Heat Stress Effects and Tolerance in Wheat: A Review

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ABSTRACT

Wheat is a major cereal crop and considered as source of basic calories and protein for more than 80% of the world population. Regarding the global climate change at the past few decades, the impact of rising temperature on wheat production is gaining concern worldwide. Heat and drought are the major abiotic stress limiting the wheat production. Heat stress interrupts the important physiological and biochemical process of the plant. High temperature stress reduces grain number, photosynthetic activity and chlorophyll content and starch synthesis in the endosperm. Reactive oxygen species accumulated under heat stress cause severe oxidative damage to the crop. Plant rapidly produces heat shock proteins to minimize the effect of heat stress. Several traits such as day green, chlorophyll fluorescence and canopy temperature play significant role in heat tolerance. In order to develop new crop varieties that can cope with future climate, knowledge of heat stress effect and tolerance at physiological, biochemical and morphological level is highly important.

Keywords: Heat stress, Heat shock proteins, Oxidative stress, Wheat.

INTRODUCTION

Wheat (\textit{Triticum} spp.) is one of the major cereal crops belonging to Poaceae family which contributes about 30% of world grain production and 50% of the world grain trade [1]. Wheat is considered as staple food in more than 40 countries of the world which provides basic calories and protein for 85% and 82% of the world population respectively [2,3]. FAO estimated that, the annual cereal production have to grow by almost one billion to feed the projected population of 9.1 billion by 2050. In order to meet the increase food requirement, increase in crop production and productivity is the demand of 21\(^{st}\) century [4]. Wheat is grown in tropical and sub-tropical region of the world which experiences various abiotic stresses. Adverse environmental stress significantly reduces crop production [5]. The major abiotic stresses include heat, drought, salinity cold, chemical and water excess. However, heat and drought are the main abiotic stresses affecting the wheat production worldwide [6,7]. Considering global climate model, the mean ambient temperature is likely to rise by 6\(^\circ\)C by the end of 21\(^{st}\) century [8].

Wheat is much sensitive to heat stress. It is estimated that per 1\(^\circ\)C increase in temperature cause decrease in global wheat production by 6\% [9]. Even 1\(^\circ\)C temperature increase over mean temperature during reproductive stage may leads to higher loss in grain yield [10,11]. High temperature alters different physiological, biological and biochemical process in wheat [12]. Heat stress (HS) in wheat cause poor seed germination, decrease in grain filling duration, reduction in grain number, deactivation of Rubisco enzyme, decrease in photosynthetic capacity, reduction in rate of assimilate translocation, premature leaf senescence, decrease chlorophyll content and ultimately decrease in yield [13-21]. HS also affect the starch and protein content in grain. HS induce production of reactive oxygen species (ROS) which cause change in membrane stability along with lipid peroxidation, protein oxidation and damage to nucleic acids [22,23]. However, in order to avoid injury and damage associated with HS, wheat has evolved different tolerance mechanisms to maintain its survival and growth. HS induced heat shock proteins (HSPs) maintain correct protein folding, refolding, synthesis and it also degrade the protein aggregate [2,24,25]. The accumulated ROS is detoxified by the antioxidative defense system through various enzymatic and non-enzymatic antioxidants [26]. Stay green (SG), chlorophyll fluorescence and canopy temperature are traits that are associated with heat tolerance in wheat [20].

This review covers the effect of HS on wheat morphology, physiology and biochemistry. Furthermore, we explained the different HS tolerance mechanisms such as antioxidative defense system and HS induced HSPs production along with SG traits associated with heat tolerance.

EFFECT OF HEAT STRESS ON WHEAT

HS affects the different growth and development stages of wheat which leads to high yield loss. However, effect of HS in plant depends upon the length of heat exposure and growth stage during the high temperature [27,28]. Poor germination, reduced leaf area, early leaf senescence and damaged photosynthetic machinery associated with heat stress cause decrease in photosynthesis in wheat [12,29,30]. Heat stress brings certain alteration on wheat morphology, physiology and biochemistry.

Effect on wheat morphology

In various crops, including wheat, HS negatively influence the seed germination and plant establishment [13]. High temperature
(45°C) has negative impact on embryonic cells, followed by improper germination and emergence which leads to poor crop stand [31]. High temperature affects the survivability of the productive tiller, which result in decrease in yield. HS in wheat result in decrease grain yield (53.57%) and tiller number (15.38%) [21]. HS causes decrease in root growth which ultimately affects the crop production [32]. The effect of HS is highly significant during reproductive phase [33]. Increase in average temperature by 1°C during reproductive stage may lead to higher loss in grain yield [10,11]. The optimum temperature for flowering and grain filling ranges from 12°C to 22°C [2]. Early stage of gametogenesis is harmed when HS occur during meiosis [34]. Microspore and pollen cell development is affected negatively due to HS at the time of floral initiation [35]. The grain development phenomenon depends upon the grain filling rate and duration which is highly sensitive to HS [36,37]. The life cycle of wheat shortens in HS than in normal temperature situation [38]. 1°C-2°C rise in temperature lowers seed weight due to decrease in grain filling duration [39]. Short term heat stress during grain filling may result in grain yield loss up to 23% [40]. HS negatively influence number of grain and grain quality. In HS condition, grain number is decreased causing reduction in harvest index [15]. Heat stress associated decrease in assimilate production and remobilization result in reduced grain quality [41]. Wheat productivity is reduced remarkably due to harmful effect of high temperature in growth process [42]. When wheat is subjected to ambient temperature (>35°C) for a short period of time can result in significant loss in grain yield [43].

**Effect on wheat physiology**

Photosynthesis is most important physiological process in plant which is highly influenced by high temperature. Stroma and thylakoid lamellae are most sensitive to heat stress in wheat [30]. High temperature (~ 40°C) results in permanent alternation of RuBisCO, Rubisco Activase and Photosystem II [44]. Upon exposure of wheat in HS condition, the RuBisCO enzyme was found to be deactivated in less than 7 days [16]. Rubisco activase breakdown under heat stress cause decrease in photosynthetic capacity [17]. HS cause change in the fluidity of thylakoid membrane and separation of light harvesting complex II from the photosystem II [45]. The photosynthetic product is necessary to be translocated to different plant parts for its growth and development. The rate of assimilate translocation from source to sink is reduced under high temperature stress cause by decrease in membrane stability [18]. Mobilization of water soluble carbohydrate to reproductive sink support grain growth and development [46]. Source and/or sink limitation reduce seed set and seed filling [47]. In case of source limitation caused by HS, plant to find another way to translocate the photosynthetic product into the grain [1]. There is increase in carbohydrate remobilization from stem to developing grain during pre-anthesis HS, which help to recover the effect on grain starch content in post-anthesis HS [48]. The availability of high O$_2$ concentration promotes photorespiration. The change in solubility of O$_2$ and CO$_2$ gases was observed under HS condition causing increase photospiration in flag leaf in wheat [49].

Plant senescence is the process of aging in plant. Avacuolar collapse, loss in membrane integrity, disturbance of cellular homeostasis are distinctive feature of leaf senescence [50]. Moderate but extended duration of HS result in gradual senescence while intensive HS for short period of time leads to protein denaturation and aggregation, causing death of the plant [24]. HS during maturity promotes the leaf senescence in plant [19]. Also, high temperature (>34°C) accelerates the leaf senescence due to reduction in biosynthesis of chlorophyll [20]. High temperature affects the water relation and content in the plant. Cell dehydration is observed under HS due to reduction in osmotic potential [51]. Canopy temperature affects the leaf relative water content, stomatal conductance and rate of transpiration [2]. Whereas chlorophyll fluorescence is highly associated with yield which aid in the measurement of photosynthetic efficiency. Thus, chlorophyll fluorescence and canopy temperature traits can be used for selection of heat tolerant genotypes [20]. During drought condition and high temperature, canopy temperature is linked with deeper roots [52]. A research was conducted by Dhyani et al. on heat tolerant and heat sensitive wheat genotypes grown under normal and late sown condition and revealed that chlorophyll content and leaf area index was significantly decreased in heat sensitive genotypes but proline content was increased in heat tolerant genotypes grown under late sown situation [53]. Under HS, plant highly produce reactive element known as Reactive Oxygen Species (ROS). The ROS interrupt the cell function by their negative action on lipid, protein and DNA. Oxidative damage associated with heat stress cause decrease in membrane thermostability by 54% [54]. ROS accumulated under HS promotes protein denaturation and formation of unsaturated fatty acid, which finally increases cell membrane permeability [55].

**Effect on wheat biochemistry**

Starch is the major constituents of wheat and is made up of amylose and amylpectin. Amylose content is key parameter to mark starch quality. Starch characteristics are affected by variation in amylose content. High temperature is associated with increase in amylose content and amylose: amylpectin ratio [56]. ADP-Glucose Pyrophosphorylase (AGPase) and starch synthase is significant enzyme involved in starch biosynthesis. Soluble Starch Synthase and Granule bound starch synthase are the two forms of starch synthase [2]. At high temperature, there is decrease in starch content in grain up to one-third of total endosperm starch, which is caused due to decrease efficiency of enzymes involving in starch biosynthesis [57]. Lower grain size and decrease in starch deposition is caused by reduce activity of soluble starch synthase at high temperature around 40°C [58]. However, Sharma et al. reported that, starch deposition is not affected by the reduction of Soluble Starch Synthase activity up to 30°C, but it affects the starch composition. He also mentioned that HS in wheat, not remarkably affect the granule bound starch synthase activity [59]. Asthir and Bhatia observed remarkable decrease of starch biosynthesis in wheat grain under HS but there was increase in total soluble sugar and protein [60]. Wheat grain quality is highly dependent upon protein content and composition. Lizana and Calderini observed no significant effect on protein concentration under HS [41]. In contrast, Iqbal et al. reported that, in HS condition, there is increase in grain protein content with increase in essential amino acids fractions, leaf nitrogen content and sedimentation index [4].

**HEAT TOLERANCE MECHANISM IN WHEAT**

Plants have different adaptation mechanism to adapt under HS. Avoidance, Escape and Tolerance are main three mechanisms that allow plant to survive and grow in high temperature environment. Heat tolerance is defined as the capability of plant to survive, grow and produce economic yield under HS. Antioxidant defense,
generation of Heat Shock Proteins (HSPs) and stay green are major heat tolerance mechanism in wheat.

**Heat shock proteins**

Protein function is highly dependent upon its synthesis and folding. Protein misfolding significantly affects the working mechanism of the cell. At HS condition, protein folding and synthesis is interrupted [2]. Stressing agents are produced in cell under HS. These agents instantly disturbs the major metabolism processes as well as DNA replication, transcription, mRNA transport and translation till the cell recuperate [61]. To overcome this plant speed up production of HS induced proteins as a defense mechanism which is known as Heat Shock Proteins (HSPs) [62]. HSPs can be classified into different families on the basis of their molecular mass, amino acid sequence homologies and functions [63]. The families include HSP100 family, HSP90 family, HSP70 family, HSP60 family and small HSPs family. These HSPs are associated with different function under HS condition (Table 1). Heat Stress transcription factors (Hsfs) are present in the cytoplasm in an inactive condition which acts as regulatory protein in the transcription of the genes which encodes for HSPs. Under HS, these Hsfs acts as transcriptional activators [64].

Various mechanisms are involved in the expression of genes that encodes for HSPs, particularly temperature sensing mechanism followed by mechanism of signal transfer to Hsfs and finally binding of Hsfs to heat shock element (HSE) for DNA for the initiation of gene expression [65]. Under HS, HSPs function as molecular chaperons to prevent protein denaturation, and aggregation [24,66].

**Reactive oxygen species and antioxidative defense mechanism**

HS affects the plant by producing unfavourable reactive oxygen species (ROS) which include singlet oxygen (\(O_2^\bullet\)) and hydroxyl radical (•OH) [67,68]. In normal cell, there exists equilibrium between production and scavenging of ROS which is known as redox homeostasis [69]. When there is more production of ROS then the scavenging capacity of cell, the cell comes under stress which is known as oxidative stress [70]. Also oxidative stress either can be occurred due to decrease in free radicals scavenging capacity of cell [71]. HS induced increased ROS production cause change in membrane potential (depolarization), lipid peroxidation, protein oxidation, damage in nuclei acids, obstruct enzyme function and activates the programmed cell death [22,23,72]. HS associated increase in ROS signals to switch on the antioxidative defense mechanism by activating the free radical scavenging related enzymes [73]. Detoxification of ROS by antioxidative defense system is necessary to save plant from oxidative damage [71]. In plant the antioxidative defense system is highly effective and is obtained through involvement of different enzymatic and non-enzymatic antioxidants [74]. The enzymatic antioxidant includes superoxide dismutase (SOD), ascorbate peroxidase, catalase (CAT), glutathione peroxidase (GPX), glutathione reductase (GR) and peroxidase (POX) while non-enzymatic antioxidants includes ascorbic acid, glutathione, tocopherols, carotenoids and phenolic compounds [69,75]. These antioxidants have different role in scavenging ROS (Table 2). The production of type of antioxidant enzymes depends upon the type of stress associated with plant. Under HS, there is increase in activity of SOD, CAT, POX [63,76], Balla et al. Reported that, the activity of S-transferase (GST), APX and CAT is increased in the cultivar which showed tolerance to HS [77].

There is unavoidable leakage of electrons from electron transport chain occurring in mitochondria, chloroplast and plasma membrane. The ROS is produced from the acceptance of leaked electron by \(O_2\) or as by product of several metabolic process limited to different cellular regions [78,79]. When oxygen molecule accepts the leaked electron, superoxide or singlet oxygen is produced. Superoxide radical is converted to hydrogen peroxide by two ways either by spontaneous dismutation or by catalytic action of SOD or otherwise metal ions (\(Fe^{2+}\) and \(Cu^{2+}\)) present in cell is reduced by superoxide radicals. The hydrogen peroxide is converted to •OH by Haber-Wiss reaction. There are two steps governing this reaction. In first step, the metal ion is reduced by superoxide radical and in second step, the reduced metal ion react with hydrogen peroxide to form •OH. The later step is known as Fenton reaction. •OH are very reactive than other ROS [26]. There is no any enzymatic mechanism that can eliminate •OH, thus higher production of •OH can result in cell death [80]. However, the •OH can be decreased by scavenging of hydrogen peroxide by

### Table 1: Role of different heat shock proteins under heat stress.

<table>
<thead>
<tr>
<th>Heat Shock Proteins</th>
<th>Functions</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>HSP100</td>
<td>Degradation of protein aggregate. It is ATP dependent process.</td>
<td>[2]</td>
</tr>
<tr>
<td>HSP90</td>
<td>Mediate HS associated signal transduction.</td>
<td>[60]</td>
</tr>
<tr>
<td>HSP70</td>
<td>Facilitate proper protein folding and stabilizes newly synthesized protein by preventing aggregate formation.</td>
<td>[88]</td>
</tr>
<tr>
<td>HSP60</td>
<td>Helps in Protein refolding and prevent denatured protein accumulation.</td>
<td>[2]</td>
</tr>
<tr>
<td>HSP40</td>
<td>Small HSPs involved in refolding are set free by HSP40, HSP70, HSP100 after the formation of fully refolded protein.</td>
<td>[24]</td>
</tr>
<tr>
<td>Small HSPa</td>
<td>Helps in refolding of denatured proteins, thus prevent thermal aggregation.</td>
<td>[62]</td>
</tr>
</tbody>
</table>

### Table 2: Different role of antioxidants in scavenging ROS.

<table>
<thead>
<tr>
<th>Antioxidants</th>
<th>Functions</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Enzymatic antioxidants</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SOD</td>
<td>Catalyzes the dismutation of (O_2^{•−}) to (H_2O_2) and (O_2)</td>
<td>[2]</td>
</tr>
<tr>
<td>CAT</td>
<td>Convert (H_2O_2) into water and oxygen without using any reducing power.</td>
<td>[87,89]</td>
</tr>
<tr>
<td>GPX</td>
<td>Catalyzes the removal of (H_2O_2)</td>
<td>[74]</td>
</tr>
<tr>
<td>APX</td>
<td>Scavenging (H_2O_2) by oxidizing ascorbate.</td>
<td>[80]</td>
</tr>
<tr>
<td><strong>Non-enzymatic antioxidants</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ascorbic Acid</td>
<td>Donate electron in various enzymatic and non-enzymatic reaction.</td>
<td>[26]</td>
</tr>
<tr>
<td>Glutathione</td>
<td>Scavengers of singlet oxygen, hydrogen peroxide and hydroxyl radical</td>
<td>[74]</td>
</tr>
<tr>
<td>Tocopherol</td>
<td>Scavengers of (H_2O_2); up regulation of APX and GR</td>
<td>[80]</td>
</tr>
<tr>
<td>Carotenoids</td>
<td>Inhibit singlet oxygen formation</td>
<td>[80]</td>
</tr>
</tbody>
</table>
Stay green

Stay green (SG) associated genotype maintains photosynthesis and grain filling in HS condition through late expression of senescence related genes [82]. SG is an important mechanism for HS tolerance in wheat as it conserve photosynthetic area and increase nitrogen remobilization to the maturing grains [81]. During growing phases of ovaries, starch content in the ovary is depleted rapidly but under HS the accumulation of sugar decreases due to reduced photosynthetic activity which helps to seed abortion [82]. Increased photosynthetic activity due to SG, helps to maintain continuous sugar supply in growing anther and pollen , thus helps to retain pollen and ovules viability [83]. A research was conducted by to relate SG traits with canopy temperature depression (CTD) [84]. They observed higher value of CTD (air temperature-canopy temperature) in SG genotypes under HS condition and concluded that SG is highly associated with CTD. Therefore, SG trait can be used as selection criteria under heat stress in wheat genotypes [32].

CONCLUSION

Regarding the global warming, the frequency of heat stress in wheat is projected to increase worldwide. HS significantly affect grain setting, duration, rate, quality and finally grain yield. The effect of HS is genotype specific and also depends upon the intensity, timing, and duration of HS. Therefore, the development of tolerant varieties helps to minimize the effect of HS. Plant produces different metabolites such as antioxidants and HSPs under HS condition. Molecular studies of such metabolites play crucial role to know the mechanism underlying stress tolerance [86-90].

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