WHEAT PERFORMS IN HEAT STRESS CONDITION: A REVIEW

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Abstract-Wheat (Triticum aestivum L.) is the most widely grown in the world. It has long been known that average wheat yield reduces by 4% for every one degree rise in ambient temperature during grain filling. High temperature drastically reduces both yield and quality of wheat. Heat stress is one of the major abiotic factor limiting production and productivity of Wheat in several regions round the world. In spite of variation in susceptibility of different stages to heat stress, almost all stages of plant life are affected by heat stress. High temperatures cause an array of morpho-anatomical, physiological and biochemical changes in plants, which affect wheat plant growth and development and may lead to a drastic reduction in economic yield. Plants have evolved various mechanisms for flourishing under higher prevailing temperatures. They include short term avoidance/acclimation mechanism or long term evolutionary adaptations. Some major tolerance mechanisms, including ion transporters, Late Embryogenesis Abundant (LEA) proteins, osmo-protectants, antioxidant defence and factors involved in signalling cascades and transcriptional control are essentially significant to counteract the stress effects. Increasing temperature there observed that Catalase (CAT), Ascorbate Peroxidase (APX) and Superoxide Dismutase (SOD) showed an initial increase before declining at 50°C, while Peroxidase (POX) and Glutathione Reductase (GR) activities declined at all temperatures. The activity of the enzymes Glutathione S-Transferase (GST), Ascorbate Peroxidase (APX) and Catalase (CAT) was more enhanced in the cultivar showed better tolerance to heat stress and projection against Reactive Oxygen Species (ROS) production. Different environmental stresses, including high temperature, result in increased levels of (Abscisic Acid) ABA in wheat. In heat stress condition there finds Heat Shock Proteins (HSPs) in wheat plant. The HSPs are extremely heterogeneous in nature and this dynamic protein family is expanding continuously as per the recent researches are going on. The expression of HSPs is restricted to certain developmental stages of plant like seed germination, embryogenesis, micro sporogenesis and fruit maturation.

Keywords: Late Embryogenesis Abundant (LEA), Catalase (CAT), Ascorbate Peroxidase (APX), Superoxide Dismutase (SOD), Glutathione S-Transferase (GST), Heat Shock Proteins (HSPs)

Introduction:

The domestication of wheat around 10,000 years ago marked a dramatic turn in the development and evolution of human civilization, as it enabled the transition from a hunter gatherer and nomadic pastoral society to a more sedentary agrarian one. Two of the most important traits in the evolution of bread wheat and other cultivated grasses were an increase in grain size and shape of grain are independently inherited traits and that wheat domestication resulted in a switch from production of a relatively small grain with a long, thin shape to a more uniform larger grain with a short, wide shape (Figure 1). These data illustrate the complex history of domesticated wheat evolution, suggesting that various traits (even some that are closely related) arose independently at different stages. For example, the authors suggest that grain size increased early in domestication through alterations both in grain width and length, followed at later stages by further modifications in grain shape largely through changes in grain length. In addition, the decrease in phenotypic diversity in grain morphology in modern commercial wheat is shown to be the result of a relatively recent and severe bottleneck that may have occurred either during the transition from hulled wheat to the modern non hulled varieties or more recently during modern breeding programs (Gegas et al., 2010).

Figure 1. Domestication of wheat led to changes in grain size, shape, and range of phenotypic variation. Grains are representative of modern elite varieties (top) and ancestral wheat species (bottom) (Gegas et al., 2010).
Wheat cultivars belong to one of two polyploid species, hexaploid wheat (bread or common wheat, *T. aestivum*, 2n=6x=42, AABBDD genomes) or tetraploid wheat (durum or pasta wheat, *T. turgidum* ssp. durum, 2n=4x=28, AABB genomes). *T. aestivum* and hereafter refer to it as ‘wheat’.

![Diagram](https://via.placeholder.com/150)

**Figure 2.** Schematic representation of the evolution of hexaploid wheat (*Triticum aestivum* L.) (Harris *et al.*, 2014)

Wheat (*Triticum aestivum* L.) “King of the cereals” is the most widely grown in the world (Kimber *et al.*, 1987). It belongs to family Poaceae (Gramineae) and used as staple food by about 35% of the world population and its demand is growing faster than other major food crops (Ali *et al.*, 2016). Wheat is the most important cereal crop world-wide, with annual production amounting to more than 651 million tons (FAO, 2010). In 2014-15, world production of wheat was 720 million tons and in 2015-16 it is again 720 million tons, and 760 million tons in 2016-17 (Food and Agriculture Organization of the United state), making it the third most-produced cereal after maize (1,016 million tons) and rice (745 million tons). In Uttar Pradesh production of wheat is 30301.942 thousand tons (FAO STAT, 2016-17).

Almost all stages of wheat growth and development are adversely affected by heat stress. It has long been known that average wheat yield reduces by 4% for every one degree rise in ambient temperature during grain filling. High temperature drastically reduces both yield and quality of wheat (Wardlaw *et al.*, 2002). Effects of heat (high temperature) stress on different plants were investigated by scientists such as on Potato (*Solanum tuberosum* L.), and on cereals. That rice yield declined with higher night temperature. That corn and soybean yield decreased as much as 17% for each degree increase in the growing season temperature (Iqbal *et al.*, 2017). Annual yield loss in wheat due to global warming is expected to be 7.7 billion dollars, by 2025, this would be around 18 billion dollars (William, 2007). This decrease in wheat production might be due to several reasons such as improper agronomic practices, poor management and unfavorable weather conditions such as high temperature, drought and salinity (Laghari *et al.*, 2012).

High temperature is one of the limiting factors affecting crop production. Combining with drought stress, the elevated temperature often causes yield loss and reduces the quality of crops. Wheat is a major crop in the world, and the high temperature stress can reduce the yield of wheat by as much as 15% (Dandan Qin *et al.*, 2008). According to Intergovernmental Panel on Climate Change, the expected changes in temperature over the next 30-50 years are predicted to be in the range of 2-3°C (IPCC, 2007). The cultivation of wheat is limiting by temperature at both ends of the cropping season and high temperature stress has an adverse effect on wheat productivity (Chandra *et al.*, 2017).

Heat waves or extreme temperature events are projected to become more intense, more frequent, and last longer than what is being currently been observed in recent years. Heat stress is one of the major abiotic factor limiting production and productivity of crops in several regions round the world. In spite of variation in susceptibility of different stages to heat stress, almost all stages of plant life are affected by heat stress. Global climate models predict an increase in mean ambient temperatures between 1.8 and 5.8°C by the end of this century (IPCC, 2007). Using an ensemble of crop model simulations, (Lobell *et al.*, 2015) estimated for the period 1980–2008a 5.5% reduction of global wheat production due to changes in temperature and precipitation. Future
climates will also be affected by greater variability in temperature and increased frequency of hot days. 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 (Muhammad Farooq et al., 2011).

Transitory or constantly high temperatures cause an array of morpho-anatomical, physiological and biochemical changes in plants, which affect plant growth and development and may lead to a drastic reduction in economic yield. The adverse effects of heat stress can be mitigated by developing crop plants with improved thermo tolerance using various genetic approaches. For this purpose, however, a thorough understanding of physiological responses of plants to high temperature, mechanisms of heat tolerance and possible strategies for improving crop thermostolerance is imperative. Heat stress affects plant growth throughout its ontogeny, though heat-threshold level varies considerably at different developmental stages (Wahid et al., 2007). The developmental stage at which the plant is exposed to the stress may determine the severity of possible damages experienced by the crop. During heat stress modifications in different plant processes takes place in such a way to minimize the effect and develop tolerance to sustain stressful environment (Trivedi, 2014).

High temperature is often accompanied with drought and the combination show detrimental effect on reproductive development such as flower initiation, ovary and pollen development, below average fertilization and subsequently yield loss due to reduced sink potential (Mishra et al., 2014). High day temperatures can cause harm to components of leaf photosynthesis by reducing carbon dioxide assimilation rates. A perception of photosynthesis to heat is largely due to damage to Photosystem II constituents positioned in the thylakoid membranes of the chloroplast and membrane belongings. Membrane thermostability has been evaluated by measuring electrolyte leakage (Hemantaranjan et al., 2014).

Cytogenetic and Taxonomic Background:

The tribe Triticeae is economically the most important group of the family Gramineae. It has given rise to cultivated wheat, barley, ryes, oats, and a number of important range grasses. Hybridization among genera within the tribe has allowed the exchange of genetic material and given rise to polyploidy in the form of amphiploidy. The wheat (genus Triticum) comprise a series of diploid, tetraploid, and hexaploid forms, the polyploids having arisen by amphiploidy between Triticum species and diploid species of the genus Aegilops (Nevo et al., 2002).

Abiotic Stress in wheat

Abiotic stresses, such as, extreme temperatures and water availability, high salt, and deficiencies or toxicity of minerals, severely affect productivity of cereal crops worldwide. Wheat is grown in adverse environments, especially high temperature and low water availability, gets greatly affected in terms of yield. There is ample variation available in abiotic stress tolerance in germplasms of wheat and its wild relatives, which are not fully exploited due to complexity of wheat genome and lack of understanding of its molecular basis of stress response. Functional genomics that involves approaches, such as, gene expression profiling and identification of responsive genes/alleles, followed by mutant analysis or transgenic approaches to assign the function of specific gene or its product protein is the new tool to deal with this issue (Grewal and Goel 2015).

Mechanism of heat tolerance

Heat tolerance is the ability of the plant to grow and produce economic yield under high temperature. Plants have evolved various mechanisms for flourishing under higher prevailing temperatures. They include short term avoidance/acclimation mechanism or long term evolutionary adaptations. Some major tolerance mechanisms, including ion transporters, late embryogenesis abundant (LEA) proteins, osmo-protectants, antioxidant defense and factors involved in signaling cascades and transcriptional control are essentially significant to counteract the stress effects. The stress responsive mechanism is established by an initial stress signal that may be in the form of ionic and osmotic effect or changes in the membrane fluidity. This helps to re-establish homeostasis and to protect and repair damaged proteins and membranes (Hemantaranjan et al., 2014).

Activities of different antioxidant enzymes are temperature sensitive and activation occurs at different temperature ranges but the activities of these enzymes increase with increasing temperature (Chakrabortty and Pradhan 2011) observed that catalase (CAT), ascorbate peroxidase (APX) and superoxide dismutase (SOD) showed an initial increase before declining at 50°C, while peroxidase (POX) and glutathione reductase (GR) activities declined at all temperatures ranging from 20 to 50°C. In addition, total antioxidant activity was at a maximum at 35-40°C in the tolerant varieties and at 30°C in the susceptible ones. Their activities also differ depending upon tolerance or susceptibility of different crop varieties, their growth stages and growing season. The activity of the enzymes glutathione S-transferase (GST), ascorbate peroxidase (APX) and catalase (CAT) was more enhanced in the cultivar showed better tolerance to heat stress and projection against ROS production. They reported that the tolerance of the wheat varieties appeared to be correlated with the antioxidant level, though changes in activity were observed for different antioxidant enzymes. Antioxidant defence mechanism plays an important role in the heat stress tolerance of wheat genotypes and it was observed that the activities of SOD, APX, CAT, GR and POX increased significantly at all stages of growth in heat tolerant cultivars (C-306) in response to heat stress treatment, while susceptible cultivar (PBW 343) showed a significant reduction in CAT, GR and POX activities in the heat tolerance treatment. Further, to create response in specific cellular compartments or tissues against a certain stimuli, interaction compartments or tissues against a certain stimuli, interaction of cofactors and signalling molecules are required. Signalling molecules are involved in activation of stress responsive genes (Hemantaranjan et al., 2014).
Effects of high temperature on wheat

Heat stress implies alteration in diverse metabolic processes, with qualitative and quantitative losses in the produce, in extreme cases can result in plant death. Effect of heat stress on wheat can be categorized as follows (Mishra et al., 2014).

Effects on yield and quality of wheat

High temperature is often accompanied with drought and the combination show detrimental effect on reproductive development such as flower initiation, ovary and pollen development, below average fertilization and subsequently yield loss due to reduced sink potential (Mishra et al., 2014). A recombinant inbred line population derived from the cross of Kauzand MTRWA116 showed significant decrease in grain yield (46.7%), thousand grains weight (20.6%), grain filling duration (20.4%), kernel per spike (23.6%) and spikelet per spike (11.7%) due to heat stress (Modarresi et al., 2010).

Water Relations

Water status of tissues is most crucial factor for survival of plants. Plants tend to maintain stable water status of tissues but high temperature impairs this particularly if water is limiting. To enhance stress tolerance, plants accumulate different osmolytes such as sugars and sugar-alcohols (polyols), proline, tertiary and quaternary ammonium compounds and tertiary sulphonium compounds. These compounds help to maintain stable water status of tissues by absorbing and retaining water (Trivedi, 2014). Reduced number of tillers with promoted shoot elongation was observed in wheat plant under heat stress. In wheat green leaf area and productive tillers/plant were drastically reduced under high temperature (30/25 °C, day/night). In T. aestivum high temperature (28 °C to 30 °C) reduced the germination period, days to anthesis booting, maturity that is ultimate the total growth duration (Hasanuzzaman et al., 2013).

Photosynthesis

High temperature (HT) has a greater influence on the photosynthetic capacity of plants especially of C3 plants than C4 plants. In chloroplast, carbon metabolism of the stroma and photochemical reactions inthylakoid lamellae are considered as the primary sites of injury at HTs. Thylakoid membrane is highly susceptible to HT. Major alterations occur in chloroplasts like altered structural organization of thylakoids, loss of grana stacking and swelling of grana under heat stress. Again, the photosystem II (PSII) activity is greatly reduced or even stops under HTs. Heat shock reduces the amount of photosynthetic pigments (Hasanuzzaman et al., 2013).
Any constraint in photosynthesis at high temperature may limit plant growth. Sensitivity of photosynthesis to heat may be due to damage to components of photosystem II located in the thylakoid membranes of the chloroplast as well as membrane properties. Photochemical reactions in thylakoid lamellae and carbon metabolism in the stroma of chloroplast are the primary sites of injury at high temperature. PSII is highly thermo labile in heat stress condition and its activity decreases drastically and sometimes high temperature stops its activity. This is due to the properties of thylakoid membrane where PSII is located. Under high temperature, leaf photosynthesis is found to be functionally limited by photosynthetic electron transport and ribulose-1,5-bisphosphate (RuBP) regeneration capacity (Trivedi 2014).

Heat stress inhibits photosynthesis. Inhibition of net photosynthesis (Pn) by moderate heat stress has been attributed to an inability of Rubisco activase to maintain Rubisco in an active form (Hemantarjan et al., 2014).

### Thermo stability of cell membrane

Heat stress causes loss of integrity and functions of biological membranes due to alteration in the tertiary and quaternary structures of membrane proteins. Such alterations enhance the permeability of membranes and cause increased leakage of solutes. It is an indication of decreased cell membrane thermo stability (CMT). CMT has been used as an indirect measure of heat stress tolerance in different plant species such as cotton, barley and wheat (Trivedi 2014).

Membrane thermal stability (MTS) can be a significant selection criterion for heat stress tolerance. MTS is determined by measuring of electrical conductivity of aqueous phase in which leaf tissue exposure to high temperature. Membrane stability parameters of genotypes decreased during the later developmental stages. Genetic variation among genotypes for membrane stability can be utilized in wheat breeding in heat-stressed environments (Hemantarjan et al., 2014). The relationship between CMT and crop yield under high temperatures may vary from plant to plant and invokes for study of individual crops before using it as an important physiological selection criterion. For example, whereas a significant relationship between CMT and yield was observed in a few plant species such as sorghum, no such relationship was observed in soybean or wheat. Thus, the major causes of yield suppression under heat stress remain largely elusive and deserve further experimentation (Wahid et al., 2007).

![Figure 4. Major effects of high temperature on plants (Hasanuzzaman et al., 2013)](image-url)

### Accumulation of compatible osmolytes / Antioxidant

A key adaptive mechanism in many plants grown under abiotic stresses, including salinity, water deficit and extreme temperatures, is accumulation of certain organic compounds of low molecular mass, generally referred to as compatible osmolytes. Under stress, different plant species may accumulate a variety of osmolytes such as sugars and sugar alcohols (polyols), proline, tertiary and quaternary ammonium compounds, and tertiary sulphonium compounds (Wahid et al., 2007). Heat stress also causes oxidative stress in plants by the generation and the production of reactive oxygen species (ROS). Plants get rid of these harmful ROS products by converting them to less reactive chemicals (Khan et al., 2013).

Production rate of reactive oxygen species is low under normal conditions; however, environmental stresses such as high temperature, drought, salinity and cold disrupt cellular homeostasis by enhancing the production of reactive oxygen species. The sources of production of these reactive oxygen species include photorespiration and mitochondrial respiration in plants. Plant cell maintains cellular homeostasis by scavenging reactive oxygen species using enzymes such as superoxide dismutase, catalase, peroxidase, ascorbate peroxidase and glutathione reductase and non-enzymatic antioxidants such as tocopherols, ascorbic acid, glutathione and carotenoids. In wheat seedling exposed to heat stress, diminished activity of catalase and increased activity of
superoxide dismutase, peroxidase, ascorbate peroxidase and proteases were observed during heat induced programmed cell death (Mihsra et al., 2014).

One of the most common responses of crop plants to high temperature stress is increase in proline accumulation. Free proline is involved in osmotic adjustment, protecting pollen and several plant enzymes from heat injury and serves as a source of nitrogen and other metabolites. Accumulation of proline occurs in wheat under heat Stress (Khan et al., 2013). In addition, total antioxidant activity was at a maximum at 35–40°C in the tolerant varieties and at 30°C in the susceptible ones. Their activities also differ depending upon tolerance or susceptibility of different crop varieties, their growth stages and growing season generally, an increase in temperature leads to an increased expression of the anti-oxidative enzymes until a particular temperature after which they decline (Chakraborty & Pradhan 2011).

Enviromental cues | Primary affects | Secondary signal
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Temperature stress | Protein stability cytoskeleton instability | Calcium signaling phosphorylation
 | | Transcriptional change hormone response
Drought stress | Chromatin structure changes | ROS production metabolic uncoupling

Figure 5. Environmental signalling pathways with external cues and internal repercussions.

Environmental cues are on the left with initial cellular effects central and the organisable signals are shown right (Bita and Gerats 2013)

Hormonal Regulation
Plants have the ability to monitor and adapt to adverse environmental conditions, though the degree of adaptability or tolerance to specific stresses varies among species and genotypes. Hormones play an important role in this regard. Cross-talk in hormone signaling reflects an organism’s ability to integrate different inputs and respond appropriately. Hormonal homeostasis, stability, content, biosynthesis and compartmentalization are altered under heat stress. Abscisic acid (ABA) and ethylene (C$_2$H$_4$), as stress hormones, are involved in the regulation of many physiological properties by acting as signal molecules. Different environmental stresses, including high temperature, result in increased levels of ABA.

Under field conditions, where heat and drought stresses usually coincide, ABA induction is an important component of thermo-tolerance, suggesting its involvement in biochemical pathways essential for survival under heat-induced desiccation stress. Other studies also suggest that induction of several HSPs (e.g., HSP70) by ABA may be one mechanism whereby it confers thermo-tolerance. More so, heat shock transcription factor 3 acts synergistically with chimeric genes with a small HSP promoter, which is ABA inducible (Wahid et al., 2007).

A gaseous hormone, ethylene regulates almost all growth and developmental processes in plants, ranging from seed germination to flowering and fruiting as well as tolerance to environmental stresses. Heat stress changes ethylene production differently in different plant species. For example, while ethylene production in wheat leaves was inhibited slightly at 35°C and severely at 40°C, in soybean ethylene production in hypocotyls increased by increasing temperature up to 40°C and it showed inhibition at 45°C. Despite the fact that ACC accumulated in both species at 40°C, its conversion into ethylene occurred only in soybean hypocotyls but not in wheat. Wheat leaves transferred to 18°C followed by a short exposure to 40°C showed an increase in ethylene production after 1 h lag period, possibly due to conversion of accumulated ACC to ethylene during that period (Tan et al., 1988).

Among other hormones, salicylic acid (SA) has been suggested to be involved in heat-stress responses elicited by plants. SA is an important component of signaling pathways in response to systemic acquired resistance (SAR) and the hypersensitive response (HR). SA stabilizes the trimers of heat shock transcription factors and aids them bind heat shock elements to the promoter of heat shock related genes. Long term thermo-tolerance can be induced by SA, in which both Ca$^{2+}$ homeostasis and antioxidant systems are thought to be involved. Sulpho-salicylic acid (SSA), a derivative of SA, treatment can effectively remove H$_2$O$_2$ and increase heat tolerance. In this regard, Catalase (CAT) plays a key role in removing H$_2$O$_2$ in cucumber (Cucumis sativus) seedlings treated with SSA under heat stress. In contrast, while glutathione peroxidase (GPX), Ascorbate Peroxidase (APX) and Glutathione Reductase (GR) showed higher activities in all SSA treatments under heat stress, they were not key enzymes in removing H$_2$O$_2$. The effects of Gibberellins and Cytokinins on high temperature tolerance are opposite to that of ABA. An inherently heat-tolerant dwarf mutant of barley impaired in the synthesis of gibberellins was repaired by application of Gibberellic acid, whereas application of Triazole Paclobutrazol, a Gibberellins antagonist, conferred heat tolerance (Vettakkorumakankavil et al., 1999).

Secondary metabolites
Heat stress induces production of phenolic compounds such as flavonoids and phenylpropanoids. Phenylalanine Ammonia lyase (PAL) is considered to be the principal enzyme of the Phenylpropanoid pathway. Increased activity of PAL in response to thermal stress is considered as the main acclimatory response of cells to heat stress. Thermal stress induces the biosynthesis of
Phenolics and suppresses their oxidation, which is considered to trigger the acclimation to heat stress. Moreover, under heat stress condition carotenoids protect cellular structures of plants. When plants are exposed to harmful environmental conditions, like heat stress, xanthophylls including violaxanthin, antheraxanthin and zeaxanthin partition between the light-harvesting complexes and the lipid phase of the thylakoid membranes (Trivedi, 2014).

Phenolics, including flavonoids, anthocyanins, lignins, etc., are the most important class of secondary metabolites in plants and play a variety of roles including tolerance to abiotic stresses (Wahid, 2007). Studies suggest that accumulation of soluble phenolics under heat stress was accompanied with increased Phenyl Ammonia Lyase (PAL) and decreased peroxidase and polyphenol lyase activities (Gill, 2014).

Heat Shock Proteins (HSPs)

In general, heat stress is responsible for the up-regulation of several heat inducible genes, commonly referred as “heat shock genes” (HSGs) that encode HSPs and these active products are very much necessary for plant’s survival under fatal high temperature. High temperature induced constitutive expression of most of these proteins protect intracellular proteins from being denaturation and preserve their stability and function through protein folding; thus it acts as chaperones (Baniwal et al., 2004). The HSPs are extremely heterogeneous in nature and this dynamic protein family is expanding continuously as per the recent researches are going on. The expression of HSPs is restricted to certain developmental stages of plant like seed germination, embryogenesis, micro sporogenesis and fruit maturation. In plants, well-characterized HSPs can be grouped into five different families: HSP100 (or ClpB), HSP90, HSP70 (or DnaK), HSP60 (or GroE) and HSP 20 (or small HSP, sHSP). The HSP70 and HSP60 proteins are among the most highly conserved proteins in nature, consistent with a fundamental role in response to heat stress (Kulzet et al., 2003).

Conclusion:

Abiotic stresses such as heat and drought are the primary cause for yield loss, and are getting more severe with change in climate. Therefore, plant breeders should get well equipped with understanding mechanism of heat tolerance in crops and transferring it to cultivars with the help of physiological, biochemical and molecular tools (Mishra et al., 2014). Heat stress significantly reduced growth, chlorophyll, starch content and yield of wheat varieties. There is a need to implement standardized phenotyping protocols to physiologically evaluate breeding lines for heat tolerance. Identification of genetic resources with heat tolerance attributes is an important approach to stabilize or maintain food production in heat stress condition. Screening different genotypes of crop wild relatives or wild accessions for growth under heat stress, distinction must be made between heat tolerance and growth potential. Usually plants with higher growth potential perform better regardless of the growing conditions. During screening and breeding for heat stress tolerance, it is needed to opt for a two pronged strategy i.e., availability of genetic framework for grain size and shape variation in wheat. Plant Cell 22: 1046.

Reference:


