

Action and Reaction of Plants to High Temperature: Improving Response of Wheat to Heat Stress

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Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

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ABSTRACT

All estimates suggest that by 2050, upto 50% increase in food production will be required to feed the world population. Wheat is the second most important crop after rice and by 2050, wheat production needs to be increased by 60% for socio-economic stability. However, the climate change induced global warming will have adverse effect on crop plants including wheat. To deal with the crop yield decrease influenced by global warming, an indepth study of heat induced morpho-physiological and molecular changes in wheat will result in better understanding of the plant. This review focuses on the impact of high temperature on the morphological, physiological, reproductive development and signaling in plants.

Keywords: Climate change; fluorescence; heat stress; photosynthesis; yield; wheat.

1. INTRODUCTION

The second most important crop after rice is wheat (*Triticum aestivum*) [1] contributing approximately 20% of the total calorie intake [1]. In last few decades the negative effect of climate

change induced high temperature have become highly significant [2]. Two processes that are directly affected by increased ambient temperature includes respiration and photosynthesis [3]. An increase in the photosynthetic yield is expected in the first half of

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this century, although a decrease is predicted in the second half due to high [4-5]. On the basis of severity, temperature stress can be divided into four main categories: Heat *shock*, chronically high temperature, chilling at low temperature and freezing temperature stress. To cope with extremes of temperature, plants have evolved the ability to survive under seasonal extremes of temperature. The phenomenon is known as acquired temperature stress tolerance [6]. The underlying mechanism to tolerate high temperature stress by plants is brought about by the changing transcriptome of the plant cell [7]. Earlier studies have predicted higher expression of the stress induced genes in response to high temperature [7-8]. The increased susceptibility of photosynthesis in response to high temperature stress have been shown in wheat [9-11].

This review will mainly focus on the selection of traits for the improvement of wheat under high temperature conditions and the involvement of stress induced genes in ameliorating heat stress induced damages.

2. NEGATIVE EFFECT OF CLIMATE CHANGE ON CROP YIELD AND PRODUCTIVITY

In the past 10,000 years since humans have cultivated the land, the atmospheric CO₂ concentration have hovered between 260 and 280 $\mu\text{mol mol}^{-1}$ [12]. Beginning of 1900, a spike in atmospheric CO₂ level has been observed, with the current value reaching about 370 $\mu\text{mol mol}^{-1}$ resulting in a spike in the ambient temperature thus negatively affecting crop yield [13].

2.1 Effects of Climate Change on Plants

Plants respond to increased temperature in a short or long scale depending on the temperature severity [14]. Major effect of increased temperature result in deleterious effects on key enzyme activities, due to differential thermo-sensitivity or result in accumulation of key metabolites. Further, short term effects result in altered transcriptome, involving stress associated genes including HSP, ROS scavengers and transcription factors [15]. Longer term responses involve modulation in the rate of photosynthesis per unit leaf area, with impaired sugar metabolism, carbon and nitrogen partitioning within and between organs [16].

Temperature induced damage depend upon developmental stage [17], although experimental

studies on effect of temperature variability on crop yield are scarce. This is primarily due to the difficulty of mimicking the environment [18]. A solution to this is to examine the effects of extreme conditions at particular development stages [19], in which the temperature extremes are defined with reference to literature [20]. Wheat being a cool season crop plant is highly susceptible at the spikelet stage [21]; anthesis stage [21] and grain filling stage [7].

2.2 High Temperature Effect on Wheat

Wheat is an important cereal crop cultivated in an area of 220 million ha worldwide. Wheat is highly susceptible to high temperature stress especially at the flowering and grain filling stage. Due to climate change induced global warming, more than half of the wheat producing area worldwide is being exposed to heat stress. At present, more than half of the total wheat producing area in the world is susceptible to periodic heat stress [3,22]. Earlier workers have shown the effect of consecutive heat stress mimicking heat wave like scenario on Indian bread wheat varieties [10].

2.3 Membrane Stability

Earlier the membrane stability have been shown to be directly correlated with yield [21]. Reports have suggested a significant heritability and variability of this trait in wheat [7]. Temperature affects directly on the physical properties of biological membranes. In response to these changes, plants regulate the level of saturation of membrane glycerolipids, as the presence of unsaturated bond decreases the phase transition temperature [23]. For instance, under low temperature, plant cells are often associated with an increase in the production of polyunsaturated fatty acids (PUFAs) such as linoleic acids and α -linoleic acids, both of which are thought to help maintain membrane fluidity, because of their low melting temperatures, as well as, the content and position of fatty acids, attached to the glycerol backbone. A combine effect of these changes to the type and amount of glycerolipids and their associated fatty acid components represent a central part of the molecular adaptation of plants to temperature. Under high temperature, grass *Agrostis stolonifera*, shows high levels of saturated lipids while tolerant varieties have greater amounts of saturated lipids at normal temperature [24]. Similar increase in the saturated fatty acids has also been observed in other plant species [25].

2.4 Heat Stress Effects on Thylakoid Membranes Reactions

Moderately high temperature is shown to stimulate photosynthetic electron flow in leaves exposed to heat stress for the first time [25], but substantial inhibition in the capacity for photosynthetic electron flow is seen returning the leaf to the pre-stress temperature compared to the control situation [25]. Due to frequent and wide fluctuations observed by individual leaf temperature, the inhibition of electron transport capacity following heat stress is physiologically relevant. Studies on heat stress should include examination of the consequences of consecutive heat stress episodes separated by a recovery phase, not simply the rate of photosynthesis during the first heat stress episode experienced by the leaf. Earlier effect of consecutive heat stresses interrupted by a recovery phase were reported in *Aegilops sp.* and wheat cultivars [9-10].

Earlier, workers have proposed an increase in thylakoid proton conductance and increased cyclic electron flow around PSI in response to moderate heat stress [26]. Results have indicated an induction of Zeaxanthin synthesis as a counteraction to increased thylakoid leakiness [26]. An increase in Zeaxanthin level have shown to alter the physical state of thylakoid membrane [27]. Importance of thylakoid membranes during temperature stress was also supported by the finding that mutants lacking trienoic fatty acids in their thylakoid membrane are merely tolerant to the heat stress [28]. Therefore, moderate heat stress induces damage to thylakoid reactions is not due to PSII, but, probably involves different pathways related to cyclic electron flow and perhaps, the cytochrome complex. PSI mediated cyclic electron flow can occur by either antimycin A sensitive route involving ferredoxin plastoquinone reductase or a second route involving the NAD(P)H dehydrogenase complex [29].

2.5 Fluorescence

Chlorophyll fluorescence analysis due to its simplicity has become a widely used technique available to plant physiologists, molecular botanists, and eco-physiologists. The principle behind fluorescence is quite straight forward. Light energy absorbed by the chlorophyll molecule may end up in three fates: It can be used during photosynthesis or dissipated as heat or can be reemitted back in the form of light of

longer wavelength, i.e., fluorescence. These three processes are in equilibrium; any change in the efficiency of one will affect the other two. By measuring any the chlorophyll fluorescence, the information about the heat dissipation and photochemistry can easily be deciphered. Kautsky and co-workers in, 1960 have explained fluorescence in great details [22]. The effect of heat stress on the fluorescence in wheat and *Aegilops sp.* was earlier reported [7-10].

2.6 Temperature Affects Spike Fertility

Even without stress, grain set is dependent on carbohydrate supply. Data indicates that under conditions of high ambient temperature, abortion of grains has been linked to increased ethylene levels inducing programmed cell death at high temperature [30]. Heat stress at gametogenesis can further impair fertility [31]. Heat stress affects the overall health of pollen, affecting such processes like composition, metabolism, morphology and quantity of pollen [32]. Differential pollen viability under heat stress has been identified in different cotton cultivars (*Gossypium hirsutum*) [33]. QTL's have been identified for grain numbers under hot environments in wheat [34].

2.7 Effect of High Temperature on Floral Development and Function

Heat stress stimulate flowering, with the mechanism being uncovered in *Arabidopsis thaliana* [35]. Temperature stress at times creates asynchrony between male and female reproductive development [32]. Further high temperature stress can shorten the duration for which stigma is receptive to pollen in *Prunus persica L.* and thereby decreasing the chances of successful fertilization [33]. Increased percentage of flower abortion in response to low temperature is observed in chickpea (*Cicer arietinum*) [34]. Fewer studies have been done in female reproductive organs as compared to male. A decrease in the number of ovules and increased ovule abortion is seen in *Arabidopsis* under high temperature [35].

Heat stress related abnormalities are specific to particular stages. Heat stress during microspore meiosis can induce tapetum degradation in wheat [36], resulting in pollen sterility. High temperature reduces pollen dispersal in rice and tomato (*Solanum lycopersicum*) by tight closure of lodicules and hence poor anther dehiscence [37].

A decrease in carbohydrate reserve and ATP production was observed in pistils of cotton (*Gossypium hirsutum*) under moderate heat stress, resulting in decrease in pollen tube growth [38]. Temperature induced negative effects were observed in the development of female and male gametes including delayed pollen viability, germination ability, maturation, and pollen tube growth in response to heat stress [39].

High temperature in *B. napus*, tomato and wheat showed complimentary effect on both male and female tissue [39-41]. Earlier dynamic interaction between pollen and pistil were reported [42]. A 10% larger transcriptome was observed in pollen tube through pistil when compared with pollen germinated in-vitro in *Arabidopsis* [42].

Pollen transcript analysis revealed calcium dependent protein kinase 2 (CDPK2) up regulated in microspore under heat stress [43]. Microarray analysis showed differentially expressed genes under heat stressed microspores, with increased expression of SIAPX3 (a ROS scavenger), ethylene responsive genes (including the MBF1 homologue ER24, HSFA2, A3 and HSP family members, with higher levels of HSF2A and LeHSP17.4-C11 (a HSP) in tolerant cultivars of tomatoes as compared to sensitive cultivars [43].

2.8 Ca²⁺ in Sensing and Signalling

The plants cell senses diverse extracellular stimuli by the Ca²⁺ that acts as a secondary messenger thus bringing about various intracellular responses [44]. A number of Ca²⁺ sensors have been characterized in plants including CBL- interacting protein kinase (CIPKs), calmodulin (CaM), and Calcineurin B-like protein (CBLs) [45].

Earlier reports have emphasized on the role of Ca²⁺ as sensors in stress signal transduction [46]. Tight regulation of Ca²⁺ is required for maintenance of homeostasis, to increase the specificity of Ca²⁺ peaks in response to different levels of stresses [47]. For e.g., the magnitude of cytosolic Ca²⁺ levels showed cell specificity in *Arabidopsis* root cells in response to salt, osmotic and low temperature stresses [48].

2.9 Role of Ca²⁺ in Heat Sensing

In response to heat stress, transient peaks of Ca²⁺ have been reported across the plasma membrane, thus highlighting the role of Ca²⁺ in heat stress sensing by plasma membrane [49].

Earlier reports have shown a rapid influx of Ca²⁺ in response to benzyl alcohol treatment (a known membrane fluidizer), followed by induction of HSP's resulting in developing acquired thermo-tolerance [49]. Higher expression of Cam3 and Cam7 was reported in response to thermal stress which further resulted in the expression of HSP's [50]. Cams are shown to interact with calcium dependent kinases such as AtCBK3, thus resulting in the induction of HSFs, which act as a regulator of HSP and thus impart thermo-tolerance to plants [51]. The HSF expression/regulation seems to be governed by membrane physiological state and perhaps triggered by increased fluidity of membrane, thus resulting in expression of different HSP's and also the change in proportion of saturated and unsaturated fatty acid.

2.10 Stress Induced Genes

Plants shows tolerance towards various stresses by expressing a number of stress induced genes that ultimately impart tolerance towards various stresses. Some of the stress induced genes that are extensively studied includes LEA (Late embryogenesis abundant proteins), ERDs, LTPs, HSPs besides others. Late embryogenesis abundant (LEA) proteins, first identified in plants, are a family of proteins characterized by their extremely hydrophilic nature, belonging to 7 different groups. These proteins accumulate under stress and stabilizes other proteins and membrane [52]. Another important regulators for stress induced genes are the transcription factors like ZnFi, bZIP, CBF/DREBs (C-repeat-binding factor/ dehydration responsive element binding proteins). Overexpressing lines of TFs in transgenic plants resulted in better tolerance towards drought, salinity, heat and freezing stress [53]. The probable mechanism in ameliorating stress in plants might be by acting as hydration buffers, molecular chaperones, ion sinks or membrane stabilizers [54]. In *A. thaliana*, Early Response to Dehydration (ERD) genes induction was reported in response to cold, drought and salt stresses. In-vitro studies with these proteins have shown their chaperone activity on several substrates due to an "entropy transfer" mechanism [55,55-56]. Hence these proteins are believed to play crucial roles in stress tolerance mechanism in plants. Another important family of protein having role in imparting tolerance towards various abiotic as well as biotic stress is Lipid Transfer Protein gene family [57]. A number of recent finding have highlighted the induction of LTPs in response to abiotic stresses [8].

2.11 Heat Shock Proteins (HSPs)

A known adaptive response to thermal stress is the expression of HSPs [58] ranging in molecular weight of about 10-200kDa. These molecules have chaperone-like functions and are involved in signal-transduction during stress [59]. Over expression of different HSPs have shown to result in improved photosynthetic efficiency, assimilate partitioning, water and nutrient use and membrane stability [60]. Their expression is triggered by either abrupt or a gradual increase in temperature [61]. Although, all HSPs till date have not been characterized, but their correlation with thermo-tolerance is attributed to the observations that they are rapidly induced in organism exposed to heat stress and are induced in a variety of cells across diverse organism. HSPs are classified into three classes based on their molecular mass, i.e., HSP90, HSP70 and low molecular proteins of 15-30 kDa, also called as small HSPs. Small HSPs shows tremendous abundance and diversity. The basic function remains conserved in all the three classes of HSPs across plant species. Small HSPs in plants are encoded by six nuclear gene families, with each gene family corresponding to proteins found in distinct cellular compartments like cytosol, chloroplast, endoplasmic reticulum (ER), mitochondria and membranes. There are differential expressions of HSP production in different species and even between genotypes within species [62]. Rapid synthesis of HSPs in sensitive organs/tissues can play an important role in protection of metabolic apparatus of the cell, thereby enhancing its chances of adaptation and survival under stress.

Although a number of roles have been ascribed to HSPs but their exact role remains elusive. Recent reports suggests HSPs to be acting as molecular chaperones, thus helping in maintaining the functionality and native configuration of cell proteins under heat stress. Studies show that acquisition of thermo-tolerance is directly related to the synthesis and accumulation of HSPs [63]. HSPs aid in folding of new or distorted proteins for normal functions and also transporting old proteins to garbage disposal inside the cell.

2.12 HSF and HSP Mediated Response to Protein Misfolding

Severe heat stress result in misfolding of protein thus disrupting cellular homeostasis and growth in plants and in yeast [64], further inducing

cytoplasmic protein response regulated by HSFA2, as is revealed by HSFA2 knockout and overexpression plants [65]. High temperature results in the unfolded protein accumulation in ER. This triggers unfolded protein response, resulting in overexpression of HSP70, HSP90 and other chaperones along with ER-associated degradation mechanism [66].

2.13 Future Prospects of Crop Production

For sustaining agriculture in a harsher climate, short term sectorial and long term structural adaptive changes will be required including plant breeding, along with integration of transgenic approach to produce stress tolerant plants [15].

Traits important for abiotic stress including heat and drought stress will include early flowering, mainly known as escapers [35], deeper roots, for efficient soil water extraction [67] along with a smaller canopy size to minimize evaporation [67]. Although such traits are associated with increased tolerance to plants experiencing stress, unfortunately such traits in general are associated with reduced yield. Another player of significant importance is stomatal movements. Earlier closure under severe heat stress ensure that the crop avoided a heat induced decreased yield substantially. To maintain leaf water potential, plants synthesize osmolytes resulting in continued evapotranspiration and increased the likelihood of the crop experiencing a lethal stress before reaching maturity.

3. CONCLUSIONS

In the coming decades the global warming induced increase in atmospheric temperature will have drastic effect on crop yield. For sustainable crop production in the coming decades, extensive human intervention will be required to control the microenvironments of the crop plants. This review has highlighted the traits that are affected in response to high temperature stress in crop plants. To achieve the crop yield under high temperature conditions, a combination of classical as well as advanced molecular techniques will help in phenotyping and genotyping of the uncharacterized accession and their application in breeding for generation of stress tolerant high yielding lines.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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