



ISSN (E): 2277- 7695

ISSN (P): 2349-8242

NAAS Rating: 5.03

TPI 2019; 8(2): 714-724

© 2019 TPI

www.thepharmajournal.com

Received: 29-12-2018

Accepted: 30-01-2019

W Nisa

Division of Genetics and Pant
Breeding, Faculty of Agriculture,
SKUAST-K, Jammu and
Kashmir, India

V Nisa

Division of Genetics and Pant
Breeding, Faculty of Agriculture,
SKUAST-K, Jammu and
Kashmir, India

SA Nagoo

Dryland Agriculture Research
Institute, Kashmir, Jammu &
Kashmir, India

ZA Dar

Dryland Agriculture Research
Institute, Kashmir, Jammu &
Kashmir, India

Correspondence

W Nisa

Division of Genetics and Pant
Breeding, Faculty of Agriculture,
SKUAST-K, Jammu and
Kashmir, India

Drought tolerance mechanism in wheat: A Review

W Nisa, V Nisa, SA Nagoo and ZA Dar

Abstract

Drought is one of the most important phenomena which limit crops' production and yield, Crops demonstrate various morphological, physiological, biochemical, and molecular responses to tackle drought stress, Plant's vegetative and reproductive stages are intensively influenced by drought stress, Drought tolerance is a complicated trait which is controlled by polygenes and their expressions are influenced by various environmental elements, In wheat, there are several genes which are responsible for drought stress tolerance and produce different types of enzymes and proteins for instance, late embryogenesis abundant (lea), responsive to abscisic acid (Rab), proline, glutathione-S-transferase (GST), and carbohydrates during drought stress, Drought stress can also influence plants in terms of protein changes, antioxidant production, osmotic adjustment, hormone composition, root depth and extension, opening and closing of stomata, cuticle thickness, inhibition of photosynthesis, decrease in chlorophyll content, reduction in transpiration, and growth inhibition (Yordanov *et al*) to stand with some osmotic changes in their organs, Drought affects photosynthesis negatively by changing inner structure of chloroplast, destruction of photosystem II releasing complex can disturb production and use of electrons, causing lipid peroxidation thus reduction in biomass and in turn yield,

Keywords: Late embryogenesis proteins, abscisic acid, photosystem II, osmotic adjustment,

Introduction

Drought tolerance

Potential of crop plants to maintain their growth and development under drought stress is termed as drought tolerance, Yield stability is also associated with drought tolerance under prevailing drought conditions, Tolerance is very complex mechanism and plants have evolved numerous adaptations at physiological and molecular levels to confer drought tolerance, Higher economic yield under drought stress is the characteristic feature of drought tolerant accessions, Survival is important at seedling stages whereas, later on just survival without economic yield have no importance for breeders and farmers (Bänziger *et al*, 2000) [3], Plant growth and development, plant phenology, grain filling and translocation of photo assimilate reserves are important traits to be targeted for improvement of drought tolerance in maize (Edmeades 2013) [10], Osmo protection by osmotic adjustment and antioxidant scavenging defence system, plant growth regulators, water channel proteins, stress responsive proteins, transcription factors and signaling pathways actively participate in conferring drought tolerance in crop plants

Drought in wheat

Drought is one of the major abiotic stresses that affect at least 60% of wheat production in high-income countries and about 32% of 99 million hectares in low-income least developed countries (Chen *et al*, 2012) [5], Water deficit might decrease wheat grain yield from 17 to 70% (Nouri-Ganbalani *et al*, 2009), Daryanto *et al*, 2016) [8] reported 20,6% yield losses in 40% reduced water, Double ridge to anthesis stage is the most sensitive growth period regarding wheat yield to water deficit because of the negative influence on number of spikelets and ultimately kernels per spike, Water deficit decreases grain yield by affecting anthesis and grain-filling period, Drought stress may decrease leaf water potential, consequently lowering turgor, stomatal conductance, and photosynthesis, and, finally, lessening growth and yield of wheat (Chen *et al*, 2012) [14], Therefore, the study of wheat plant traits in response of drought stress is crucial for its genetic improvement to ensure high yield in water-deficit conditions,

Mechanisms for tolerance

1. Reduction in leaf area

Typically, as the water content of the plant decreases, its cells shrink and the cell walls relax,

This decrease in cell volume results in lower turgor pressure and the subsequent concentration of solutes in the cells, The plasma membrane becomes thicker and more compressed because it covers a smaller area than before, Because turgor reduction is the earliest significant biophysical effect of water stress, turgor-dependent activities such as leaf expansion and root elongation are the most sensitive to water deficits Cell expansion is a turgor-driven process Because leaf expansion depends mostly on cell expansion, the principles that underlie the two processes are similar, Inhibition of cell expansion results in a slowing of leaf expansion early in the development of water deficits, The smaller leaf area transpires less water, effectively conserving a limited water supply in the soil over a longer period, Reduction in leaf area can thus be considered a first line of defense against drought,

2. Closure of Stomata (Hydro passive)

When the onset of stress is more rapid or the plant has reached its full leaf area before initiation of stress, other responses protect the plant against immediate desiccation, Under these conditions, stomata closure reduces evaporation from the existing leaf area, Thus, stomatal closure can be considered a third line of defense against drought, Uptake and loss of water in guard cells changes their turgor and modulates stomatal opening and closing, Because guard cells are located in the leaf epidermis, they can lose turgor as a result of a direct loss of water by evaporation to the atmosphere, The decrease in turgor causes stomatal closure by hydro passive closure, This closing mechanism is likely to operate in air of low humidity, when direct water loss from the guard cells is too rapid to be balanced by water movement into the guard cells from adjacent epidermal cells,

3. Reduction in photosynthesis

As stomata close during early stages of water stress, water-use efficiency may increase (i.e., more CO₂ may be taken upper unit of water transpired) because stomatal closure inhibits transpiration more than it decreases intercellular CO₂ concentrations, As stress becomes severe, however, the dehydration of mesophyll cells inhibits photosynthesis, mesophyll metabolism is impaired, and water-use efficiency usually decreases, Results from many studies have shown that the relative effect of water stress on stomatal conductance is significantly larger than that on photosynthesis,

4. Water relations

Relative water content (RWC) is an important indicator of water status as compared to leaf water potential in wheat under water deficit (Lugojan and Ciulca 2011) and has been utilized for the selection of drought tolerant cultivars in wheat (Bayoumi et al, 2008), Drought applied at later stage of plant growth (after 6 weeks of emergence) has more deleterious effects on water relations, nutrient uptake, growth, and yield than early imposed drought (after 3 weeks of seedling emergence) in wheat (Nawaz et al, 2014), Drought significantly reduces chlorophyll content, membrane stability and RWC of wheat cultivars at flowering stage (Moayedi et al, 2010), Drought stress reduced relative water content by 43% (from 88 to 45%) in four genotypes of bread wheat (Siddique et al, 2000), Reduction of RWC closes stomata that will reduce photosynthesis rate, The scarcity of water impedes osmotic regulation, whereas alternate drying and re-watering induced osmotic regulation that improved plant's water use efficiency under drought conditions, High relative moisture

content is a tolerance approach to water deficit and is due to more osmotic regulation (Keyvan 2010), Drought tolerant genotypes maintained high turgor potential and relative water content to signify that limited water had a little effect on their protoplasmic structure as compared to sensitive genotypes which indicate a highly positive correlation between RWC and photosynthetic rate (Moayedi et al, 2010), Maintenance of leaf turgor is an important adaptive mechanism that plays an important role in stomatal regulation and photosynthetic activities under water-deficit conditions (Lipiec et al, 2013)

Signal Transduction

The machinery leading to the expression of drought-stress genes conforms to the general cellular model, with a complex signal transduction cascade that can be divided into the following basic steps:

- (a) Perception of stimulus
- (b) processing, including amplification and integration of the signal
- (c) a response reaction in the form of de novo gene expression,

The drought-activated signal transmission process has begun to be dissected at the molecular level, mostly on the basis of studies of isolated drought-responsive genes, Endogenous ABA levels have been reported to increase as a result of water deficit in many physiological studies, and therefore ABA is thought to be involved in the signal transduction (15, 43), Many of the drought-related genes can be induced by exogenous ABA; however, this does not necessarily imply that all these genes are also regulated by ABA in vivo,

1. Transcription factors: Natural master regulators of cellular processes and modifier of traits in response Transcription factors (TF s) have the potential to regulate multistep complex pathways by modifying the metabolite fluxes in predictable pattern, Stress responsive pathways are regulated at the level of transcription factors, Studies of transcriptional factor regulation were mostly conducted on model plant *Arabidopsis thaliana*, TFs of more than 50 different families encoded by 1700 different genes were reported in *Arabidopsis* (Yang et al, 2010) ^[60], In present study we are going to discuss only those TFs which are responsive to drought stress and confer drought tolerance, ABA responsive element binding factors (AREB/ABF) are member of basic leucine zipper (bZIP) TF family; they are involved in ABA signaling under drought stress and seed maturation, AREB/ABF recognizes and binds ABA responsive 2 element (ABRE) and conserves cis-element to regulate the expression of downstream genes (Mundy et al, 1990), ABRE is located in the promoter region of ABA responsive genes (Yamaguchi-Shi nozaki and Shinozaki 2006) ^[59], Stomatal closure and reduced transpirational losses are the result of increased ABA contents due to over expression of AREB 1/ABF 2, ABF3 or ARE B2/ABF4 (Kang et al, 2002) ^[24], ABA-independent dehydration responsive TF family is known as DREB TF family, These TFs act as response regulator under drought stress, cold stress and for the developments of leaf, flower and seed, For improvement of stress tolerance in crops DREB1 signaling pathway is extensively explored, d by Yang et al, 2010) ^[60], Two types of DREB (DREB1 and DREB2) are found responsive for different stresses, DREB1 is responsive to cold stress whereas, DREB2 is responsive to drought, heat and salt

stresses, Zinc Finger Protein (ZFP) TFs, are strongly induced by salinity, drought, ABA and cold treatments which depicts that these TFs are dynamically involved in stress responses through functioning as transcriptional repressors or activators (Sakamoto et al, 2000, 2004), Members of ZFP TF family like Drought and Salt Tolerance (DST; Huang et al, 2009) ^[18], OsZFP252 (Xu et al, 2008) and ZAT10 (Xiao et al, 2009) ^[57] are actively involved in regulation of dehydration responses, ZFP252 is found to be located upstream of DREB1A TF and upregulated the accumulation of soluble sugars and proline, TaRZF38 and TaRZF70 were expressed in the wheat root while TaRZF74 and TaRZF59 were expressed in embryo and endosperm at the highest level,

2. Promoter elements: cis - regulatory elements are the regions of non- coding DNA which regulates the transcription neighbouring genes, These regulate gene transcription by binding to transcription factors, Promoters are CREs consisting of relatively short sequences of DNA which include site where transcription is initiated, The best-characterized *cis*-element in the context of drought stress is the ABA-responsive element (ABRE), which contains the palindromic motif CACGTG with the G-box ACGT core element, In wheat The best-studied examples of these ABRE promoter elements are Em1a for Em gene, The *rd29A* gene has at least two *cis*-acting elements, The 9-bp direct repeat sequence, TACCGACAT, termed the dehydration-responsive element (DRE), functions in the initial rapid response of *rd29A* to drought, salt, or low temperature (144)

3. Signaling pathway: Adaptive responses in plants are broadly categorized into three categorical groups ,(a) osmotic adjustment or osmotic homeostasis; (b) stress damage control, detoxification and repair, (c) growth control (reviewed by Zhu 2002) ^[62], Depending on plant responses, drought stress signaling is again categorized into three functional characteristics groups ; (a) osmotic stress signaling for restoration of cellular homeostasis; (b) detoxification stress signaling to prevent cell damage and to repair cell damages; (c) signaling to maintain cell division and cell expansion to sustain growth, Homeostasis and detoxification signaling confer drought tolerance and regulate the stress responses to maintain growth, Osmotic stress signaling is accompanied by protein phosphorylation, Protein kinases are activated in response of osmotic stress, Calcium signaling in response of osmotic stress stimulates calcium- dependent protein kinases (CDPK) which further regulates downstream responses, Constitutive overexpression of CDPK protoplast regulates the expression of certain genes which are responsive to ABA , cold and osmotic stresses (Sheen 1996) ^[50], These findings link the induction of gene expression in response of osmotic

stress with calcium signaling, Transcriptome for protein kinases like , MAPK, MAPKK, MAPKKK and histidine kinase is increased

Osmotic Adjustment

Osmotic adjustment is described as development of water gradient to increase the water influx for maintaining turgor by lowering osmotic potential, Osmotic adjustment help to maintain the tissue water status, Damaging effects of drought are minimized by accumulation of solutes in cellular cytoplasm and vacuole, Protection is provided by maintaining the turgor potential and physiological processes with the help of osmotic adjustment (Taiz and Zeiger 2006) ^[52], Plant water status is determined by water potential, osmotic potential, turgor potential and relative water contents, Relative water contents act as integrative index for estimation of drought tolerance, Stomata are closed followed by reduction in CO₂ accumulation which is the result of reduction in relative water contents under drought stress, It permits cell expansion and plant growth with severe water deficit, It also permits stomata to stay partially open and CO₂ fixation to continue during water deficit, The mechanism is achieved by accumulation of compatible solutes or osmolytes, Osmolytes or osmoprotectants are neutral, organic and non-toxic compounds for plants, These osmolytes protect the cellular proteins and cellular membranes against the dehydrating effects of drought stress, Osmotic adjustment enables the plant to extract more of this tightly held water, but the increase in total available water is small, Thus the cost of osmotic adjustment in the leaf is offset by rapidly diminishing returns in terms of water availability to the plant, as can be seen by a comparison of the water relations of adjusting and non-adjusting species (Teiz & Zeiger),The wheat plant accumulates several inorganic and organic solutes in its cytosol to lessen its osmotic potential for maintenance of cell turgor,

1 Organic solutes

1, 1 Proline

Proline is an amino acid, Wheat plants accumulate proline to a greater extent than the other osmoregulators, especially in leaves (Farshadfar et al, 2008) ^[12] as a consequence of increasing collapse of proteins with immediate decline in its synthesis during the grain filling stage under water deficit (Nazarli and Faraji 2011) ^[39], It is osmotically active, controls storage of useful N, and plays a major part in membrane stability (Bandurska et al, 2008) ^[4], scavenging free radicals and buffering cellular redox potential that help wheat plants to combat abiotic stresses, As a signaling controller molecule, it initiates many mechanisms that help in adaptation to drought (Marcinińska et al, 2013) ^[34],

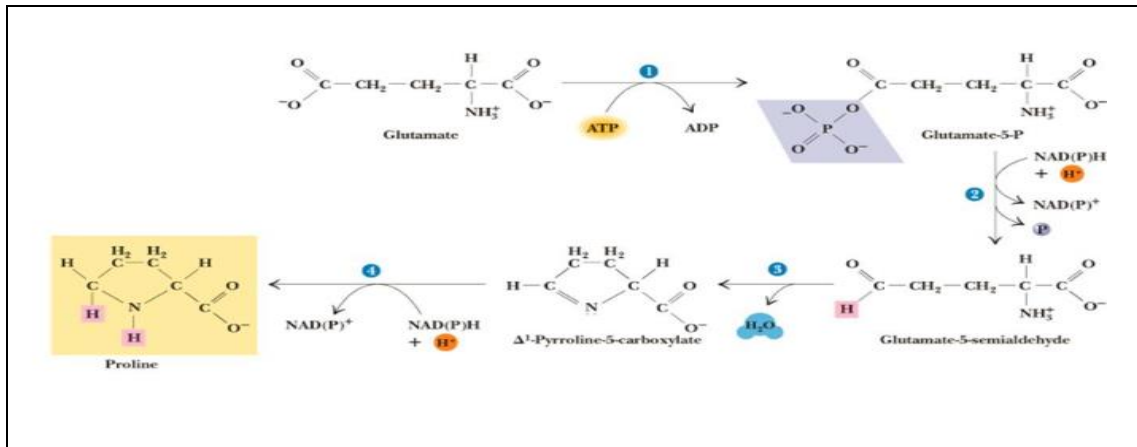


Fig 1: Pathway of proline synthesis

Proline oxidation pathway is suppressed by down-regulation of proline dehydrogenase (PDH) enzyme (first enzyme for proline oxidation) in maize under drought stress. Down-regulation of PDH is ABA independent regulation which showed that ABA is not contributor for its down-regulation under drought stress

1,2 Glycine betaine

Glycine betaine is organic, water soluble and non-toxic for plants and has very important role in protection of plants against drought, salinity, cold and heat stresses by acting as osmoprotectant. Glycine betaine shields cells from water deficit by preserving the osmotic balance between extra and intra cellular environment, alleviating quaternary structure of proteins, e.g., antioxidant enzyme protection and membrane proteins and the oxygen releasing complex of photosystem II (Gou et al, 2015) [15]. It also regulates intra cellular osmotic potential, controls pH of cytoplasm, and stabilizes cell membrane structure of wheat in drought stress (Huseynova et al, 2016) [21].

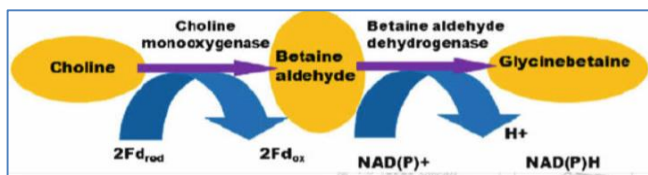


Fig 2: Synthesis of glycine betaine

1,3 Sugars

Soluble carbohydrates accumulate in plants as a result of drought (Zhang et al, 2009) [57] in addition to a decline in the net CO₂ integration rate. In extreme dehydrated states, sugars become an essential replacement for water, even more than proline, providing a hydration shell around proteins. Wheat genotypes accumulate more soluble sugars during the grain filling period than the pre-anthesis stage under drought stress, and the best stages for the screening of drought tolerant cultivars are grain filling and post-anthesis periods (Farshadfar et al, 2008) [12]. High osmotic stress reported to enhance the endogenous level of soluble sugars in wheat from 1,49 mg in control to 2,65 mg per gram of leaves under osmotic stress of - 8 bars (Qayyum et al, 2011) [41]. One way sugars may protect the cell during severe desiccation is by glass formation: Rather than solutes crystallizing, through the presence of sugars a supersaturated liquid is produced with the mechanical properties of a solid. During desiccation, glass

would fill space, thus preventing cellular collapse, and in restricting the molecular diffusion required by chemical reactions would permit a stable quiescent state. Among sugars trehalose is mostly found in wheat during drought which is a disaccharide. It not only act as carbohydrate storage molecule but also stabilizes proteins during desiccation by replacing water through hydrogen bonding to polar residues and prevents fusion of membranes. It also forms glass i.e. vitrification in dry state, a process that may be required for stabilization of macromolecules. It is synthesized by Trehalose-6-phosphate synthase encoded by gene TPS1 (found in cereals).

2, Inorganic Solutes

Like organic solutes, inorganic solutes also have a potential significance in water homeostasis and growth during water deficit.

2,1 Potassium: K has several functions that include protein biosynthesis, energy status, charge-balance, osmoregulation, and stomatal regulation. It also reduces transpiration and upholds turgor pressure under water-deficit environment.

2,2 Calcium: Ca also affects stress reactions of plants and growth by regulating different physiological processes including cell division, cell wall synthesis, stomatal regulation, water and solute movements, respiration, and translocation. These vital elements absorbed by roots are used for water conservation of plants under water deficit as direct inorganic osmotic solutes or indirect as possible regulators in biosynthesis of the organic solutes (Marcinińska et al, 2013) [34].

2,3 Silicon: It enhances photosynthetic gas exchange in wheat by improving water status, inorganic phosphate concentration in leaves and phosphoenolpyruvate (PEP) carboxylase activity under water-deficit environment. It was also reported that the alleviation of drought stress in wheat plants using silicon depends on the upsurge of antioxidant defense capabilities (Pei et al, 2010; Gong and Chen 2012) [41, 14], Ratnakumar et al, (2016) [45] observed that foliar application of 32 ppm of silicon increases RWC, leaf chlorophyll content, and also lower canopy temperatures.

2,4 Silicyclic acid: Ortho-silicyc acid had a robust influence on lessening drought and reduced the yield losses in wheat under water deficit. The phenolic compound salicylic acid (SA) (Kang et al, 2013) [25] is a phytohormone and growth regulator

that has a vital role in growth and development, ethylene biosynthesis, stomatal behavior, flower induction, and respiration in many plants (Kang et al, 2012) [27], It performs a critical role in plant biotic stress tolerance and is now generally recognized as chief signal transducer during biotic stress (Loutfy et al, 2012) [29], External application of SA also improves plant's abiotic stress tolerance (Kang et al, 2013) [25] including drought, These studies have mostly been done at physiological levels, proposing that SA induced drought tolerance is linked with an improved antioxidant defense mechanism (Horváth et al, 2007) [20], However, some studies have revealed that alleviation of abiotic stress by SA could be the result of changed expression of the genes encoding heat

shock proteins, osmotin, and pathogenesis-related proteins (Kang et al, 2013) [25], It is reported that application of SA at seedling stage to alleviate drought could produce real economic yields of wheat genotypes grown under water deficit, Role of SA on growth improvement of wheat seedlings has also been reported for other stressed environments (Loutfy et al, 2012) [29],

Role of ABA

ABA as a stress hormone is actively involved in modulation of growth, development and responses against stresses, ABA biosynthesis takes place in chloroplasts via carotenoid, pathway:

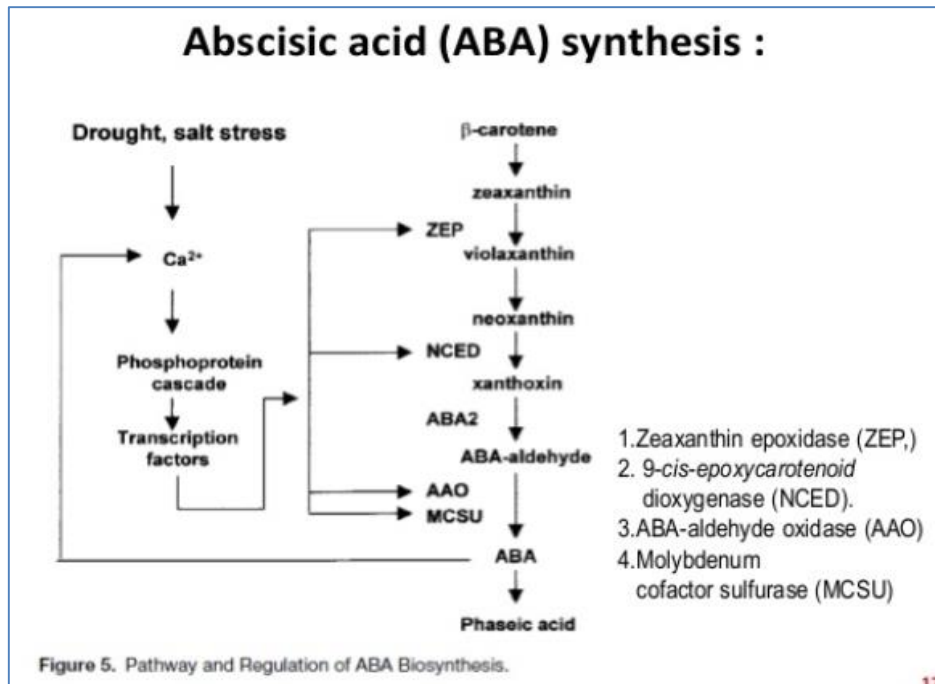


Fig 3: Synthesis of ABA via carotene

Under drought synthesis occurs in the leaf, redistribution within the mesophyll cell, import from the roots, and recirculation from other leaves, The concentration of ABA declines after rewatering because of degradation and export from the leaf, as well as a decrease in the rate of synthesis

1, Stomatal closure

High ABA concentration around guard cell results in stomata closure and helps to conserve water ABA also can act as a long distance communication signal between water stressed roots and leaves, which induces stomata closure, Since under drought conditions stomatal closure due to ABA formation prevents the intracellular water loss; ABA is aptly called as a "plant stress hormone", Li and Xu (2014) [30] ABA decreased significantly stomatal conductance, net photosynthetic rate and transpiration rate at all growth stages, Some factors such as xylem pH and the duration of the day control the transport of ABA into the root xylem, The pH of the xylem sap is increased under drought stress conditions; therefore, the loading of ABA into the root xylem and its transport to the shoot is promoted, Environmental factors, which increase the transpiration rate, may also cause an increase in the leaf sap pH, Increased leaf sap pH may promote ABA accumulation,

and then lead to reduction in stomatal conductance, Abscisic acid (ABA) produced in the roots and leaves during water stress is transported to the guard cells and activates signaling pathways leading to stomatal closure, It is transported into the guard cells by ATP- binding cassette (ABC) transporters that are located in the plasma membrane, When the ABC transporters are knocked out, ABA uptake is lower, stomata remain more open during drought and the stress tolerance is decreased (Mutava et al., 2015) [31], Abscisic acid signals are first recognized by several receptors (Mutava et al., 2015) [31], Regulation of stomatal opening is linked to transport of ions and water through channel proteins across the plasma and vacuole membrane (Arve *et al.*, 2013) [2], Abscisic acid induces the production of reactive oxygen species (ROS), which, in turn, act as a trigger for NO production, inhibition of membrane proton pumps, and Ca²⁺ influx across both the plasma and vacuole membranes, H⁺-AT Pases that hyperpolarize the plasma membranes must be inhibited to induce ABA mediated stomatal closure, The increased Ca²⁺ levels activate slow and rapid type anion channels, generating an anion efflux from the cells, The anion efflux depolarizes the membrane, which in turn causes K⁺ efflux through K⁺ out channels across both the vacuole and the plasma membrane,

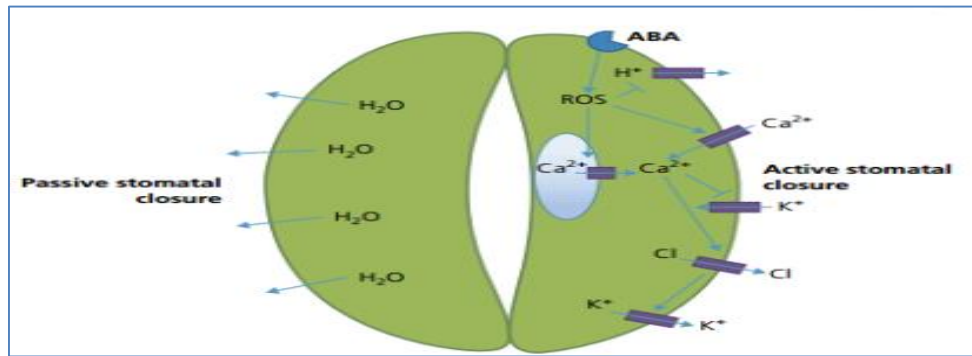


Fig 4: Two mechanisms of stomatal closure; hydro passive (left) and hydro active (right) pathways (adapted from Arve *et al.*, 2011) [2],

1,1 Genetics of closure

The increase in ABA plays a major role in stomatal closure that helps to minimize water loss by reducing transpiration occurring through stomata. This is brought about by regulating a sophisticated cascade of biochemical events that involves the ABA signal some complex (PYR/PYL-PP2C-SnRK2), as shown in Figure: 5 Chemical genetic screens have become pivotal in identifying the crosstalk between various signaling networks of major hormones (Sreenivasulu *et al.*, 2012) [48]. The stomatal closure is brought about through the well-described sophisticated cascade of ABA signal some complex (PYR/PYL-PP2C-SnRK2) mediated in a calcium-independent way (Sreenivasulu *et al.*, 2012) [48]. Abscisic acid-activated SnRK2 protein kinase functions in the ABA signal transduction pathway that controls stomatal closure,

SnRK2 is a member of the SNF1-related PK ase family, SnRK2s are activated by drought and ABA, The receptors interact with PP2C phosphatases, which are subsequently inhibited in their function of blocking downstream SnRK2/CDPK, It is distinguished that Ca²⁺ independent (left scheme) and Ca²⁺ dependent signalling (right scheme), SnRK2 proteins auto phosphorylate to come to an active state and further phosphorylate downstream targets such as AREB/ABF transcription factors or ion channels subsequently leading to ABA responses such as stomatal closure in guard cells, CDPKs on the other hand are released by PYR/PYL-PP2C complex and are activated by an increase in Ca²⁺ concentration and further phosphorylate ion channels (Sreenivasulu *et al.*, 2012) [48],

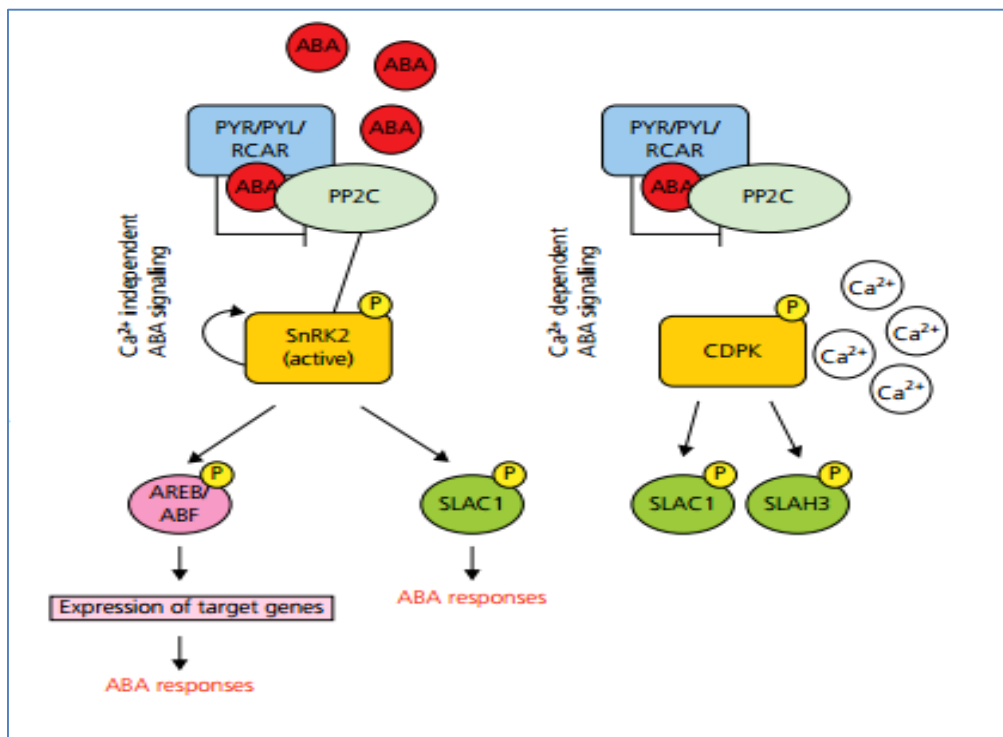


Fig 5: Signaling by ABA, (Sreenivasulu *et al.*, 2012), [48]

Degradation and Repair

During early drought in *A. thaliana*, there is an increase in levels of mRNA encoding ubiquitin extension protein (66), a fusion protein from which active ubiquitin is derived by proteolysis processing. This increase may be significant in terms of protein degradation, because ubiquitin has a role in tagging proteins for destruction. During drought stress,

protein residues may be modified by chemical processes such as deamination, isomerization, or oxidation, and it is thus likely that enzymes with functions in protein repair are upregulated in response to drought. Indeed, the response to desiccation in mosses may largely be repair based. An example of such repair processed in wheat is the observation that L-isopartyl methyltransferases may convert modified

L-isoaspartyl residues in damaged proteins back to L-aspartyl residues

Antioxidant Defence Mechanism

A decline in the net-photosynthetic process under water-deficit conditions is also associated with conflicts in biochemical routes of a non-stomatal nature, triggered by oxidation of chloroplast lipids and variations in the assembly of pigments and proteins, Production of reactive oxygen species (ROS) enhanced in response to drought stress however, the major source of ROS production is electron transport chain which operates in chloroplasts, Destruction of the photosystem II (PSII) oxygen releasing complex and reaction center can disturb production and use of electrons, resulting in the production of ROS that subjected cell membrane to lipid peroxidation (Wang et al, 2014), High concentrations of singlet oxygen (1O_2), superoxide radicals

(O_2), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH) resulted in oxidative damages to plants depending upon their endogenous levels, ROS may react with deoxyribonucleic acid, lipids, and proteins, leading to oxidative damage, inactivation of enzymes, and destroyed cellular structures associated with photosynthesis by impairing the normal functions of cells (Miller et al, 2010 [36]; ROS production is linear with the severity of water stress that triggered the peroxidation of membrane lipids and break down of nucleic acids, Cell organelles, i.e., chloroplasts, mitochondria, and peroxisomes are cytological locations and first target of active oxygen species, as well, Nitric oxide-mediated alternative pathways boosted photosynthesis under water deficit by circumventing severe decrease in electron transport chain of photosynthesis and finally inhibiting ROS production and oxidative damage in wheat leaves (Wang et al, 2016) [8],

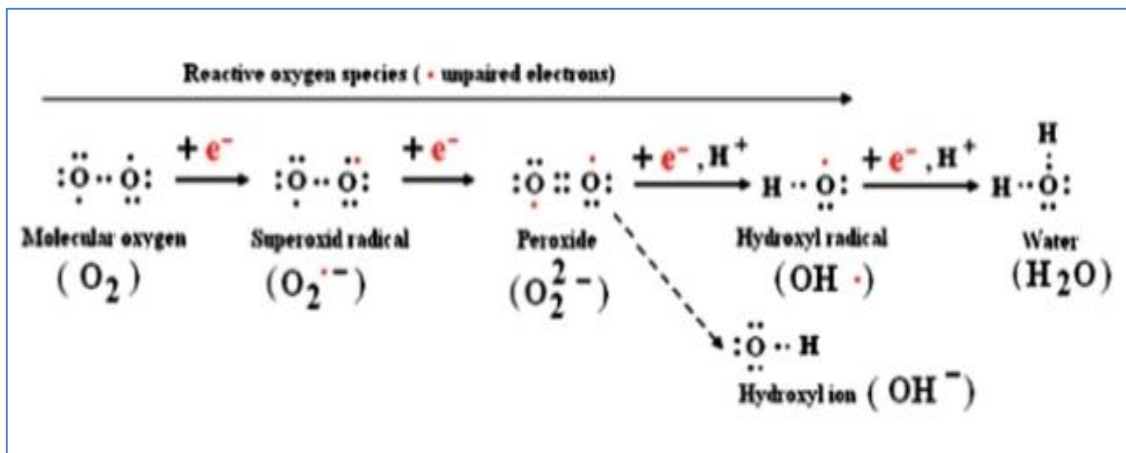


Fig 6: Generation of reactive oxygen species (Christin et al, 2012)

1, Antioxidation enzymes

Production of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), and glutathione peroxidase (GPx) in response to water stress is an adaptive mechanism well known in plants, Plants enhance the activity of peroxidases and glutathione against water stress induced oxidative damage, APX is the most important antioxidant enzyme of water-water and ascorbate–glutathione (ASH-GSH) cycles which scavenge superoxide radicals and H_2O_2 in the chloroplast under water-deficit conditions (Gill and Tuteja 2010), in wheat cultivars, APX activity varied depending on leaf developmental stage and duration of drought, Wheat plants subjected to mild drought enhance leaves' APX activity, whereas prolonged water deficit decreased its activity because of the increased production of malonic dialdehyde (MDA)

(Nikolaeva et al 2010) [38], Being scavengers of hydrogen peroxide, CAT and POD converts toxic levels of endogenous H_2O_2 into water and oxygen, Likewise, CAT activities were examined in wheat leaves subjected to severe drought and increased activity of CAT was noted, especially in susceptible cultivars (Simova-Stoilova et al, 2010) [46], Ascorbic acid as an antioxidant has a key influence on cell division, differentiation, and growth of plants, Foliar applied ascorbic acid alleviates drought by influencing stomatal closure, nutrient uptake, total chlorophyll content, protein synthesis, transpiration, flowering, and photosynthesis Foliar applied ascorbic acid increased wheat yield and chlorophyll content linked with leaf water potential regulation by moving minerals from leaves to flowers and by enhancing the CAT and APX activity (Hafez and Gharib 2016) [19],

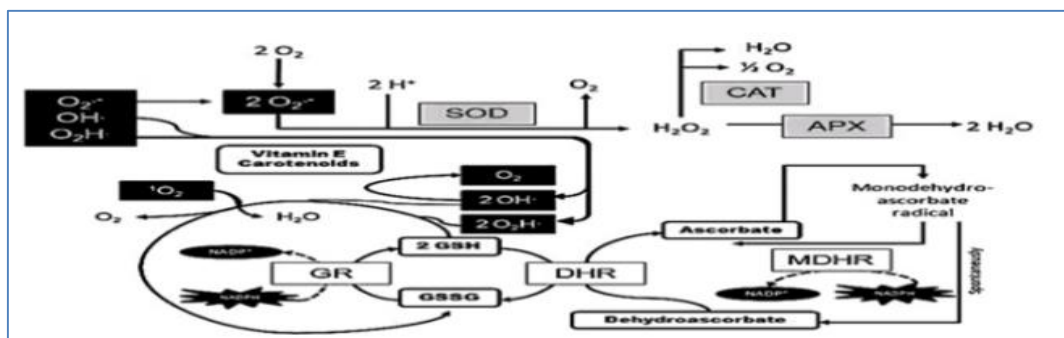


Fig 7: Scavenging of ROS (Ceron et al, 2012)

Stress Proteins

Certain proteins have critical role in imparting tolerance against drought stress, broadly these are known as stress proteins, Stress proteins are mostly water soluble and ensure tolerance by hydration of cellular contents,

1, late embryogenesis proteins (LEA)

LEA is a group of proteins which naturally accumulate in pollen grains, seeds and vegetative tissues during prevalence of abiotic stresses. Among these different groups, 1, 2 and 3 are main groups which consist of large number of LEA proteins. Proteins belonging to Group 1 undergo complex post-translational modifications (PTMs) including, acetylation, phosphorylation, deamination and methylation and these PTMs depict their seed specific role. Anti-aggregative properties are characteristic features of group- 2 and group- 3 LEA proteins, Groups 2 LEA proteins provide protection to membranes by preventing their denaturation, Groups 3 LEA proteins are linked in dehydration tolerance and prevent the cell shrinkage which is the result of water loss. During the mid- to late stages of seed development, specific mRNAs accumulate in embryos at the time of high levels of endogenous ABA, These mRNAs encode so-called

Late-Embryogenesis-Abundant (LEA)

proteins thought to be involved in desiccation tolerance, In wheat *HVA1* (D7 LEA group gene assists to increase growth under drought stress, *HVA1* gene produce a kind of protein which is in group 3 LEA and has 11 amino acid motifs in nine repeats, this gene was isolated from aleurone layer of barley and inserted in wheat embryos through particle bombardment method, LEA proteins are influenced by drought stress and their size in wheat reaches 200 kDa (Wcs200), Wheat LEA genes, PMA1959 (encoding group one of LEA protein) and PMA80 (encoding LEA protein's second group) improved water deficit resistance in rice. The *Em* gene of wheat which encodes LEA protein first group has been vastly researched [105]. In durum wheat, protein of groups two (dehydrins) and four of LEA proteins were studied by Ali-Benali et al, 2005 [33], *Td27e*, *Td29b*, and *Td16* gene transcripts were saved late in embryogenesis and throughout seed development, Transcripts of *Td11* gene were presented whereas no transcripts of *Td25a* gene were detected in seeds (Ali-Benali et al, 2005) [33].

A general structural feature of the LEA proteins is their biased amino acid composition, which results in highly hydrophilic polypeptides, with just a few residues providing 20–30% of their total complement, D19 protein from cotton contains 13% glycine and 11% glutamic acid.

1.1 Role

The randomly coiled moieties of some LEA proteins are consistent with a role in binding water, Total desiccation is probably lethal, and therefore such proteins could help maintain the minimum cellular water requirement, McCubbin & Kay in 1985 [35] have found that the Em protein (D19-group) from wheat is considerably more hydrated than most globular polypeptides because it is over 70% random coil in normal physiological conditions, A major problem under severe dehydration is that the loss of water leads to crystallization of cellular components, which in consequence damages cellular structures, This may be counteracted by LEA proteins, and some of the LEA proteins could essentially be considered compatible solutes, which supports the likely

role of sugars in maintaining the structure of the cytoplasm in the absence of water, They are involved in the “solvation” of cytosolic structures, The random coiling would permit their shape to conform to that of other structures and provide a cohesive layer with possibly greater stability than would be formed by sugars, Their hydroxylated groups would solvate structural surfaces. Crystallization of cellular components, which in consequence damages cellular structures, They also counter the effects of increasing ionic strength in the cytosol during desiccation, Such problems could be mitigated by the formation of salt bridges with amino acid residues of highly charged proteins, The repeating elements most likely exist as amphiphilic helices (Dure et al, 1993) [9], which means that hydrophobic and hydrophilic amino acids are contained in particular sectors of the helix, The helices probably form intramolecular bundles, which would present a surface capable of binding both anions and cations, eg, D7 LEA group,

Aquaporins

Aquaporins are membrane channel proteins ubiquitously present in all kingdoms of life, Although aquaporins were originally discovered as water channels, their roles in the transport of small neutral solutes, gases, and metal ions are now well established, Plants contain the largest number and greatest diversity of aquaporin homologs with diverse subcellular localization patterns, gating properties, and solute specificity, the transport of water across biological membranes through specialized pores rather than by simple diffusion was first proposed by Koefoed Johnsen *et al*, in 1953 [28] and then confirmed by Macey *et al*, in 1970, The molecular identity of the first water channel protein, aquaporin 1 (AQP1) was established by Agre and coworkers in 1992 based upon its ability to dramatically increase the water permeability of *Xenopus oocytes* expressing the *CHIP28* gene (Preston et al,1992), Although the first aquaporin member, Nodulin-26, GmNOD26 was identified in soybeans as early as 1987 (Fortin et al,1987) [13], the existence of water channels in plants was not clearly hypothesized until 1993 when Maurel *et al*, demonstrated the functional expression of the first plant aquaporin, Arabidopsis tonoplast intrinsic protein homolog (AtTIP1;1), in *Xenopus laevis* oocytes (Preston et al,1992) [40]. Aquaporins include seven subfamilies categorized according to their intracellular locations and sequence similarities: the plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), NOD26-like intrinsic proteins (NIPs) and small, basic intrinsic proteins (SIPs), the GlpF-like intrinsic proteins (GIPs), hybrid intrinsic protein (HIP), and the uncategorized X intrinsic protein (XIP), They are involved in symplast water movement (movement from one cell to another through plasmodesmata),

1, Role: It is widely accepted that, in most plant species, water uptake and transcellular water flow in roots are largely mediated by PIPs and TIPs, These are the most abundant aquaporins in the plasma membrane and tonoplast of the plant cells, respectively. All of these *PIP* genes that are down-regulated in response to drought are highly expressed in the roots, On the basis of transcriptome data, it is difficult to identify a concerted pattern of aquaporin expression in response to drought stress, Reverse genetics approaches based on one or a few genes provide a better snapshot than the whole transcriptome studies, Crucial involvement of PIPs in

modulating *Lpr* in response to various environmental stresses has been widely observed (Choumet et al,1994), Increased susceptibility of plants to water stress due to reduction in *Lpr* by silencing PIPs has been reported extensively in various plant species, Consistently, transgenic plants overexpressing aquaporins showed enhanced drought tolerance, For example, the overexpression of a BnPIP1 from *Brassica napus* in transgenic tobacco plants resulted in increased tolerance to drought stress (Yu et al, 2005) ^[58], Similarly, transgenic tobacco plants overexpressing the wheat aquaporin gene *TaAQP7* (*PIP2*) were more drought tolerant in comparison to non-transgenic tobacco plants due to enhanced water retention capabilities of transgenic plants, *TaAQP7* also increase water uptake in wheat,

Breeding for Drought Tolerance through Markers

Different molecular marker are currently available for genome mapping and tagging of different traits which is useful for Marker-assisted breeding (MAB) technique in wheat in stress conditions DNA markers can track presence of QTLs for drought tolerance (Thoday et al, 1996), For development of, In winter wheat, with the use of amplified fragment length polymorphism (AFLP) and simple sequence repeat (SSR) markers, QTL mappings for senescence of flag leaf (FLS) in normal and water-stressed environments have been studied, The responsible gene for this characteristic is revealed and the QTL is also detected on chromosome 2D associated with better performance under drought (Verma et al,2004) ^[13], Drought tolerance in plants through molecular linkage maps, Some markers in durum wheat are linked to grain yield and morpho-physiological characteristics for drought tolerance (Nachit et al,1993) ^[32], Leaf water potential, canopy temperature, chlorophyll inhibition, and proline content showed strong relationships with markers

Mapping of QTLs for Drought Tolerance in Wheat

Quantitative trait loci (QTL) is a location from where some genes influence a phenotype of quantitatively inherited trait, Genetic variations of a crop can be explored through QTL mapping (polygenes) (Ashraf et al,2008), Mapping of QTL allows the estimation of the places, quantity, size of effects for the phenotype, and gene activity pattern (Vinh et al, 2005) ^[37], In 2005, the first activity was conducted for cloning QT (Salvi et al, 2005) ^[51] to know and operate the characteristics which are responsible for drought resistance, QTL mapping for water stress resistance traits has been done in wheat and other crops, In wheat, due to drought stress, the place of genes which had influence on ABA concentration was detected (Quarrie et al,1996), It is detected that 5A chromosome transports gene(s) for ABA concentration, Quarrie et al,2005) ^[49] conducted mapping of QTLs for drought resistance in hexaploid wheat placed on chromosomes 1A, 1B, 2A, 2B, 2D, 3D, 5A, 5B, 7A, and 7B, Double haploid populations serve as a permanent source of QTL mapping

Conclusion and Future Perspective

Drought stress is one of the major limitations to crop production, To develop improved cultivars with enhanced to drought stress, identification of osmotic stress related molecules and determination of their roles and locations in several physiological, biochemical, and gene regulatory networks is necessary, Several QTLs for key morpho - physiological characteristics and yield were identified under water-limited conditions through creation of linkage maps

using parentals with different drought coping abilities, Analysis of drought response has been complicated in the absence of wheat genomic sequence data, However, with the recent advances in sequencing technologies, genome sequence of bread wheat is almost complete by the efforts of ITMI (The International *Triticeae* Mapping Initiative) and IWGSC (International Wheat Genome Sequencing Consortium), Availability of whole wheat genome sequence will contribute to the ongoing studies of exploring the extensive reservoir of alleles in drought tolerant wild germplasm, and this also enables better marker development, genome analysis and large scale profiling experiments, A well-organized combination of all components is required for further application of high-throughput phenotyping to develop drought tolerant wheat varieties in future, As water requirements of wheat vary from region to region, proper water budgeting of wheat is required, For this purpose, WUE regarding yield should be considered, Aquaporin proteins should be inserted via genetic engineering in wheat as these are the principal transporter of water in plants to enhance water use efficiency of modern wheat cultivars during drought stress,

References

1. Ashraf M, Athar HR, Harris PJC, Kwon TR, Some prospective strategies for improving crop salt tolerance,” *Advances in Agronomy*, 2008; 97:45-110,
2. Arve LE, Torre S, Olsen JE, Tanino KK, Stomatal responses to drought stress and air humidity, In: *Abiotic Stress in Plants – Mechanisms and Adaptations*, Shanker A (Ed.), In Tech Publication, 2011, 267-280,
3. Bänziger M, Edmeades GO, Beck D, Bellon M, Breeding for drought and nitrogen stress tolerance in maize: from theory to practice, *CIMMYT*, Mexico, 2000,
4. Bandurska H, Górny AG, Zielezińska M, Effects of water deficit on the relative water content, proline accumulation and injury of cell membranes in leaves of old and modern cultivars of winter wheat, *Acta Physiol*, 2008; 524:115-125,
5. Chen X, Min D, Yasir TA, Hu YG, Field crops research evaluation of 14 morphological, yield-related and physiological traits as indicators of drought tolerance in Chinese winter bread wheat revealed by analysis of the membership function value of drought tolerance (MFVD), *F Crop Res*. 2012; 137:195-201,
6. Chaumont FO, Barrieu FO, Wojcik E, Chrispeels MJ, Jung R, Aquaporins constitute a large and highly divergent protein family in maize, *Plant Physiol*, 2001; 125:1206-1215,
7. Chandler PM, Robertson M, Gene expression regulated by abscisic acid and its relation to stress tolerance, *Annu, Rev, Plant Physiol, Plant Mol, Biol*, 1994; 45(11):3-41,
8. Daryanto S, Wang L, Jacinthe PA, Cordain L, Simopoulos A, Ray D *et al*, Global synthesis of drought effects on maize and wheat production, Hui D, editor, *PLoS One*, 2016; 11:e0156362,
9. Dure L III, Arepeating 11-mer amino acid motif and plant desiccation, *Plant J*, 1993; 3(3):363-69,
10. Edmeades GO, Progress in achieving and delivering drought tolerance in maize-an update, Ithaca, ISAAA, 2013,
11. Sivamani E, Bahieldin A, Wraith JM *et al*, Improved biomass productivity and water use efficiency under water deficit conditions in transgenic wheat constitutively

- expressing the barley *HVA1* gene,” *Plant Science*, 2000; 155(1):1-9,
12. Farshadfar E, Ghasempour H, Vaezi H, Molecular aspects of drought tolerance in bread wheat (*T. aestivum*), *Pak J Biol Sci*, 2008; 11:118-122,
 13. Fortin MG, Morrison NA, Verma DPS, Nodulin-26, a peribacteroid membrane nodulin is expressed independently of the development of the peribacteroid compartment, *Nucleic Acids Res.* 1987; 15:813–824,
 14. Gong H, Chen K, The regulatory role of silicon on water relations, photosynthetic gas exchange, and carboxylation activities of wheat leaves in field drought conditions, *Acta Physiol Plant*, 2012; 34:1589-1594,
 15. Gou W, Tian L, Ruan Z, Zheng P, Chen F, Zhang L, *et al*, Accumulation of choline and glycinebetaine and drought stress tolerance induced in maize (*Zea mays*) by three plant growth promoting rhizobacteria (PGPR) strains, *Pak J Bot*, 2015; 47:581-586,
 16. Giraudat J, Parcy F, Bertauche N, Gosti F, Leung J *et al*, Current advances in abscisic acid action and signalling, *Plant Mol, Biol*, 1994; 26:1557-77,
 17. Gill S, Tuteja N, Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants, *Plant Physiol Biochem*, 2010; 48:909-930
 18. Huang XY, Chao DY, Gao JP, Zhu MZ, Shi M, Lin HX, A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control, *Genes Dev*, 2009; 23:1805-1817,
 19. Hafez EM, Gharib HS, Effect of exogenous application of ascorbic acid on physiological and biochemical characteristics of wheat under water stress, *GUASNR Int J Plant Prod*, 2016; 10:579–59
 20. Horváth E, Pál M, Szalai G, Páldi E, Janda T, Exogenous 4-hydroxybenzoic acid and salicylic acid modulate the effect of short-term drought and freezing stress on wheat plants, *Biol Plant*, 2007; 51:480-487,
 21. Huseynova IM, Rustamova SM, Suleymanov SY, Aliyeva DR, Mammadov AC, Aliyev JA, Drought-induced changes in photosynthetic apparatus and antioxidant components of wheat (*Triticum durum* Desf.) varieties, *Photosynth Res*, 2016; 130:215–223
 22. Thoday JM, Location of polygenes, *Nature*, 1961; 191(4786):368-370,
 23. Litts JC, Colwell GW, Chakerian RL, Quatrano RS, “The nucleotide sequence of a cDNA clone encoding the wheat Em protein,” *Nucleic Acids Research*, 1987; 15(8):3607-3618,
 24. Kang JY, Choi HI, Im MY, Kim SY, Arabidopsis basic leucine zipper proteins that mediate stress-responsive abscisic acid signaling, *Plant Cell*, 2002; 14:343-357,
 25. Kang GZ, Li GZ, Liu GQ, Xu W, Peng XQ, Wang CY, Zhu YJ, *et al*, Exogenous salicylic acid enhances wheat drought tolerance by influence on the expression of genes related to ascorbate-glutathione cycle, *Biol Plant*, 2013; 57:718-724,
 26. Kiyosue T, Yamaguchi-Shinozaki K, Shinozaki K, Cloning of cDNAs for genes that are early-responsive to dehydration stress (ERDs) in *Arabidopsis thaliana* L.; identification of three ERDs as HSP cognate genes, *Plant Mol, Biol*, 1994; 25:791-98,
 27. Kang G, Li G, Xu W, Peng X, Han Q, Zhu Y, *et al*, Proteomics reveals the effects of salicylic acid on growth and tolerance to subsequent drought stress in wheat, *J Proteome Res.* 2012; 11:6066-6079,
 28. Koefoed-Johnsen V, The contributions of diffusion and flow to the passage of D2O through living membranes: Effect of neurohypophysial hormone O11 isolated anuran skin, *Acta Physiol, Scand.*1953; 28:60–76, [Cross Ref] [Pub Med]
 29. Loutfy N, El-Tayeb MA, Hassanen AM, Moustafa MFM, Sakuma Y, Inouhe M, Changes in the water status and osmotic solute contents in response to drought and salicylic acid treatments in four different cultivars of wheat (*Triticum aestivum*), *J Plant Res*, 2012; 125:173-184
 30. Li X, Xu K, Effects of exogenous hormones on leaf photosynthesis of *Panax ginseng*, *Photosynthetica*, 2014; 52:152-156,
 31. Mutava RN, Prince SJK, Syed NH, Song L, Valliyodan B, Chen W, *et al*, Understanding abiotic stress tolerance mechanisms in soybean: A comparative evaluation of soybean response to drought and flooding stress, *Plant Physiol Biochem*, 2015; 86:109-120,
 32. Nachit MM, Baum M, Autrique E, Sorrells ME, Ali Dib T, Monneveux P, “Association of morphophysiological traits with RFLP markers in durum wheat,” in *Tolerance à la Sécheresse des Céréales en Zone Méditerranéenne*, P, Monneveux and M, Ben Salem, Eds., 159-171, *Diversité Génétique et Amélioration Variétale*, Montpellier, France, 1993,
 33. Ali-Benali MA, Alary R, Joudrier P, Gautier MF, Comparative expression of five LEA genes during wheat seed development and in response to abiotic stresses by real-time quantitative RT-PCR,” *Biochimica et Biophysica Acta*, 2005; 1730(1):56-65,
 34. Marcińska I, Czyczyło-Mysza I, Skrzypek E, Filek M, Grzesiak S, Grzesiak MT *et al*, Impact of osmotic stress on physiological and biochemical characteristics in drought-susceptible and drought-resistant genotypes, *Acta Physiol Plant*, 2013; 35:451-461
 35. McCubbin WD, Kay CM, Hydrodynamic and optical properties of the wheat Em protein, *Can, J, Biochem*, 1985; 63:803-10,
 36. Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R, Reactive oxygen species homeostasis and signaling during drought and salinity stresses, *Plant Cell Environ.* 2010; 33:453-467,
 37. Vinh NT, Paterson AH, Genome mapping and its implication for stress resistance in plants,” in *Abiotic Stresses: Plant Resistance through Breeding and Molecular Approaches*, M, Ashraf and P, J, C, Harris, Eds., Haworth Press, New York, NY, USA, 2005,
 38. Nikolaeva MK, Maevskaya SN, Shugaev AG, Bukhov NG, Effect of drought on chlorophyll content and antioxidant enzyme activities in leaves of three wheat cultivars varying in productivity, *Russ J Plant Physiol*, 2010; 57:87-95,
 39. Nazarli H, Faraji F, Response of proline, soluble sugars and antioxidant enzymes in wheat (*Triticum aestivum* L.) to different irrigation regimes in greenhouse condition, *Cercet Agron în Mold*, 2011; 44:27-33,
 40. Preston GM, Carroll TP, Guggino WB, Agre P, Appearance of water channels in xenopus oocytes red cell chip 28 protein, *Science.* 1992; 256:385–387, [Cross Ref] [Pub Med]
 41. Pei ZF, Ming DF, Liu D, Wan GL, Geng XX, Gong HJ, *et al*, Silicon improves the tolerance to water-deficit stress induced by polyethylene glycol in wheat (*Triticum*

- aestivum* L.) seedlings, *J Plant Growth Regul*, 2010; 29:106-115,
42. Pilon-Smits EAH, Ebskamp MJM, Paul MJ, Jeuken MJW, Weisbeek PJ, Smeekens SCM, Improved performance of transgenic fructan-accumulating tobacco under drought stress, *Plant Physiol*, 1995; 107:125-30,
 43. Qayyum A, Razzaq A, Ahmad M, Jenks MA, Water stress causes differential effects on germination indices, total soluble sugar and proline content in wheat (*Triticum aestivum* L.) genotypes, *Afr J Biotechnol*, 2011; 10:14038-14045,
 44. Robertson M, Chandler PM, Pea dehydrins: identification, characterisation and expression, *Plant Mol Biol*, 1992; 19:1031-44,
 45. Ratnakumar P, Deokate PP, Rane J, Jain N, Kumar V, Berge DV *et al*, Effect of ortho-silicic acid exogenous application on wheat (*Triticum aestivum* L.) under drought, *J Funct Environ Bot*, 2016; 6:34-42,
 46. Simova-Stoilova L, Demirevska K, Petrova T, Tsenov N, Feller U, Antioxidative protection and proteolytic activity in tolerant and sensitive wheat (*Triticum aestivum* L.) varieties subjected to long-term field drought, *Plant Growth Regul*, 2009; 58:107-117,
 47. Quarrie SA, Gulli M, Calestani C, Steed A, Marmioli N, "Location of a gene regulating drought-induced abscisic acid production on the long arm of chromosome 5A of wheat," *Theoretical and Applied Genetics*, 1994; 89(6):794-800,
 48. Sreenivasulu N, Harshavardhan VT, Govind G, Seiler C, Kohli A, Contrapuntal role of ABA: Does it mediate stress tolerance or plant growth retardation under long-term drought stress? *Gene*, 2012; 506:265-273,
 49. SA Quarrie, A Steed, C Calestani *et al*, "A high-density map of hexaploid wheat (*Triticum aestivum* L.) from the cross Chinese Spring x SQ1 and its use to compare QTLs for grain yield across a range of environments," *Theoretical and Applied Genetics*, 2005; 110(5):865-880,
 50. Sheen J, Ca²⁺ dependent protein kinases and stress signal transduction in plants, *Science*, 1996; 274:1900-1902,
 51. Salvi S, Tuberosa R, "To clone or not to clone plant QTLs: present and future challenges," *Trends in Plant Science*, 2005; 10(6):297-304,
 52. Teiz and Zeiger, 2006,
 53. Verma V, Foulkes MJ, Worland AJ, Sylvester-Bradley R, Caligari PDS, Snape JW, "Mapping quantitative trait loci for flg leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments," *Euphytica*, 2004; 135(3):255-263,
 54. Wang H, Huang J, Li Y, Li C, Hou J, Liang W, Involvement of nitric oxide-mediated alternative pathway in tolerance of wheat to drought stress by optimizing photosynthesis, *Plant Cell Rep*, 2016; 35:2033-2044,
 55. Wang X, Vignjevic M, Jiang D, Jacobsen S, Wollenweber B, Improved tolerance to drought stress after anthesis due to priming before anthesis in wheat (*Triticum aestivum* L.) var, Vinjett, *J Exp Bot*, 2014; 65:6441-6456
 56. Xu Y, Skinner DJ, Wu H, Palacios-Rojas N, Araus JL, Yan J, *et al*, Advances in maize genomics and their value for enhancing genetic gains from breeding, *Int J Plant Genomics*, 2009, 1-30,
 57. Xiao BZ, Chen X, Xiang CB, Tang N, Zhang QF, Xiong LZ, (2009) Evaluation of seven function-known candidate genes for their effects on improving drought resistance of transgenic rice under field conditions, *Mol Plant*, 2009; 2:73-83,
 58. Yu Q, Hu Y, Li J, Wu Q, Lin Z, Sense and antisense expression of plasma membrane aquaporin bnp1p1 from brassica napus in tobacco and its effects on plant drought resistance, *Plant Sci*, 2005,
 59. Yamaguchi-Shinozaki K, Shinozaki K, Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses, *Annu Rev Plant Biol*, 2006; 57:781-803
 60. Yang S, Vanderbeld B, Wan J, Huang Y, Narrowing down the targets: towards successful genetic engineering of drought-tolerant crops, *Mol Plant*, 2010; 3(3):469-490
 61. Zhou S, Hu W, Deng X, Ma Z, Chen L, Huang C, Wang C *et al*, Overexpression of the wheat aquaporin gene, TaAQP7, enhances drought tolerance in transgenic tobacco, *PLoS ONE*, 2012; 7:e52439,
 62. Zhu JK, Plant salt tolerance, *Trends Plant Sci*. 2002; 6:66-71