. *Plant Signal Behav.*, 7(11): 1456-1466.
- Hieng, B., K. Ugrinovic, J. Sustar-Vozlic and M. Kidric. 2004. Different classes of proteases are involved in the response to drought of *Phaseolus vulgaris* L. cultivars differing in sensitivity. *J. Plant Physiol.*, 161(5): 519.
- Hincha, D.K., A.V. Popova and C. Cacula. 2006. Effects of sugars on the stability and structure of lipid membranes during drying. *Adv. in Planar Lipid Bilayers & Liposomes.*, 3: 189-217.
- Jang, J.C. and J. Sheen. 1997. Sugar sensing in higher plants. *Tree Plant Sci.*, 2(6): 208-214.
- Kameli, A. and D.M. Lösel. 1996. Growth and sugar accumulation in durum wheat plants under water stress. *New Phytol.*, 132(1): 57-62.
- Khan, N., A. Bano and P. Zandi. 2018b. Effects of exogenously applied plant growth regulators in combination with PGPR on the physiology and root growth of chickpea (*Cicer arietinum*) and their role in drought tolerance. *J. Plant Interact.*, 13(1): 239-247.
- Khan, N., A. Bano, M.A. Rahman, B. Rathinasabapathi and M.A. Babar. 2018a. UPLC-HRMS-based untargeted metabolic profiling reveals changes in chickpea (*Cicer arietinum*) metabolome following long-term drought stress. *Plant Cell Environ.* doi: 10.1111/pce.13195.
- Khan, N., S. Ali, M.A. Shahid and A. Kharabian-Masouleh. 2017. Advances in detection of stress tolerance in plants through metabolomics approaches. *Plant Omics.*, 10(3): 153.
- Kim, K.H., R. Tsao, R. Yang and S.W. Cui. 2006. Phenolic acid profiles and antioxidant activities of wheat bran extracts and the effect of hydrolysis conditions. *Food Chem.*, 95(3): 466-473.
- Kishor, P.K., S. Sangam, R.N. Amrutha, P.S. Laxmi, K.R. Naidu, K.R. Rao, S. Rao, K.J. Reddy, P. Theriappan and N. Sreenivasulu. 2005. Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: its implications in plant growth and abiotic stress tolerance. *Curr. Sci.*, 10: 424-438.
- Krishnamurthy, R. and K.A. Bhagwat. 1989. Polyamines as modulators of salt tolerance in rice cultivars. *Plant Physiol.*, 91(2): 500-504.
- Kuldau, G. and C. Bacon. 2008. Clavicipitaceous endophytes: their ability to enhance resistance of grasses to multiple stresses. *Bio. Control*, 46(1): 57-71.
- Kumar, V. and D.R. Sharma. 1989. Isolation and characterization of sodium chloride-resistant callus culture of *Vigna radiata* (L.) Wilczek var. radiata. *J. Exp. Bot.*, 40(1): 143-147.
- Lewin, L.G., D.H. Sparrow and D. Aspinall. 1977. Proline accumulation and drought resistance in barley. *Plant Breeding Papers; Int Congr of the Society for the Advancement of Breeding Researches in Asia & Oceania.*
- Maeda, H. and N. Dudareva. 2012. The shikimate pathway and aromatic amino acid biosynthesis in plants. *Ann. Rev. Plant Biol.*, 63: 73-105.
- Mishra, S. and R.S. Dubey. 2006. Inhibition of ribonuclease and protease activities in arsenic exposed rice seedlings: role of proline as enzyme protectant. *J. Plant Physiol.*, 25; 163(9): 927-936.
- Mo, H. and E.C. Pua. 2002. Up-regulation of arginine decarboxylase gene expression and accumulation of polyamines in mustard (*Brassica juncea*) in response to stress. *Physiol. Plant.*, 114(3): 439-449.
- Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.*, 35(1): 299-319.
- Morsy, M.R., L. Jouve, J.F. Hausman, L. Hoffmann and J.M. Stewart. 2007. Alteration of oxidative and carbohydrate metabolism under abiotic stress in two rice (*Oryza sativa* L.) genotypes contrasting in chilling tolerance. *J. Plant Physiol.*, 164(2): 157-167.
- Naya, L., R. Ladrera, J. Ramos, E.M. González, C. Arrese-Igor, F.R. Minchin and M. Becana. 2007. The response of carbon metabolism and antioxidant defenses of alfalfa nodules to drought stress and to the subsequent recovery of plants. *Plant Physiol.*, 144(2): 1104-1114.

- Nishiyama, Y., S.I. Allakhverdiev, H. Yamamoto, H. Hayashi and N. Murata. 2004. Singlet oxygen inhibits the repair of photosystem II by suppressing the translation elongation of the D1 protein in *Synechocystis* sp. PCC 6803. *Biochem.*, 43(35): 11321-11330.
- Obata, T., S. Witt, J. Lisek, N. Palacios-Rojas, I. Florez-Sarasa, J.L. Araus, J.E. Cairns, S. Yousfi and A.R. Fernie. 2015. Metabolite profiles of maize leaves in drought, heat and combined stress field trials reveal the relationship between metabolism and grain yield. *Plant Physiol.*, 1: 01164.
- Ottow, E.A., M. Brinker, T. Teichmann, E. Fritz, W. Kaiser, M. Brosché, J. Kangasjärvi, X. Jiang and A. Polle. 2005. *Populus euphratica* displays apoplastic sodium accumulation, osmotic adjustment by decreases in calcium and soluble carbohydrates, and develops leaf succulence under salt stress. *Plant Physiol.*, 139(4): 1762-1772.
- Pelleschi, S., A. Leonardi, J.P. Rocher, G. Cornic, D. De Vienne, C. Thevenot and J.L. Prioul. 2006. Analysis of the relationships between growth, photosynthesis and carbohydrate metabolism using quantitative trait loci (QTLs) in young maize plants subjected to water deprivation. *Mol. Breed.*, 17(1): 21-39.
- Pinheiro, C., J.A. Passarinho and C.P. Ricardo. 2004. Effect of drought and rewatering on the metabolism of *Lupinus albus* organs. *J. Plant Physiol.*, 161(11): 1203-1210.
- Quintero, F.J., M. Ohta, H. Shi, J.K. Zhu and J.M. Pardo. 2002. Reconstitution in yeast of the Arabidopsis SOS signaling pathway for Na⁺ homeostasis. *Proc. Nat. Acad. Sci.*, 99(13): 9061-9066.
- Rai, M., A. Yadav and A. Gade. 2009. Silver nanoparticles as a new generation of antimicrobials. *Biotech. Adv.*, 27(1): 76-83.
- Rizhsky, L., H. Liang, J. Shuman, V. Shulaev, S. Davletova and R. Mittler. 2004. When defense pathways collide. The response of Arabidopsis to a combination of drought and heat stress. *Plant Physiol.*, 134(4): 1683-1696.
- Rolland, F., E. Baena-Gonzalez and J. Sheen. 2006. Sugar sensing and signaling in plants: conserved and novel mechanisms. *Ann. Rev. Plant Biol.*, 57: 675-709.
- Rosa, M., C. Prado, G. Podazza, R. Interdonato, J.A. González, M. Hilal and F.E. Prado. 2009. Soluble sugars: Metabolism, sensing and abiotic stress: A complex network in the life of plants. *Plant Signal Behav.*, 4(5): 388-393.
- Rus A., B.H. Lee, A. Muñoz-Mayor, A. Sharkhuu, K. Miura, J.K. Zhu, R.A. Bressan and P.M. Hasegawa. 2004. AtHKT1 facilitates Na⁺ homeostasis and K⁺ nutrition in planta. *Plant Physiol.*, 136(1): 2500-2511.
- Sakamoto, A. and N. Murata. 2002. The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. *Plant Cell Environ.*, 25(2): 163-171.
- Sami, F., M. Yusuf, M. Faizan, A. Faraz and S. Hayat. 2016. Role of sugars under abiotic stress. *Plant Physiol Biochem*, 1; 109: 54-61.
- Sanchez, D.H., F.L. Pieckenstain, F. Escaray, A. Erban, U.T. Kraemer, M.K. Udvardi and J. Kopka. 2011. Comparative ionomics and metabolomics in extremophile and glycophytic *Lotus* species under salt stress challenge the metabolic pre-adaptation hypothesis. *Plant Cell Environ.*, 34(4): 605-617.
- Sassi, S., S. Aydi, E.M. Gonzalez, C. Arrese-Igor and C. Abdelly. 2010. Understanding osmotic stress tolerance in leaves and nodules of two *Phaseolus vulgaris* cultivars with contrasting drought tolerance. *Symbiosis.*, 52(1): 1-0.
- Seifert, G.J. 2004. Nucleotide sugar interconversions and cell wall biosynthesis: how to bring the inside to the outside. *Curr. Opin. Plant Biol.*, 7(3): 277-284.
- Seki, M., T. Umezawa, K. Urano and K. Shinozaki. 2007. Regulatory metabolic networks in drought stress responses. *Curr. Opin. Plant Biol.*, 10(3): 296-302.
- Shabala, S.N and R.R. Lew. 2002. Turgor regulation in osmotically stressed Arabidopsis epidermal root cells. Direct support for the role of inorganic ion uptake as revealed by concurrent flux and cell turgor measurements. *Plant Physiol.*, 129(1): 290-299.
- Sharma, P. and R.S. Dubey. 2005. Modulation of nitrate reductase activity in rice seedlings under aluminium toxicity and water stress: Role of osmolytes as enzyme protectant. *J. Plant Physiol.*, 23; 162(8): 854-864.
- Shen, B., R.G. Jensen and H.J. Bohnert. 1997. Mannitol protects against oxidation by hydroxyl radicals. *Plant Physiol.*, 115(2): 527-32.
- Sheveleva, E.V., R.G. Jensen and H.J. Bohnert. 2000. Disturbance in the allocation of carbohydrates to regenerative organs in transgenic *Nicotiana tabacum* L. *J. Exp. Bot.*, 51(342): 115-122.
- Shewry, P.R., V. Piironen, A.M. Lampi, M. Edelmann, S. Kariluoto, T. Nurmi, R. Fernandez-Orozco, C. Ravel, G. Charmet, A.A. Andersson and P. Åman. 2010. The healthgrain wheat diversity screen: Effects of genotype and environment on phytochemicals and dietary fiber components, 9291-9298.
- Shi, H., M. Ishitani, C. Kim and J.K. Zhu. 2000. The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na⁺/H⁺ antiporter. *Proc. Nat. Acad. Sci.*, 97(12): 6896-6901.
- Shulaev, V., D. Cortes, G. Miller and R. Mittler. 2008. Metabolomics for plant stress response. *Physiol. Plant.*, 132(2): 199-208.
- Siripornadulsil, S., S. Traina, D.P. Verma and R.T. Sayre. 2002. Molecular mechanisms of proline-mediated tolerance to toxic heavy metals in transgenic microalgae. *Plant Cell.*, 14(11): 2837-2847.
- Steuer, R., A.N. Nesi, A.R. Fernie, T. Gross, B. Blasius and J. Selbig. 2007. From structure to dynamics of metabolic pathways: application to the plant mitochondrial TCA cycle. *Bioinformatics*, 23(11): 1378-1385.
- Suguiyama, V.F., E.A. Silva, S.T. Meirelles, D.C. Centeno and M.R. Braga. 2014. Leaf metabolite profile of the brazilian resurrection plant *barbarea purpurea* hook. (Velloziaceae) Shows Two Time-Dependent Responses during Desiccation and Recovering. *Front. Plant Sci.*, 5: 96.
- Sumner, L.W., P. Mendes and R.A. Dixon. 2003. Plant metabolomics: large-scale phytochemistry in the functional genomics era. *Phytochem.*, 62(6): 817-836.
- Suzuki, N., R.M. Rivero, V. Shulaev, E. Blumwald and R. Mittler. 2014. Abiotic and biotic stress combinations. *New Phytol.*, 203(1): 32-43.
- Szabados, L. and A. Savoure. 2010. Proline: a multifunctional amino acid. *Tree Plant Sci.*, 15(2): 89-97.
- Tanaka, O., Y. Nakayama, K. Emori, G. Takeba, K. Sato and M. Sugino. 1997. Flower-inducing activity of lysine in *Lemna paucicostata* 6746. *Plant Cell Physiol.*, 38(2): 124-128.
- Texier, A.C., Y. Andres, M. Illemassene and P. Le Cloirec. 2000. Characterization of lanthanide ions binding sites in the cell wall of *Pseudomonas aeruginosa*. *Environ. Sci. Technol.*, 15; 34(4): 610-615.
- Torres, M.A. and J.L. Dangl. 2005. Functions of the respiratory burst oxidase in biotic interactions, abiotic stress and development. *Curr. Opin. Plant Biol.*, 1; 8(4): 397-403.
- Trouverie, J., C. Thévenot, J.P. Rocher, B. Sotta and J.L. Prioul. 2003. The role of abscisic acid in the response of a specific vacuolar invertase to water stress in the adult maize leaf. *J. Exp. Bot.*, 54(390): 2177-2186.
- Umezawa, T., M. Fujita, Y. Fujita, K. Yamaguchi-Shinozaki and K. Shinozaki. 2006. Engineering drought tolerance in plants: discovering and tailoring genes to unlock the future. *Curr. Opin. Biotech.*, 17(2): 113-122.

- Uozumi, N., E.J. Kim, F. Rubio, T. Yamaguchi, S. Muto, A. Tsuboi, E.P. Bakker and T. Nakamura. 2000. The Arabidopsis HKT1 gene homolog mediates inward Na⁺ currents in *Xenopus laevis* oocytes and Na⁺ uptake in *Saccharomyces cerevisiae*. *Plant Physiol.*, 122(4): 1249-1260.
- Urano, K., Y. Yoshida, T. Nanjo, Y. Igarashi, M. Seki, F. Sekiguchi, K. Yamaguchi-Shinozaki and K. Shinozaki. 2003. Characterization of Arabidopsis genes involved in biosynthesis of polyamines in abiotic stress responses and developmental stages. *Plant Cell Environ.*, 26(11): 1917-1926.
- Valliyodan, B. and H.T. Nguyen. 2006. Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Curr. Opin. Plant Biol.*, 9(2): 189-195.
- Van Oosten, M.J., O. Pepe, S. De Pascale, S. Silletti and A. Maggio. 2017. The role of biostimulants and bioeffectors as alleviators of abiotic stress in crop plants. *Chem. & Biol. Technol. Agri.*, 4(1): 5.
- Wang, W., B. Vinocur and A. Altman. 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta*, 218(1): 1-4.
- Warth, B., Parich, A. Bueschl, C. Schoefbeck, D. Neumann, N.K. Kluger, B. Schuster, K. Krska, R. Adam, G. Lemmens, M. and R. Schuhmacher. 2015. GC-MS based targeted metabolic profiling identifies changes in the wheat metabolome following deoxynivalenol treatment. *Metabolomics*, 11(3): 722-738.
- Witt, S., L. Galicia, J. Lisek, J. Cairns, A. Tiessen, J.L. Araus, N. Palacios-Rojas and A.R. Fernie. 2012. Metabolic and phenotypic responses of greenhouse-grown maize hybrids to experimentally controlled drought stress. *Mol. Plant.*, 5(2): 401-417.
- Yancey, P.H. 2005. Organic osmolytes as compatible, metabolic and counteracting cytoprotectants in high osmolarity and other stresses. *J. Exp. Biol.*, 208(15): 2819-2830.
- Zieliński, H. and H. Kozłowska. 2000. Antioxidant activity and total phenolics in selected cereal grains and their different morphological fractions. *J. Agri. Food Chem.*, 48(6): 2008-2016.

(Received for publication 3 September 2018)