Asian J Agri Biol, 2013, 1(1):29-37.

A COMPREHENSIVE OVERVIEW OF RECENT ADVANCES IN DROUGHT STRESS TOLERANCE RESEARCH IN WHEAT (*TRITICUM AESTIVUM* L.)

Rashid Mehmood Rana*[1], Shoaib Ur Rehman[1], Junaid Ahmed[1] and Muhammad Bilal[1]
[1] Department of Plant Breeding & Genetics, PMAS-Arid Agriculture University Rawalpindi, Pakistan

ABSTRACT

Wheat is an important food crop grown worldwide and used as staple food in many countries. Its production is affected by several factors including abiotic stresses and drought is one of the most damaging and frequently occurring abiotic stresses. Several efforts have been made to address and cope with it at morphological, physiological and molecular levels, have been summarized. Different morphological and physiological traits identified through successive efforts include osmotic adjustment, cell membrane stability and stomatal conductance and showed positive correlation with drought tolerance. Some quantitative trait loci have also been discovered in wheat genome on chromosome 4A that showed significant association with this mechanism. Proteomic and gene functional analysis revealed the genes involved in vital biological pathways (e.g., reactive oxygen species scavenging, etc.) and showed significant correlation with drought tolerance. Therefore, the information generated through both the QTLs and gene functional analysis could be utilized to achieve drought tolerance in wheat.

Keywords: Biological pathways; Gene expression; Osmotic adjustment; Quantitative trait loci

INTRODUCTION

Wheat is a major food crop grown in temperate region of world and used as staple food in most of the countries (Shewry, 2009). Crop shows its maximum yield potential in stress free environment while environmental stress causes reduction in this potential. Abiotic factors are the major threat to wheat productivity and causing up to 71% reduction in yield. Among abiotic stresses, drought is one of the most challenging threat with worldwide distribution that directly reduces the growth and development of crop plants by disturbing normal biochemical processes and gene expression (Akram et al., 2004; Jones et al., 2003)

As a consequence of severe climatic changes across the globe, threat of the occurrence of more frequent drought spells is predicted. Therefore, it became more challenging for scientists and plant breeders as it causes significant losses of crop productivity (Pan et al., 2002; Rad et al., 2012). Physiological responses of the drought stress are more complex; therefore breeding for drought tolerant cultivars has been a challenging task to the breeders (Moustafa et al., 1996). Several efforts have been made to address this problem at different levels viz. discovery of physiological and molecular responses, development of new tolerant varieties etc. The current manuscript summarizes efforts made at different level to cope with drought stress in wheat.

Breeding parameters and efforts made for drought tolerance: Plant breeders observed several traits and through intensive research, they evaluated the role of different traits/processes during drought stress. After this evaluation, the next step is to observe the heritability and manipulation of selected traits for plant improvement. Several efforts have also been made in wheat against drought tolerance and therefore the incorporation of these traits for the development of new drought tolerant varieties has been made using conventional and molecular breeding techniques. A brief overview of these traits is discussed below.

Osmotic adjustment (OA): Plants have developed some strategies to act against various stresses. Osmotic adjustment is one of them that assists the plant to get rid of ion toxicity and water uptake maintenance under drought stress (Abdelmalek and Khaled, 2011; Chen and Jiang, 2010). During osmotic adjustment, plant accumulate large amount of osmolyets viz. organic solutes and inorganic ions. Inorganic ions including sodium,

---

Corresponding author: e-mail: rashid_cabb@hotmail.com potassium, calcium and chloride ions have been found to play vital role in osmotic adjustment by ion transport processes (Chen and Jiang, 2010). In wheat genome, *P5CS* gene has been discovered on 7A chromosome and found involved in osmotic adjustment and showed positive correlation with drought tolerance in wheat (Morgan and Tan, 1996; Sawahel and Hassan, 2002).

Stomatal conductance: Plants uptake CO_2 from air and transpire water through stomata. Under water scarcity, plants regulate water transpiration by regulating the stomatal conductance (Farooq et al., 2009). Therefore, plants with lowered stomatal conductance are thought to have better adaptability under drought stress condition. Wheat genes *Rht-B1b* and *Rht-D1b* showed strong association with drought tolerance as well as stomatal conductance (Rebetzke et al., 2012).

Cell membrane stability: Cell membrane is one of the first targets of many stresses including drought and therefore the stability of cell membrane is of great importance. Hence, plant cell membrane stability (CMS) is used as an indicator of drought tolerance and the rate of injury to plasma membrane can be assayed through the measurement of electrolytes leaked from the cell (Blum and Ebercon, 1981). The wheat genotypes with higher cell membrane stability (71-80 %) have been noticed to perform better under drought (Shafeeq and Zafar, 2006).

Molecular markers and QTLs: Quantitative trait loci analysis (QTL) analysis and other subsequent study through molecular markers in wheat revealed that chromosome 5B, 4B and 7B carry important genes for drought tolerance (Dashti et al., 2007). A QTL on chromosome 5B located between two markers (M51P65 and Psr136) showed positive correlation with drought tolerance. However, QTLs discovered on chromosome 4B and 7B (between M62P64d - Rht and M83P65d - M21P76n markers respectively) showed negative effect on drought tolerance (Dashti et al., 2007).

Wheat chromosome 4A has been reported to carry important genes for production under drought stress. Several other reports on QTL in homologous Triticeae group 4 chromosomes highlight the importance of this chromosome group for drought stress tolerance. A marker located on chromosome 4A (Xwmc89) was found significantly associated with drought tolerance in tolerant wheat genotypes (Kirigwi et al., 2007).

Study on biological pathways: Recent advanced in the discovery of biological pathways and biochemicals involved in various pathways motivated the plant scientists to discover the factors affecting these vital pathways. Several studies have also been conducted in wheat and here we summarized these efforts as shown in Table 1 and described below.

Carbohydrate metabolism: During water scarcity, decreased stomatal conductance causes the reduction of CO_2 intake. This situation (lowered CO_2& O_2 ratio) provokes the oxygenase activity of Rubisco (ribulose-1,5-*bis*phosphate carboxylase/oxygenase), an enzyme of Calvin cycle, hence starts the process of photorespiration (Bowes and Ogren, 1972). Being the most abundant proteins in leaf tissue, Rubisco subunits have been reported to be susceptible to fragmentation under drought stress (Ge et al., 2012; Salekdeh et al., 2002). 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.

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). Another group of enzymes, beta-glucanases are hydrolases of beta glucans, which is the major components of plant cell walls and are involved in several processes such as endosperm development and vegetative growth (Nishizawa et al., 2003). These enzymes were reported to be up-regulated under osmotic stress (Mohammadi et al., 2007; Nishizawa et al., 2003). The breakdown of cell wall components (beta-glucanase, beta-D-glucanexohydrolase) has been implicated to reduce water potential of the cells to respond the decreased water potential gradient due to water scarcity (Mohammadi et al., 2007); as well as to provide energy by supplying resources at the time of increased ATP demand due to an impairment of the photosynthetic machinery (Mohapatra et al., 2010). A reduced level of cell wall beta-glucosidase (b-D-glucanexohydrolase) has been noticed in wheat studied under drought stress (Merewitz et al., 2011)

Energy Metabolism: Down-regulation of ATP synthase CF1 subunit and atp1 has been reported to decrease photosynthetic rates in stressed wheat plants (Caruso et al., 2009). Aconitate-hydratase is an integral member of the tricarboxylic acid cycle (TCA cycle) and, thus, closely related to the energy status of a cell. Aconitate-hydratase is reported to be affected by oxidative damage (Navarre et al., 2000) and has been reported to be up-regulated under drought stress (Gregersen and Holm, 2006). Cytochrome c oxidase is a terminal enzyme of the respiratory chain of mitochondria. Putative cytochrome c oxidase subunit II PS17 appeared to be down-regulated in response to drought in wheat as it exhibited the lowest levels of the protein under drought-stress.(Budak et al., 2013). Ferredoxin-NADP(H) oxidoreductase (FNR) isoforms are involved in the photosynthetic machinery where electrons are transferred from ferredoxins or flavodoxins to NADPH and are also implicated in protection against ROS and found up-regulated under drought stress in wheat (Caruso et al., 2008; Gregersen and Holm, 2006).

Closing of stomata under drought stress conditions promotes photorespiration leading to an increase in the abundance of glycolate in chloroplasts. In peroxisomes, glycolate is oxidized by glycolate oxidase (also known as (S)-2-hydroxy-acid oxidase) and H_2O_2 is generated in the process (Miller et al. 2010). An enzyme peroxisomal (S)-2-hydroxy-acid oxidase involved in this mechanism was induced by drought in wheat (Budak et al., 2013).

Methionine synthase catalyzes the transfer of a methyl group from 5-methyl-tetrahydrofolate to homocysteine to produce methionine which is further converted into S-adenosylmethionine (SAM) by S-adenosylmethioninesynthetase (methyl cycle). Methionine synthase was also reported to be down-regulated in flooding stress in wheat (Kong et al., 2010). Generation and re-generation of SAM is of particular importance as SAM is the universal donor in the transmethylation of nucleic acids, proteins, lipids and other metabolites such as compatible solutes glycine betaine and polyamines(Narita et al., 2004; Ravanel et al., 2004). The role of polyamines in stress responses has been extensively studied in a number of recent studies and foundup-regulated in wheat and other crop plants (Budak et al., 2013).

Cellular processes: Resistant genotypes may cope with drought stress through alternate ROS scavengers' e.g. catalase-1, GST, MnSOD as noticed in some drought resistant wheat genotypes (Budak et al., 2013). In addition to detoxification via the tripeptide glutathione, GST isoforms may also act as glutathione peroxidases and thus are considered as an integral part of oxidative stress responses (Gallé et al., 2009). Similarly, superoxide dismutases (SOD) aid in alleviating the oxidative via conversion of superoxide ion to hydrogen peroxide (Zhang et al., 2008). It is involved in post-translational modification and reported to play key role in drought tolerance (Budak et al., 2013; Jang et al., 2003).

Information storage: Membrane constituents including lipids and proteins are primarily damaged by drought stress, chloroplast envelope was previously found to harbor several proteins with scavenging and antioxidant capacities which may be involved in defense against oxidative stress (Ferro et al., 2003). A higher level of putative chloroplast envelope protein was observed in drought tolerant wheat genotype (Budak et al., 2013).

Mitochondrial alternative oxidase (AOX) is involved in the protection of photosynthesis during drought in wheat leaves. Drought increased the amount of AOX protein in leaf and also enhanced the rate of AOX-dependent O_2 uptake by the respiratory electron transport chain. The amount of the reduced, active form of the AOX protein was specifically increased by drought and hence conferred tolerance against drought stress (Bartoli et al., 2005).

Castiglioni et al. (2008) reported that CMSO was involved in the synthesis of glycine-betaine. Transgenic plants of several species (maize, soybean, rice, and wheat) with increased level of CSMO had a significantly increased glycinebetaine content, and gained tolerance to water deficit (Bensen et al., 2008).

Table 1 Pathways involved in drought tolerance in wheat

Functional category	Gene/Protein	Scientist reported
Energy metabolism	atp1 F1-ATP synthase subunit α	Caruso et al., 2009
	Peroxisomal S-2-hydroxy-acid oxidase	Budak et al., 2013
	aconitate hydratase protein	Gregersen and Holm, 2006
	ATP synthase CF1 alpha subunit	Caruso et al., 2009
	cytochrome c oxidase	Budak et al., 2013
	Ferredoxin-NADPH oxidoreductase FNR	Caruso et al., 2008
	Putative inorganic pyrophosphatase	Tetlow et al., 2003
	Glyoxysomal malate dehydrogenase	
Carbohydrate metabolism	Triosephosphate isomerase, cytosolic	Xue et al., 2008
	Putative aconitate hydratase, cytoplasmic	Budak et al., 2013
	Beta-D-glucan exohydrolase	Mohammadi et al., 2007
	Cell wall beta-glucosidase	Mohammadi et al., 2007
	Ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit	Demirevska et al., 2009
	Ribulosebisphosphate carboxylase	Salekdeh et al., 2002
	1,3;1,4 Beta glucanase	Mohammadi et al., 2007
	Xyloglucan endotransglycosylase XET	Nishizawa et al. 2003.
Cellular processes	Catalase-1	Budak et al., 2013
	UTP-glucose-1-phosphate uridylyltransferase	Budak et al., 2013
	Carbonic anhydrase	Budak et al., 2013
	Glutathione transferase	Budak et al., 2013
	Manganese superoxide dismutase	-do-
Amino acid metabolism	methionine synthase	Kong et al., 2010
	polyamine oxidases	Budak et al., 2013
	Serine hydroxymethyl transferase	
translational machinery	Putative chloroplast envelope protein	Ferro et al., 2003
Oxidative phosphorylation	cytochrome c oxidase	Budak et al., 2013
Cytoskeleton related	1,3;1,4 Beta glucanase	Mohammadi et al., 2007; Nishizawa et al., 2003
ROS	Glutathione transferase	Budak et al., 2013
Photosynthesis & Respiration	Mitochondrial alternative oxidase AOX	Bartoli et al., 2005
synthesis of glycine-betaine	CMSO gene	Castigioni et al. 2005
ABA regulatory pathway	bZIP gene	Ergen et al., 2009
	HD-ZIP	Ergen et al., 2009
1,4,5-triphosphate IP3 signalling	phospholipase C gene	Ergen et al., 2009

Table 2 Genes involved in drought tolerance in wheat

Sr.No.	Genes	Reference
1	*Dreb 1*	Huseynova and Rustamova, 2010; Sakuma et al., 2006 Lopato and Langridge; Wei et al., 2009
2	*Dreb 2*	Liu et al., 1998; Nakashima and Yamaguchi-Shinozaki, 2005
4	*LEA*	Lopato and Langridge
5	*Rht 8*	Gasperini et al., 2012
6	*TaAQP7*	Zhou et al., 2012
7	*TaSnRK2.8*	Zhang et al., 2010
9	TaMYB33	Qin et al., 2012
10	TaMYB2	Garg et al., 2012
11	R2R3-MYB	Zhang et al., 2012
12	TaNAC2a	Tang et al., 2012
13	TaNAC4a	Do
14	TaNAC6	Do
15	TaNAC7	Do
16	TaNAC13	Do
17	TaNTL	Do
18	TaEXPB23	Han et al., 2012
19	$TaSRK_2C_1$	Du et al., 2013b
20	TaASR1	Hu et al., 2013
21	*TaHPS*	Xiao et al., 2012
22	*TaSRHP*	Hou X. et al., 2013
23	*TaSIP*	Du et al., 2013a
24	TaWRKY2	Niu et al., 2012
25	TaWRKY19	Niu et al., 2012
26	R2R3-MYB	Zhang et al., 2012
27	TaMYB30-B	Do

FUNCTIONAL ANALYSIS OF DROUGHT RESPONSIVE GENES

The advent of genomics has offered a comprehensive profiling the changes in gene expression result from exposure to drought. A number of genes have shown their involvement in drought response mechanism (Table 2). A brief description of these functionally characterized wheat genes are given as follows.

Dehydration-responsive element binding (DREB) genes belongs to largest family of transcription factors which are induced abiotic stresses. In wheat, *Dreb1* genes are located on 3A, 3B and 3D chromosomes. Mapping of *Dreb-B1* genes showed that is located between *Xmwg818* and *Xfbb117* on 3BL chromosome. *Dreb-B1* gene is responsible for abiotic stress tolerance in wheat such as it provides tolerance against drought. It provides tolerance to salinity, low temperature and ABA as well. (Wei et al., 2009). *Dreb1/Dreb2* homologous genes have been isolated from many crops i.e. *Triticum aestivum*, *Oryza sativa*, *Zea mays* and from perennial ryegrass (Lata and Prasad, 2011)

NAC (NAM, ATAF1/2 and CUC2) domain proteins are transcriptional factors conserved in plant-species and reported to play diverse roles in various processes including plant developmental, abiotic and biotic stress responses etc (Zheng et al., 2009). Rice stress-responsive NAC gene, when incorporated in wheat conferred tolerance to drought and salt stress. Molecular characterization of novel *TaNAC* genes in wheat and overexpression of *TaNAC2a*, *TaNAC4a*, *TaNAC6*, *TaNAC7*, *TaNAC13* and *TaNTL5* genes in tobacco conferred drought tolerance (Tang et al., 2012). Stress-responsive NAC 1 (SNAC1) is predominantly induced in the guard cells by water scarcity condition (Hu et al., 2006). SNAC1 gene was introduced into a superior Chinese wheat variety Yangmai12 which showed considerable enhanced tolerance against drought and salinity in multiple generations. The transgenic Yangmai12 also showed higher level of water and chlorophyll content in their leaves.

In wheat, products of late embryogenesis abundant (LEA) genes perform repairing cell components works to, such as organelles, proteins and membranes damaged due to dehydration (Lopato and Langridge). Among LEA genes, a nuclear gene *cor14b* is responsible of drought stress tolerance in wheat.

Reduced height genes (Rht) are responsible for short stature in wheat (Borojevic and Borojevic, 2005). Dwarfing wheat genes Rht-B1b, Rht-D1b and Rht8 have been identified (Gasperini et al., 2012) and found positively correlated with drought tolerance.

Myeloblastosis oncogenes (MYB) are involved in several processes of growth of plant, developmental stages of plant and response to stress. In wheat, *TaMYB30* and TaMYB30-B gene has been identified which encodes for R2R3-type MYB protein and conferred drought tolerance in transgenic *Arabidopsis*. (Zhang et al., 2012). Another wheat gene *TaMYB33* has been reported to be involved in detoxification of reactive oxygen species (ROS) and it confers tolerance in wheat against salt and drought stresses (Qin et al., 2012). TaMYB2 gene of wheat also conferred tolerance in drought stress in wheat (Garg et al., 2012).

Wheat expansis protein (EXPB) is a main regulator of cell wall extension during plant growth. In wheat, the expression of *TaEXPB23* corresponded to water stress response and coleoptiles growth in wheat (Han et al., 2012). According to Han, Li et al. 2012 transgenic tobacco overexpressing *TaEXPB23* showed enhanced water retention ability (WRA) and decreasing osmotic potential. The ability of water retention of *TaEXPB23* gene may be used in wheat cultivars to improve water retention ability in wheat so that wheat can perform better in drought condition.

Aquaporin (AQP) protein is vital for plants to contest stress caused by water scarcity. AQP protein belongs to a large family in the major intrinsic protein (MIP) and is responsible for the transport of water and other tiny molecules across living membranes. Due to allohexaploid nature wheat genome and incomplete wheat genome sequence, a very little information is available about the wheat AQPs. However, a study conducted on overexpression of *TaAQP7* conferred drought stress tolerance in transgenic tobacco, showed concurrence with observations in tolerant wheat cultivars which showed enhanced expression of the said gene.

Sucrose non-fermenting1-related protein kinases 2 (SnRK2) play a vital role in abiotic stress signaling in plants. *TaSnRK2.8* has been reported as a regulatory factor, involved in many stress response pathways as well as provides strength to plasma membrane stability. Overexpression of *TaSnRK2.8* in transgenic *Arabidopsis* showed enhanced tolerance to drought, salt and cold stresses (Zhang et al., 2010). Based on these observations, this gene can therefore be utilized in wheat improvement against drought stress.

Wheat gene coding for hypothetical HPS-like protein, showed drought and salt stress tolerance in transgenic *Arabidopsis* with a considerably lower levels of amylase, glucose and malic acid leading to stomatal closure and hence improved tolerance against salt and drought (Xiao et al., 2012).

Abscisic acid (ABA)-stress and ripening-induced (ASR) proteins, are suggested to be involved in abiotic stress. Overexpression of *TaASR1* in tobacco resulted in increased drought tolerance. Transgenic tobacco containing this gene showed ROS scavenging and higher level of relative water content, superoxide dismutase and catalase. A wheat gene *TaSIP* (*Triticum aestivum* salt-induced protein) confers tolerance in transgenic *Arabidopsis* and *Oryza sativa* against high level of salt and drought (Du et al., 2013). Overexpression of *Triticum aestivum* salt-related hypothetical protein *(TaSRHP),* in *Arabidopsis* causes enhanced resistance to salt and water scarcity condition. As a consequence of expression of this gene there is lower level of sodium ion and increased level of potassium ions and proline (Hou et al., 2013)

WRKY-type transcription factors are involved in several stages of growth of plant, response to stress and developmental stages. These WRKY genes have been reported to take part in abiotic stresses tolerance. Transgenic *Arabidopsis* having WRKY genes, TaWRKY2 and TaWRKY19 showed drought and salt stress tolerance (Niu et al., 2012).

CONCLUSION

Wheat being an important food crop has always been of interest to plant breeders. Several efforts have been made to increase its production in general as well as under drought stress. Breeders explored several useful traits including osmotic adjustment, cell membrane stability, stomatal conductance etc. and bred varieties having better performance. Although molecular markers have also been discovered through QTL analysis having positive correlation with drought tolerance, the complex nature of hexaploid wheat genome made it difficult to clearly identify the locus of extremely important markers. Several genes have been discovered from wheat and showed involvement in important biological pathways that confers drought tolerance in wheat. However, still a lot to be explored about these discovered genes as most of them has only been studied in model plants (e.g. *Arabidopsis*, tobacco, etc.). The next step could be the incorporation of drought tolerant genes either through genetic transformation or gene breeding coupled with marker assisted selection.

REFERENCES

Abdelmalek C, Khaled T. 2011. Physiological behavior of wheat genotypes from algerian semi-arid regions grown under salt stress. African J. Agri. Res. 5:636-641.

Akram HM, Iqbal MS, Saeed M, Yar A, Ali A, Sahi K, Nadeem MA. 2004. Drought tolerance studies of wheat genotypes. Pak. J. Biol. Sci. 7:90-92.

Bartoli CG, Gomez F, Gergoff G, Guiamét JJ, Puntarulo S. 2005. Up-regulation of the mitochondrial alternative oxidase pathway enhances photosynthetic electron transport under drought conditions. J. exp. bot. 56:1269-1276.

Bensen R, Castiglioni P, Korte J, Bell E, Hinchey B, Loida P, Ahrens J. 2008. Transgenic plants with increased glycine-betaine, Google Patents.

Blum A, Ebercon A. 1981. Cell membrane stability as a measure of drought and heat tolerance in wheat. Crop Sci. 21:43-47.

Borojevic K, Borojevic K. 2005. The transfer and history of "reduced height genes"(Rht) in wheat from japan to europe. J.Heredity 96:455-459.

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

Budak H, Akpinar BA, Unver T, Turktas M. 2013. Proteome changes in wild and modern wheat leaves upon drought stress by two-dimensional electrophoresis and nanolc-esi–ms/ms. Plant Mol. Biol.:1-15.

Caruso G, Cavaliere C, Foglia P, Gubbiotti R, Samperi R, Laganà A. 2009. Analysis of drought responsive proteins in wheat (*Triticum durum*) by 2D-PAGE and MALDI-TOF mass spectrometry. Plant Sci. 177:570-576.

Caruso G, Cavaliere C, Guarino C, Gubbiotti R, Foglia P, Laganà A. 2008. Identification of changes in *triticum durum* L. Leaf proteome in response to salt stress by two-dimensional electrophoresis and maldi-tof mass spectrometry. Anal. Bioanal. Chem. 391:381-390.

Chen HCH, Jiang J-GJJ. 2010. Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environ. Rev. 18:309-319.

Dashti H, Yazdi-Samadi B, Ghannadha M, Naghavi M, Quarri S. 2007. Qtl analysis for drought resistance in wheat using doubled haploid lines. Int. J. Agric. Biol. 9:98-102.

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

Du HY, Shen YZ, Huang ZJ. 2013. Function of the wheat tasip gene in enhancing drought and salt tolerance in transgenic arabidopsis and rice. Plant. Mol. Biol. 81:417-29..

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra S. 2009. Plant drought stress: Effects, mechanisms and management. Sust. Agri.:153-188.

Ferro M, Salvi D, Brugière S, Miras S, Kowalski S, Louwagie M, Garin J, Joyard J, Rolland N. 2003. Proteomics of the chloroplast envelope membranes from arabidopsis thaliana. Mol. Cell. Prot. 2:325-345.

Gallé Á, Csiszár J, Secenji M, Guóth A, Cseuz L, Tari I, Györgyey J, Erdei L. 2009. Glutathione transferase activity and expression patterns during grain filling in flag leaves of wheat genotypes differing in drought tolerance: Response to water deficit. J. Plant Physiol. 166:1878-1891.

Garg B, Lata C, Prasad M. 2012. A study of the role of gene tamyb2 and an associated snp in dehydration tolerance in common wheat. Mol. Biol. Rep. 39:10865-71.

Gasperini D, Greenland A, Hedden P, Dreos R, Harwood W, Griffiths S. 2012. Genetic and physiological analysis of rht8 in bread wheat: An alternative source of semi-dwarfism with a reduced sensitivity to brassinosteroids. J. Exp. Bot. 63:4419-36.

Ge P, Ma C, Wang S, Gao L, Li X, Guo G, Ma W, Yan Y. 2012. Comparative proteomic analysis of grain development in two spring wheat varieties under drought stress. Anal. Bioanal. Chem. 1-17.

Gregersen PL, Holm PB. 2006. Transcriptome analysis of senescence in the flag leaf of wheat (*Triticum aestivum* L.). Plant Biot. J. 5:192-206.

Han Y, Li A, Li F, Zhao M, Wang W. 2012. Characterization of a wheat (*Triticum aestivum* L.) expansin gene, taexpb23, involved in the abiotic stress response and phytohormone regulation. Plant. Physiol. Biochem. 54:49-58.

Hou X, Liang Y, He X, Shen Y, Huang Z. 2013. A novel aba-responsive tasrhp gene from wheat contributes to enhanced resistance to salt stress in arabidopsis thaliana. Plant Mol. Biol. Rep. 1-11. DOI: 10.1007/s11105-012-0549-9.

Hu H, Dai M, Yao J, Xiao B, Li X, Zhang Q, Xiong L. 2006. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. Pro. Nat. Aca. Sci. 103:12987-12992.

Jang C, Kim J, Haam J, Lee M, Kim D, Li Y, Seo Y. 2003. Expressed sequence tags from a wheat-rye translocation line (2bs/2rl) infested by larvae of hessian fly [mayetiola destructor (say)]. Plant Cell Rep. 22:150-158.

Jones C, Jacobsen J, Wraith J. 2003. The effects of p fertilization on drought tolerance of malt barley, Western Nutrient Management Conference, Salt Lake City, UT. pp. 88-93.

Kirigwi F, Van Ginkel M, Brown-Guedira G, Gill B, Paulsen G, Fritz A. 2007. Markers associated with a qtl for grain yield in wheat under drought. Mol. Breed. 20:401-413.

Kong F-J, Oyanagi A, Komatsu S. 2010. Cell wall proteome of wheat roots under flooding stress using gel-based and lc ms/ms-based proteomics approaches. Biochimica et Biophysica Acta (BBA)-Prot. Proteom. 1804:124-136.

Lata C, Prasad M. 2011. Role of drebs in regulation of abiotic stress responses in plants. J Exp Bot 62:4731-48. DOI: 10.1093/jxb/err210.

Lopato S, Langridge P. 2011. Engineering stress tolerance in cereals using dreb/cbf genes: Outcomes, problems and perspectives. ISB News Rep. April.

Merewitz EB, Gianfagna T, Huang B. 2011. Protein accumulation in leaves and roots associated with improved drought tolerance in creeping bentgrass expressing an ipt gene for cytokinin synthesis. J. Exp. Bot. 62:5311-5333.

Mohammadi M, Kav NN, Deyholos MK. 2007. Transcriptional profiling of hexaploid wheat (*Triticum aestivum* L.) roots identifies novel, dehydration- responsive genes. Plant, Cell Env. 30:630-645.

Mohapatra PK, Patro L, Raval MK, Ramaswamy NK, Biswal UC, Biswal B. 2010. Senescence- induced loss in photosynthesis enhances cell wall β- glucosidase activity. Physiol. Plant. 138:346-355.

Morgan J, Tan M. 1996. Chromosomal location of a wheat osmoregulation gene using RFLP analysis. Funct. Plant Biol. 23:803-806.

Moustafa M, Boersma L, Kronstad W. 1996. Response of four spring wheat cultivars to drought stress. Crop Sci. 36:982-986.

Narita Y, Taguchi H, Nakamura T, Ueda A, Shi W, Takabe T. 2004. Characterization of the salt-inducible methionine synthase from barley leaves. Plant Sci. 167:1009-1016.

Navarre DA, Wendehenne D, Durner J, Noad R, Klessig DF. 2000. Nitric oxide modulates the activity of tobacco aconitase. Sci. Signal. 122:573.

Nishizawa Y, Saruta M, Nakazono K, Nishio Z, Soma M, Yoshida T, Nakajima E, Hibi T. 2003. Characterization of transgenic rice plants over-expressing the stress-inducible beta-glucanase gene gns1. Plant. Mol. Biol. 51:143-52.

Niu CF, Wei W, Zhou QY, Tian AG, Hao YJ, Zhang WK, Ma B, Lin Q, Zhang ZB, Zhang JS, Chen SY. 2012. Wheat WRKY genes TAWRKY2 and TAWRKY19 regulate abiotic stress tolerance in transgenic arabidopsis plants. Plant Cell Environ. 35:1156-70.

Pan X, Wang Y, Wang G, Cao Q, Wang J. 2002. Relationship between growth redundancy and size inequality in spring wheat populations mulched with clear plastic film. Acta Phytoecol. Sinica 26:177-184.

Qin Y, Wang M, Tian Y, He W, Han L, Xia G. 2012. Over-expression of TAMYB33 encoding a novel wheat myb transcription factor increases salt and drought tolerance in arabidopsis. Mol. Biol. Rep. 39:7183-92.

Rad RN, Kadir MA, Jaafar HZ, Gement D. 2012. Physiological and biochemical relationship under drought stress in wheat (*Triticum aestivum* L.). Afr. J. Biotechnol. 11:1574-1578.

Ravanel S, Block MA, Rippert P, Jabrin S, Curien G, Rébeillé F, Douce R. 2004. Methionine metabolism in plants chloroplasts are autonomous for de novo methionine synthesis and can import s-adenosylmethionine from the cytosol. J. Biol. Chem. 279:22548-22557.

Rebetzke G, Rattey A, Farquhar G, Richards R, Condon T. 2012. Genomic regions for canopy temperature and their genetic association with stomatal conductance and grain yield in wheat. Funct. Plant Biol. 40:14-33

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

Sawahel WA, Hassan AH. 2002. Generation of transgenic wheat plants producing high levels of the osmoprotectant proline. Biotechnol. Let. 24:721-725.

Shafeeq S, Zafar Y. 2006. Genetic variability of different wheat (*Triticum aestivum* L.) genotypes/cultivars under induced water stress. Pak. J. Bot. 38: 1671-1678

Shewry P. 2009. Wheat. J. Exp. Bot. 60:1537-1553.

Tang Y, Liu M, Gao S, Zhang Z, Zhao X, Zhao C, Zhang F, Chen X. 2012. Molecular characterization of novel tanac genes in wheat and overexpression of tanac2a confers drought tolerance in tobacco. Physiol. Plant 144:210-24.

Wei B, Jing R, Wang C, Chen J, Mao X, Chang X, Jia J. 2009. Dreb1 genes in wheat (*Triticum aestivum* L.): Development of functional markers and gene mapping based on snps. Mol. Breed. 23:13-22.

Xiao Y, Huang X, Shen Y, Huang Z. 2012. A novel wheat α- amylase inhibitor gene, tahps, significantly improves the salt and drought tolerance of transgenic arabidopsis. Physiol. plant. doi: 10.1111/j.1399-3054.2012.01707.x

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

Zhang H, Guo C, Li C, Xiao K. 2008. Cloning, characterization and expression analysis of two superoxide dismutase (sod) genes in wheat (*Triticum aestivum* L.). Front. Agric. China 2:141-149.

Zhang H, Mao X, Wang C, Jing R. 2010. Overexpression of a common wheat gene TASNRK2. 8 enhances tolerance to drought, salt and low temperature in arabidopsis. PLOS One 5:e16041.

Zhang L, Zhao G, Xia C, Jia J, Liu X, Kong X. 2012. A wheat R2R3-MYB gene, tamyb30-b, improves drought stress tolerance in transgenic arabidopsis. J. Exp. Bot. 63:5873-85.

Zheng X, Chen B, Lu G, Han B. 2009. Overexpression of a nac transcription factor enhances rice drought and salt tolerance. Biochem. Biophys. Res. Commun. 379:985-9.