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Heat and Drought Tolerance in Wheat: Integration of Physiological and Genetic Platforms for Better Performance Under Stress

Vikender Kaur[1*] **Sunder Singh**[2] **Rishi Kumar Behl**[3*]

[1] Germplasm Evaluation Division, ICAR-National Bureau of Plant Genetic Resources, New Delhi-110012, India.
[2] Department of Botany, Maharishi Dayanand University, Rohtak-124001, Haryana, India.
[3] Department of Genetics and Plant Breeding, CCS Haryana Agricultural University, Hisar-125004, Haryana, India.

[*] Corresponding author e-mail: vikender@nbpgr.ernet.in; drvikender@yahoo.in; rkbehlprof@gmail.com

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ABSTRACT

Heat and drought stress are currently the leading threat on world's food supply, limiting wheat yield. The extent and severity of stress affected agricultural land is predicted to worsen as a result of inadequate irrigation resources, declining water tables and global warming. Drought/heat tolerance is crucial to stabilize and increase food production since domestication has limited the genetic diversity of crops including wild wheat, leading to cultivated species, adapted to artificial environments, and lost tolerance to stress episodes. Breeding for this trait is complicated as it is controlled by polygenes and their expressions are influenced by various environmental elements and molecular methods such as molecular markers, quantitative trait loci (QTL) mapping strategies, and expression patterns of genes should be applied to produce heat/drought tolerant genotypes. Understanding the mechanism of stress tolerance along with a plethora of genes involved in stress signaling network is important for wheat improvement. Integrating physiology and biotechnological tools with conventional breeding techniques will help to develop wheat varieties with better grain yield under stress during reproductive and grain-filling phases. We briefly consider mechanisms of adaptation and highlight recent research examples through a lens of their applicability to improve the efficiency of wheat under stressful field conditions. Improvement for stress tolerance can be achieved by the introduction of drought and or heat related genes and QTLs to modern wheat cultivars.

Keywords: drought, heat, yield, tolerance, climate change, wheat, stress.

I. Introduction

The average global temperature is reported to be increasing at a rate of 0.18°C every decade (Hansen *et al.* 2012; Annual Climate Summary, 2010).Future climates will also be affected by greater variability in temperature and increased frequency of hot days (Pittock,2003).To adapt new crop varieties to the future climate, we need to understand how crops respond to elevated temperatures and how tolerance to heat can be improved (Halford, 2009). Drought, being also a very important environmental stress, severely impairs plant growth and development, limits plant production and the performance of crop plants, more than any other environmental factor (Shao *et al.* 2009;Rad *et al.* 2012). As a consequence of severe climatic changes across the globe, threat of the occurrence of more frequent drought spells is predicted. Available water resources for successful crop production have been decreasing in recent years. Furthermore, in view of various climatic change models scientists suggested that in many regions of world, crop losses due to increasing water shortage will further aggravate its impacts.

Wheat (*Triticum aestivum* L.) is very sensitive to high temperature and trends in increasing growing season temperatures have already been reported for the major wheat-producing regions (Alexander *et al.* 2006;Hennessy *et al.* 2008). Though, heat stress affects the metabolic pathways at every stage of life of wheat finally leading to yield reduction, the effect of high temperature is particularly severe during grain filling; these losses may be up to 40% under severe stress (Wollenweber *et al.* 2003, Hays *et al.* 2007). Other effects of high temperatures are decreased grain weight, early senescence, shriveled grains, reduced starch accumulation, altered starch-lipid composition in grains, lower seed germination and loss of vigor (Balla *et al.* 2012). End-of-season or 'terminal' heat stress is also likely to increase for wheat in the near future (Mitra and Bhatia, 2008; Semenov and Halford, 2009).Also available water resources for successful crop production have been decreasing in recent years. As a consequence of severe climatic changes across the globe, threat of the occurrence of more frequent drought spells is predicted. Drought stress can influence plants in terms of membrane integrity, root depth and extension, opening and closing of stomata, cuticle thickness, inhibition of photosynthesis, decrease in chlorophyll content, reduction in transpiration, growth inhibition, hormone composition, protein changes, osmotic adjustment and antioxidant production (Szegletes *et al.* 2000; Lawlor and Cornic 2002; Yordanov *et al.* 2000; Praba *et al.* 2009) to stand with some osmotic changes in their organs. Drought can also cause pollen sterility, grain loss, accumulation of abscisic acid in spikes of drought-susceptible wheat genotypes, and abscisic acid synthesis genes in the anthers (Ji e*t al.* 2010). In relation to current development of cultivars, which are higher yielding even in water-limited environments, one of the major targets is *Triticum* species, being one of the leading human food source, accounting for more than half of total human consumption (Fleury *et al.* 2010;Habash *et al.* 2009).

II. Impacts of heat and drought stress on wheat

A. Photosynthesis and chlorophyll content: Photosynthesis is the most sensitive physiological process to elevated temperature (Wahid *et al.* 2007) and any reduction in photosynthesis affects growth and grain yield of wheat (Al-Khatib and Paulsen, 1990, 1999). Heat stress reduces photosynthesis through disruptions in the structure and function of chloroplasts, and reductions in chlorophyll content. Oxidative stress may induce lipid peroxidation leading to protein degradation, membrane rupture and enzyme inactivation (Sairam *et al.* 2000). Rubisco is more sensitive to increased temperatures than the rest of the enzymes involved in carboxylation. PSII appears to be influenced by temperatures above 45°C but is not severely affected by moderately high temperatures (<40°C) (Allakhverdiev *et al.* 2008). Prasad *et al.* (2008b) reported that the most important reasons for PSII sensitivity to high temperature are heat-induced increase in thylakoid membrane fluidity and electron-transport dependent integrity of PSII. The inhibition of PSII electron transport under heat stress is often indicated by a sharp increase in the basal level of chlorophyll fluorescence that corresponds to photosynthetic inhibition (Ristic *et al.* 2007). Heat-stress induced damage and disruption of the integrity of thylakoid membranes also causes the photophosphorylation to cease (Dias and Lidon, 2009).

Drought has a direct impact on the photosynthetic apparatus, essentially by disrupting all major components of photosynthesis including the thylakoid electron transport, the carbon reduction cycle and the stomatal control of the CO_2 supply, together with an increased accumulation of carbohydrates, peroxidative destruction of lipids and disturbance of water balance. Many studies have shown the decreased photosynthetic activity in wheat under drought stress due to stomatal or non-stomatal mechanisms (Ahmadi, 1998; Del Blanco *et al.* 2000). Stomata are the entrance of water loss and CO_2 absorbability and stomatal closure is one of the first responses to drought stress which result in declined rate of photosynthesis. Stomatal closure deprives the leaves of CO_2 and photosynthetic carbon assimilation is decreased in favor of photorespiration. Down regulation of Rubisco large subunit has been observed in drought stressed susceptible wheat lines (Bota *et al.* 2004, Demirevska *et al.* 2009) showing its involvement in drought tolerance mechanism. The activity of photosynthetic electron chain is finely tuned to the availability of CO_2 in the plant and photosystem II (PS II) often declines in parallel under drought conditions. The decrease in chlorophyll content under drought stress has been considered a typical symptom of oxidative stress and may be the result of pigment photo-oxidation and chlorophyll degradation. Both the chlorophyll a and b are prone to soil dehydration (Farooq *et al.* 2009). Drought decreased photosynthetic rate and high temperature hastened the decline in photosynthetic rate in wheat. Interactions between the two stresses are pronounced, and consequences of drought on all physiological parameters are more severe at high temperature than low temperature. The synergistic interactions indicate that productivity of wheat is reduced considerably more by the combined stress than by either stress alone, and much of the effect is on photosynthetic processes (Shah and Paulsen 2003).

Mohammadi *et al.* (2009) reported significant negative correlation between chlorophyll content and grain yield under heat and drought stresses and revealed that chlorophyll content can be a significant selection criterion for higher yielding lines under heat and drought stress.

B. Water relations: Leaf relative water contents (LRWC), leaf water potential, stomatal conductance and rate of transpiration are influenced by leaf and canopy temperature. In dry environments, higher temperatures lead to higher vapor pressure deficits, which drive higher evapotranspiration. There is limited information on the dynamics of water and heat balance for wheat during reproductive and grain-filling stages, but an example of the dynamics in seedlings occurred in the study by Machado and Paulsen (2001). During reproductive and grain-filling phases, water is needed for stem and peduncle elongation to raise the ear up through the unfolding leaf to the top of the canopy; cell expansion and growth of all parts of the ear; facets of flowering, such as pollen ripening, rapid extension of stamen filaments and fertilization; grain growth and filling.Water flow for many of these processes involves crossing membranes, possibly facilitated by aquaporins. Elevated temperature tends to increase hydraulic conductivity of membranes and plant tissues due to increased aquaporin activity, membrane fluidity and permeability (Martınez-Ballesta,2009) and, to a greater degree, reduced water viscosity with increasing temperature (Cochard *et al.* 2007). Alternatively, increased permeability of membranes may cause flowers and grains to dehydrate, particularly if gradients driving water flow into flowers or grains are disrupted by heat stress. Environmental conditions that increase the rate of transpiration also result in an increase in the pH of leaf sap, which can promote ABA accumulation and lead to reduction in stomatal conductance. Increased cytokinin concentration in the xylem sap was shown to promote stomatal opening directly as well as decrease the sensitivity of stomata towards ABA (Wilkinson and Davies, 2002). Wheat genes Rht-B1b and Rht-D1b showed strong association with drought tolerance as well as stomatal conductance (Rebetzke *et al.* 2012).

C. Grain number and size: Both grain number and weight is sensitive to elevated temperature. Elevated temperatures reduce the duration between anthesis and physiological maturity which is associated with a reduction in grain weight. Variability in terms of high temperature effects on wheat grain number and size appears to be related to genotypic differences in heat tolerance (Viswanathan and Khanna Chopra, 2001;Tahir and Nakata, 2005). Elevated temperatures can also cause grain shrinkage through ultrastructural changes in the aleurone layer and endosperm cells as observed by Dias *et al.* (2008) when day/night temperatures increased from 25/14°C to 31/20°C. In the absence of heat stress, the aleurone layer of a wheat grain has large cells surrounding a starchy endosperm. Drought related reduction in yield and yield components of plants could be ascribed to stomatal closure in response to low soil water content, which decreased the intake of CO_2 and, as a result, photosynthesis decreased (Cornic, 2000; Flexas *et al.* 2004). Drought and temperature stress applied before grain filling shortened the grain filling period and reduced grain weight and specific weight in wheat (Yang and Zhang, 2006; Ehdaie *et al.* 2006). Drought led to shortened duration of maturation, grain filling duration and reduced grain yield, mean grain weight, grain number and thousand grain weight in wheat when imposed at different phenophases (Barbanas *et al.*2008; Kaur and Behl, 2010). Water deficit during early endosperm development might inhibit kernel growth by decreasing endosperm cell division, decreasing the number of endosperm nuclei and correspondingly endosperm fresh weight, starch accumulation and dry mass at maturity (Ober *et al.* 1991). Kaur *et al.* 2011 reported that drought during endosperm cell division reduces grain sink potential and subsequently mature grain mass, mainly by disrupting cell divisions in peripheral and central endosperm and thus reducing endosperm length and breadth to a considerable extent in wheat. The interaction of high temperature and drought stresses resulted in stronger reduction of pericarp thickness and endosperm size in wheat than either stress alone. Grain filling duration has been used as a parameter to identify heat tolerant wheat genotypes (Yang *et al.* 2002b; Mohammadi *et al.* 2008b). Sadat *et al.* (2013) revealed the utility of SSR marker linked with various heat tolerant traits like grain filling duration, HSI (Heat Susceptibility Index), single kernel weight of main spike, grain filling duration under heat stress in MAS for screening 25 bread wheat genotypes to heat stress. However, limited research has been done to identify genetic markers associated with heat tolerance in different plants. Thus, there is an urgent need to understand genetic factors affecting heat tolerance as well as to identify new diagnostic markers to be deployed in MAS, which will ensure faster yield gains under stress environments.

III. Phenotyping for heat and drought tolerance in wheat with physiological traits:

For screening out transgenic wheat lines with desirable heat/drought tolerance, the physiological traits and processes which can be genetically manipulated to improve wheat adaptation to stress have to be taken into account. The genetic basis of drought tolerance in wheat is still elusive. At present the physiological traits (PTs) linked to heat tolerance appear to be a superlative accessible tool since they exhibit the favorable allele combination for drought tolerance (Table 1). Such alleles interact with the environment and genetic background which includes variation in gene expression and hence are still poorly understood through the QTL approach (Reynolds and Tuberosa, 2008). Hybridization of heat tolerance PTs may not always have a predictable outcome related to net crop yield particularly in varying environmental conditions, but breeding such varieties with complementary PTs could augment the cumulative gene effect (Reynolds and Rebetzke, 2011). Thus the physiological phenotyping along with gene discovery can be valuable to pin down desired alleles and understand their genetic mechanism.

IV. Tolerance mechanisms

The capability of crop plants to survive and produce good grain yield under stress is generally regarded as stress tolerance. Plant responses to heat/drought stress are mediated by an intrinsic capacity to endure basal thermo-tolerance and, after acclimation, the ability to gain thermo-tolerance.

A. Antioxidant defense system: The antioxidant defense system in plants involves both enzymatic and non-enzymatic antioxidant systems. To minimize the affections of oxidative stress, plants have evolved a complex enzymatic and non-enzymatic antioxidant system, such as low-molecular mass antioxidants (glutathione, ascorbate, carotenoids) and ROS scavenging enzymes e.g. superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX). Non-enzymatic antioxidants cooperate to maintain the integrity of the photosynthetic membranes under oxidative stress. The enzymatic components may directly scavenge ROS or may act by producing a non-enzymatic antioxidant. Efficient destruction of O^{2-} and H_2O_2 in plant cells requires the concerted action of antioxidants. O^{2-} can be dismutated into H_2O_2 by SOD in the chloroplast, mitochondrion, cytoplasm and peroxisome. SOD is involved in post-translational modification and reported to play key role in drought tolerance (Budak *et al.* 2013). POD plays a key role in scavenging H_2O_2. CAT is a main enzyme to eliminate H_2O_2 in the mitochondrion and microbody (Shigeoka *et al.* 2002) and thus help in ameliorating the detrimental effects of oxidative stress. It is found in peroxisomes, but considered indispensable for decomposing H_2O_2 during stress. 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. Evidences suggest that drought causes oxidation damage from increased production of ROS with deficit defense system of antioxidant in plants (Seki *et al.* 2002; Chinnusamy *et al.* 2004). The transcript of some of the antioxidant genes such as glutathione reductase (GR) or the ascorbate peroxidase (APX) is higher during the recovery of water deficit period and may play a role in the protection of cellular machinery against photo-oxidation by ROS. Resistant genotypes may cope with drought stress through alternate ROS scavengers e.g. catalase-1, GST and SOD as noticed in some drought resistant wheat genotypes (Budak *et al.* 2013). Balla *et al.* (2009) demonstrated that upon exposure to heat stress, during the reproductive phase, activities of enzymatic antioxidants were substantially increased in heat-tolerant genotypes of wheat and have been correlated with heat the capacity to acquire thermo-tolerance (Sairam *et al.* 2000; Mittler, 2002; Almeselmani *et al.* 2009).

B. Osmolyte accumulation: Osmotic adjustment is a remarkable part of plants' physiology by which they respond to water deficits. In this process, plants decrease their cellular osmotic potential by the accumulation of solutes. These compounds include proline, glutamate, glycine-betaine, mannitol, sorbitol, fructans, polyols, trehalose, sucrose, oligosaccharides and inorganic ions like K^+. These compounds help the cells to maintain their hydrated state and therefore function to provide resistance against drought and cellular dehydration (Ramanjulu and Bartels, 2002; Chaves *et al.* 2003). Osmolytes in low accumulation function in protecting macromolecules either by stabilizing the tertiary structure of protein or by scavenging ROS produced in response to drought (Zhu, 2001). In wheat, P5CS (pyrroline-5-carboxylate synthase) gene on 7A chromosome has been found to be involved in osmotic adjustment and showed positive correlation with drought tolerance (Morgan and Tan, 1996; Sawahel and Hassan, 2002).Abebe *et al.* (2003) reported the tolerance of mannitol accumulating transgenic lines of wheat to water stress and salinity.Trehalose over-expression helps in the maintenance of an elevated capacity for photosynthesis primarily due to increased protection of PS II against photo-oxidation (Garg *et al.* 2002). Proline is one of the amino acids, which appear most commonly in response to stress. Wheat is marked by low level of these compatible solutes and the accumulation and mobilization of proline was observed to enhance tolerance to water stress (Nayyar and Walia, 2003). Proline can act as a signaling molecule to modulate mitochondrial functions, influence cell proliferation or cell death and trigger specific gene expression, which can be essential for plant recovery from stress (Szabados and Savoure, 2010). Hong-Bo *et al.* 2006 investigated the role of proline as a wheat anti-drought defence protein under drought.

C. Molecular basis of tolerance: Expression of heat shock proteins (HSPs) is the most studied molecular response under heat stress. HSPs save proteins from heat-induced aggregation and thus during the recovery period, facilitates their re-folding (Maestri *et al.* 2002; Rampino *et al.* 2009). Accumulation of Hsps coincides with acquisition of stress tolerance. Hsps are induced by water stress in several plants (Coca *et al.* 1996; Campalans *et al.* 2001). Transgenic *Arabidopsis* plants overexpressing AtHSP17.7 accumulate high levels of AtHSP17.7 protein and show enhanced tolerance to drought and salinity (Sun *et al.* 2001). The concept that low RWC impairs protein structure explains the necessity of molecular chaperones to accumulate under a range of stresses. The abundance of small heat shock proteins (sHsps) in plants and their functional characteristics of binding and stabilizing denatured proteins suggest that sHsps play an important role in plant stress tolerance (reviewed in Wang *et al.* 2004).

Late embryogenesis abundant (LEA) proteins are influenced by drought stress and they help other proteins retrieve after denaturation during water stress (Campbell and Close, 1997). There have been a lot of works during the last two decades to engineer LEA producing genes for promoting crop water stress resistance. Sivamani *et al.* 2000 indicated that barley group 3 LEA gene HVA1 assists to increase wheat growth under drought stress. The over-expression of gene HVA1 in leaves and roots of rice and wheat leads to improved tolerance against osmotic stress as well as improved recovery after drought and salinity stress. Wheat LEA genes, PMA1959 (encoding group one of LEA protein) and PMA80 (encoding LEA protein's second group) improved water deficit resistance in rice (Cheng *et al.* 2002). In wheat, protein contents of groups one, two, and three of LEA have been detected. The Em gene of wheat which encodes LEA protein first group has been vastly researched (Cheng *et al.* 2002; Litts *et al.* 1987). Group three of LEA protein has also been distinguished in seedlings of wheat (Curry *et al.* 1991; Ried and Walker-Simmons, 1993). Dehydrins, also known as group 2 LEA proteins accumulate in response to both dehydration as well as low temperature In durum wheat, protein of groups two (dehydrins) and four of LEA proteins were studied by Ali-Benali *et al.* 2005.Dehydrins help to stabilize macro-molecules against heat-induced damage (Brini *et al.* 2010). Dehydration-responsive element binding (DREB)genes belong 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 viz. wheat, maize, rice and from perennial ryegrass (Lata and Prasad, 2011).

Vacuolar H+translocating pyrophosphatase (V-PPase) is an important enzyme linked to plant development as well as resistance to abiotic stress. Wheat V-PPase genes, TaVP3, TaVP2, and TaVP1 were investigated by Wang *et al.* (2009). Kam *et al.* (2007) also detected the responsible genes in wheat for water stress. They observed that TaRZF70 as a RING-H2 zinc finger gene presented various responses to drought stress which was up-regulated in the leaf and down regulated in the root. TaRZF38 and TaRZF70 were expressed in the wheat root while TaRZF74 and TaRZF59 were expressed in embryo and endosperm at the highest level. Drought stress influences RD gene (responsive to desiccation). Available information on drought responsive genes is still limited as their roles have not been thoroughly determined.

D. Quantitative trait loci (QTL) 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. 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. Recently, several QTLs have been identified in wheat for heat tolerance during the reproductive phase. Byrne *et al.* (2002) detected QTLs for heat tolerance under hot and dry conditions on chromosomes 2B and 5B in a spring wheat population. Dhanda and Munjal (2006) reported both dominant and additive types of gene action at the genetic direction of MTS. The QTL for thousand grain weight (TGW) was dissected in to single Mendelian gene and mapped on short arm of chromosome 7D by Röder *et al.* (2008). Nine QTLs across the wheat genome for effective tiller per plant were mapped by Li *et al.* (2010) using a set of 168 doubled haploid (DH) lines, derivatives of a cross between two winter wheat cultivars Huapei 3 and Yumai 57. Similarly, 3 QTLs for stay green have been mapped on chromosome 1A, 3B and 7D by Kumar *et al.* (2010). The other traits like early ground cover, leaf glaucousness (Richards, 1996), leaf rolling (Araus, 1996), biomass, canopy temperature (Reynolds *et al.* 2001), etc. have been mapped independently in various genetic backgrounds. Paliwal *et al.* (2012) used the parameter heat susceptibility index (HSI) for thousand grain weight (HSITGW), canopy tem perature (HSICT) and grain filling duration (HSIGFD) to identify the QTLs for heat tolerance.

V. Improving genetic adaptation of wheat to stress

Development and selection of crop varieties is, most often, aimed at improving yield under existing climatic conditions. With the changing climate, in particular episodes of high temperature during the reproductive phase, ideotypes with physiological, morphological, and molecular traits unique for heat tolerance are required (Semenov and Halford, 2009). Recent advances in molecular biological, functional, and comparative tools open up new opportunities for the molecular improvement of modern wheat. Recently developed techniques enable faster identification and characterization of heat/drought-related gene(s) and generegion(s). Natural variants of modern species harbor a large repertoire of potential stress related genes and hold a tremendous potential for wheat improvement. Introduction of these components of wheat can be performed either with breeding through marker-assisted selection or transgenic methods. Recent increase in sequence availability due to recently developed high-throughput sequencing strategies has provided several high quality genetic markers for breeding. Transgenic strategies with enhanced transformation and selection methods are currently being developed.

A. Marker-assisted selection: MAS is most often performed based on physio-morphological characteristics related to yield under stress conditions. Markers that are utilized in such a context include SSR (simple sequence repeat) markers, Xgwm136, and NW3106, which are linked to genes that effect tillering capacity and coleoptile length, respectively (Gulnaz *et al.* 2011). Other selection markers are linked to Rht (reduced height) genes, which are known to be associated with harvest index.Additionally, transcription factor-derived markers, especiallyDREB proteins hold a great potential as PCR-based selection markers that can be useful in MAS (Wei *et al.* 2009). However, the isolation of transcription factors is a challenge since they belong to large gene families containing members with high sequence similarities. Identification and successful isolation of a single drought-related locus is compelling also in general due to the complex genomic structure of wheat. The polyploid nature of the genome also makes molecular analysis complicated (Barnabas *et al.* 2008) due to repetitions of DNA sequences. Natural genetic variation may be used through direct selection under heat stress during the reproductive phase or through QTL mapping and subsequent marker-assisted selection.

B. Use of Transgenics: An alternative to ongoing breeding programmes is transgenic methods, which enable the transfer of only the desired loci from a source organism to elite wheat cultivars, avoiding possible decrease in yield due to the cotransfer of unwanted adjacent gene segments. Until now, transcription factors have been the most appealing targets for transgenic wheat improvement, due to their role in multiple stress-related pathways. In two different lines of research, overexpression of cotton and A. thaliana DREB was performed in wheat, resulting in transgenic lines with improved drought tolerance (Guo *et al.* 2009; Pellegrineschi *et al.* 2004; Hoisington and Ortiz,2008). In another study, a barley LEA protein, HVA1, was also overexpressed in wheat, and overexpressors were observed to have better drought tolerance (Bahieldin *et al.* 2005). It wheat will be transferred to the fields as a common is not unreasonable to predict in the following decades that GM (genetically modified) commercial crop. However, to pace this process, new transgenics methodologies should be developed since the current methods are laborious and time consuming. In a recent study, drought enhancement of bread wheat was established with the overexpression of barley HVA1, using a novel technique, which combines doubled haploid technology and *Agrobacterium* mediated genetic transformation (Chauhan and Khurana, 2011).

C. Use of Proteomics: New studies are focusing to study wheat tolerance attheproteomic level to target different proteins and understand their role in stress. The differential expression at biochemical and protein level expression could be a simpler approach to understanding and manipulating drought stress in plants (Jiang *et al.* 2012). Consequently comparative proteomics may provide a clearer picture and alternate way to evaluate and characterize drought resistant genes and proteins in wheat varieties. Global changes in the plant gene expression during growth, development and exposure to environmental variations is reflected in respect to changes at the level of various enzymes and or proteins of various metabolic pathways (Hakeem *et al.* 2012). This suggests the importance of analyzing wheat proteome to understand the molecular basis of heat tolerance in some wheat cultivars. In fact, with the availability of sensitive and accurate proteome analysis technique, proteomics has emerged as a powerful tool in discovering genes and pathways involved in abiotic stress response in crop plants (Chen and Harmon 2006; Kosová *et al.* 2011). The key proteins/enzymes and metabolic pathways identified from tolerant wheat lines could be potentially targeted for designing tolerant varieties of wheat.

VI. Conclusion and future perspectives

The wheat crop is grown in diverse agro-ecological conditions ranging from temperate to subtropical climates. Thus, considerable climatic differences in temperature and relative humidity exist in these areas and wheat crop experiences wide seasonal variations. The synergistic interactions between heat and drought indicate that productivity of wheat is reduced considerably more by the combined stress than by either stress alone. Simultaneous drought and heat stresses are more detrimental than either stress alone. The generation of novel plant varieties displaying tolerance to abiotic stress is highly expected to cope with the unfavorable environment challenges. Although molecular markers discovered through QTL, proteomic and gene functional analysis suggest positive correlation with stress tolerance, the complex nature of hexaploid wheat genome makes it difficult to clearly identify the locus of extremely important markers. Traditional breeding, utilization of germplasm resources and transgenic approaches as well as physiological breeding is advocated for significant gain in yield under abiotic stress environments. Despite the current knowledge on the scientific basis of heat/drought tolerance, more information is needed to understand and be able to manipulate such complex quantitative trait. In recent decades, application of high-throughput screening, "omics" strategies on Triticum species with differential drought tolerance copingabilities, has revealed several stressrelated candidate gene(s) or gene block(s). Furthermore, using a variety of bioinformatics, molecular biology, and functional genomics tools, drought-related candidates were characterized, and their roles in drought tolerance were studied. 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/heat tolerant wild germplasm, and this also enables better marker development, genome analysis and large scale profiling experiments. Affordable next-generation sequencing and novel transformation techniques now allow fundamental research to be performed on crops. The future efforts will be to integrate and translate these resources into practical higher yielding field products.

Table 1. List of morpho-physiological traits and adaptation mechanism under heat/drought stress.

Trait	Adaptation mechanism	Reference
Leaf rolling	Avoidance	Araus, 1996
Leaf glaucousness	Avoidance	Richards, 1996; Tsunewaki and Ebana, 1999; Bennett *et al.* 2011
Transpirational cooling (cooler canopy)	Avoidance	Reynolds and Rebetzke, 2011; Pinto *et al.* 2010
Stomatal conductance	Avoidance	Reynolds *et al.* 1994
Early maturation	Avoidance	Tewolde *et al.* 2006
Alteration of membrane lipid composition (Membrane stability)	Avoidance	Shanahan *et al.* 1990; Ciuca and Petcu, 2009
Photosynthetic rate	Tolerance	Rijven, 1986; Al-Khatib and Paulsen, 1990, 1999
Chlorophyll content	Tolerance	Al-Khatib and Paulsen, 1984; Farooq *et al.* 2009
Accumulation of osmo-protectants	Tolerance	Sawahel and Hassan, 2002; Abebe *et al.* 2003; Hong-Bo *et al.* 2006
Antioxidant defense	Tolerance	Almeselmani *et al.*, 2009; Sairam *et al.* 2000
Signaling cascade and transcriptional control	Tolerance	Kaur and Gupta, 2005
Expression of stress proteins	Tolerance	Balla *et al.* 2009; Maestri *et al.* 2002

Fig. 1. Schematic illustration of heat/drought induced signal transduction mechanism and development of stress tolerance in plants. Stress imposes injury on cellular physiology and results in metabolic dysfunction. Stress injury and ROS generated in response to stress also trigger a detoxification signaling by activating genes responsible for damage control and repair mechanism leading to stress tolerance. Partly adopted from Wahid *et al.* 2007

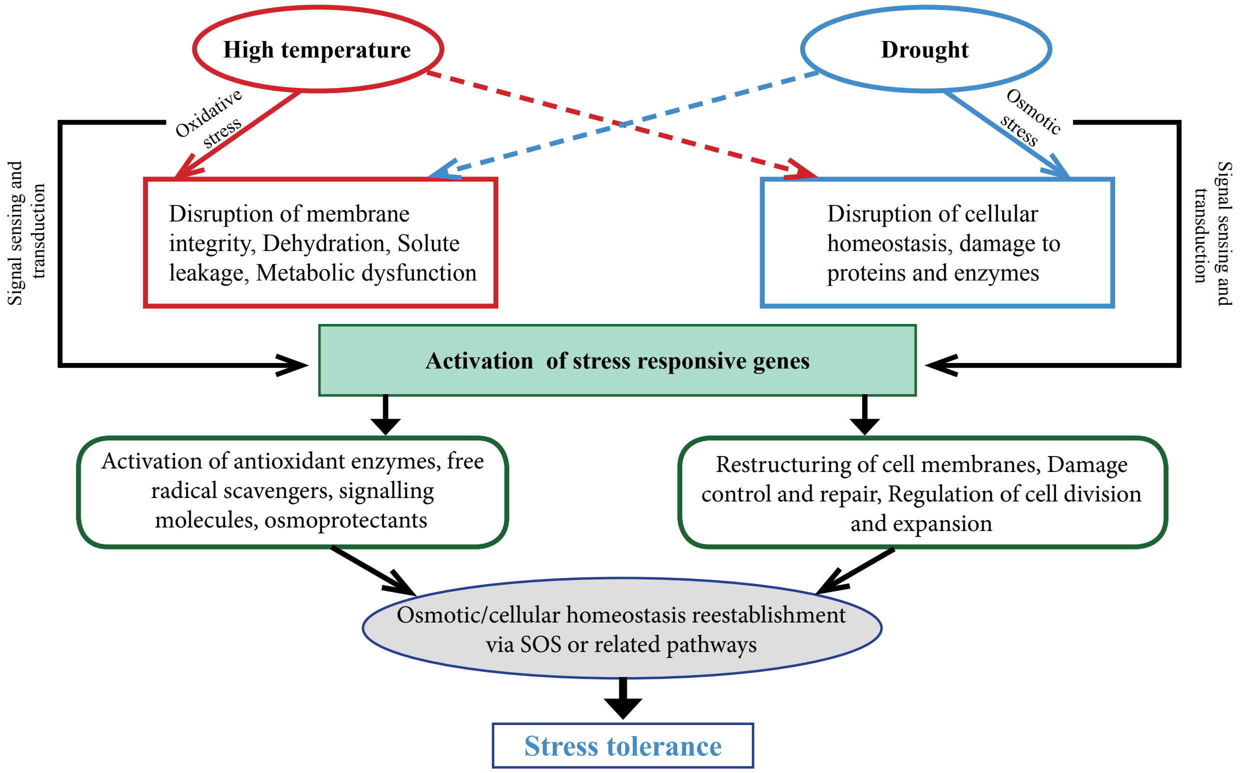
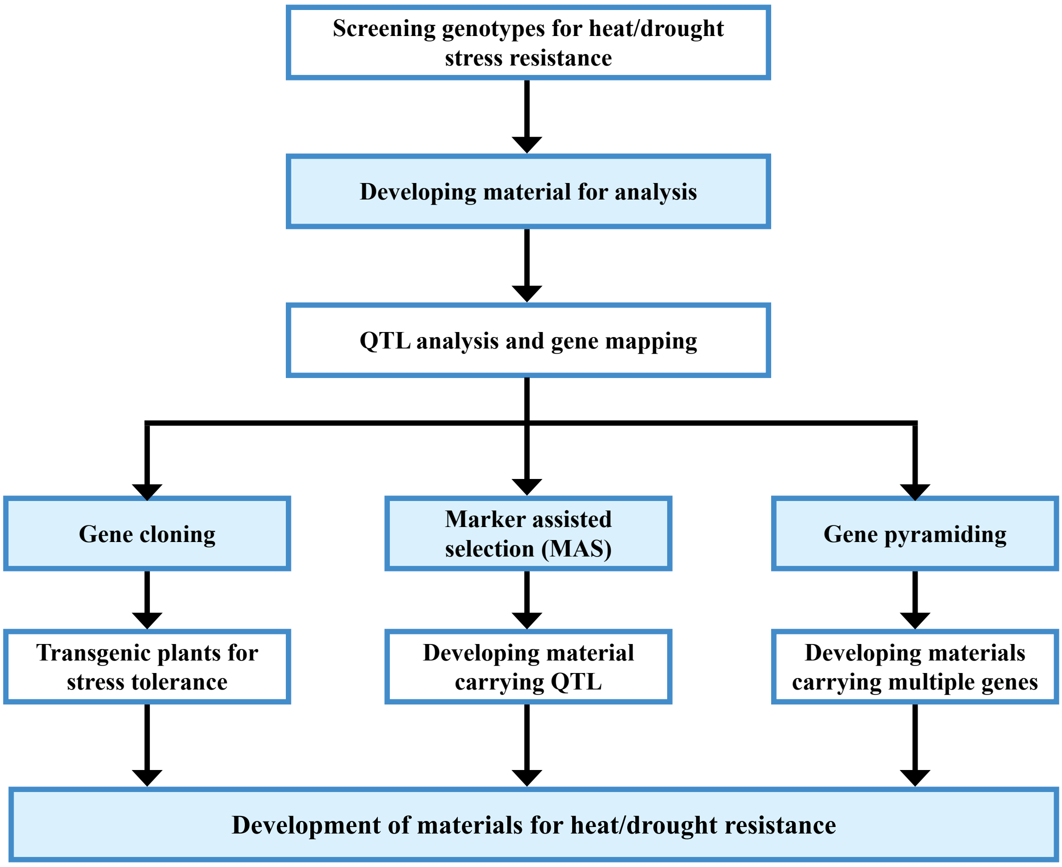


Fig. 2. Developing materials for heat/drought resistance. Genotypes are screened for stress resistance, which are used for the development of genetic materials for QTL analysis and gene mapping. For gene cloning, identified gene or major QTL are analyzed in detail using large populations. Cloned gene is transferred into widely adapted varieties. To develop materials carrying gene or QTL, DNA markers having link to QTL are used for marker-assisted selection. Likewise, marker assisted selection is used for developing materials of gene pyramiding. The gene cloning, marker assisted selection and gene pyramiding are usefull for developing materials for drought resistance. Modified from Budak *et al.* 2013.



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