



ISSN (E): 2277- 7695  
 ISSN (P): 2349-8242  
 NAAS Rating: 5.23  
 TPI 2021; 10(4): 909-917  
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 www.thepharmajournal.com  
 Received: 22-01-2021  
 Accepted: 25-03-2021

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## Heat stress: Effect and tolerance mechanism in major cereal crops

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### Abstract

Nowadays, abiotic stresses are the major area of concern for plant breeder as they are the cause of massive yield losses. Among all the stresses, escalating adverse effect of heat stress are putting global food security and nutritional security at greater risk. Temperature persistently higher than the optimal temperature induces adverse effect on growth and development of plants is called as heat stress. Heat stress induces physical damage, biochemical changes and physiological disruption and thus, increases the yield gap between potential yield and the actual yield production in crop plants. Different crop plants have varying degree of tolerance and sensitivity to the threshold temperature. Generally, the reproductive phase of crop plants is more sensitive than vegetative phase. Therefore, a better understanding of plant responses to these stresses has pragmatic implication for remedies and management.

**Keywords:** heat stress, tolerance, crop plants and heat shock protein

### Introduction

The green revolution occurred between 1950 to late 1960s increased the agricultural production throughout the globe. This was the third agricultural revolution, at the end of 1960s it breakdown the plateau reached in yield of many crops. Decades of research, modification in breeding strategies and advancement of technology led to the development of such crop varieties and hybrids which can boost the production as well as increases the income of farmers. This also helped in keeping the pace with the demand of ever-growing population. But looking at current scenarios, to achieve the same gain, we are facing a dual challenge 1) many crops are reaching to its yield plateau at a faster rate (Iizumi *et al.*, 2017; Zhao *et al.*, 2017) [21, 50] adverse global climatic changes that negatively affect the crop production (Pfleiderer *et al.*, 2019) [29]. In 2019, the earth's surface temperature was 0.95 °C warmer than the average of 20<sup>th</sup> century (Tiseo, 2020) [41]. Variation in climate can increase or decrease the length of developmental stages of crop plants (Lemma *et al.*, 2016) [23]. The areas which are more prone to heat stress are Central and East Asia, North American and the Indian subcontinent among those growing the major crops rice, wheat and maize (Teixeira *et al.*, 2013) [62]. Among all the environmental factors which adversely affects the plants, temperature is the preliminary factor which affects plant activities like seed germination, photosynthesis, evapotranspiration, stomatal conductance, reproduction, growth and development (Hasanuzzaman *et al.*, 2012) [12]. Each degree rise in average seasonal temperature can decrease the yield by 4.1 % to 10.0 % (Wang *et al.*, 2012) [44]. By assessing the impact of increased global temperature on crop production, it has been found out that increase in each degree Celsius of temperature reduces the global yield of wheat by 6.0%, rice by 3.2% and maize by 7.4% (Zhao *et al.*, 2017) [50]. The reduction in yield may negatively affect our food and nutritional security and in return increases the rate of hunger in the most vulnerable parts of the globe which are majorly dependent on agriculture like Hindu Kush Himalayan region, encompassing parts of Pakistan, India, and Nepal (Rasul *et al.*, 2019) [32]. That's why development of heat stress tolerant cultivars will be an effective and ideal solution to achieve the desired crop yield. But before going for any breeding programme we need to understand the effect of heat on crop plants and how they combat this effect and mechanism they adopt to protect themselves from stress conditions.

### Heat stress and its effect on crop plants

Temperature and photoperiod plays a crucial role in phenological development of plants. The sudden increase or decrease in temperature leaves negative impact on the metabolic processes inside the plant. There is an optimal range of temperature for each plant species below or

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above which plant growth and development are affected (Table 1). The temperature above the threshold causes irreversible damage to the growth and development of plant are called as heat stress, it varies at different stages of life cycle and ultimately results in yield reduction in crop plants (Djanaguiraman *et al.*, 2018) [14, 15]. There are number of factors which lead to heat stress namely intensity, duration, temperature increasing rate and sensitivity of the developmental stage of plant to increased temperature (Wahid *et al.*, 2007) [65]. The high temperature leads to multifarious effect on plant like shortens the duration of growth duration, accelerates the onset of reproductive stage, increased pollen sterility percentage, reduced accumulation of sufficient resources in grain and ultimately results in catastrophic loss in grain productivity (de Souza *et al.*, 2012) [13]. The reason behind increasing sterility could be abnormal meiosis in male and female organs, anomaly stigmatic and style position, disturbed fertilization process, disrupted pollen tube growth and impaired pollen germination. The increased ambient temperature can leads to collapse of cellular organization by the denaturation of proteins, increased fluidity of membrane lipids, inactivation of crucial enzymes in chloroplast and mitochondria, halting of photosynthesis, reduced ion flux, production of toxic compounds, production of reactive oxygen species (ROS) most commonly single oxygen, superoxide radical, hydrogen peroxide and hydroxyl radical, eventually leads to the cell death (Ashraf *et al.*, 2005) [6]. The cereal crop responds differentially to the variable heat stress conditions occurring at different stages of their growth duration. In sorghum, heat stress conditions when created artificially led to the accumulation of reactive oxygen species (ROS) in pollens, damages the pollen membrane and showed 62-90 % reduction in seed set (Djanaguiraman *et al.*, 2018) [14, 15]. In most of the cereal crops, reproductive stages are more sensitive to heat stress as compared to vegetative stage. This causes severe reduction in seed set because of reduced water and nutrient transport during reproductive development. Basically, male gametophyte is found sensitive to high temperature while pistil and female gametophyte is tolerant whereas, in pearl millet the situation is reversed (Gupta *et al.*,

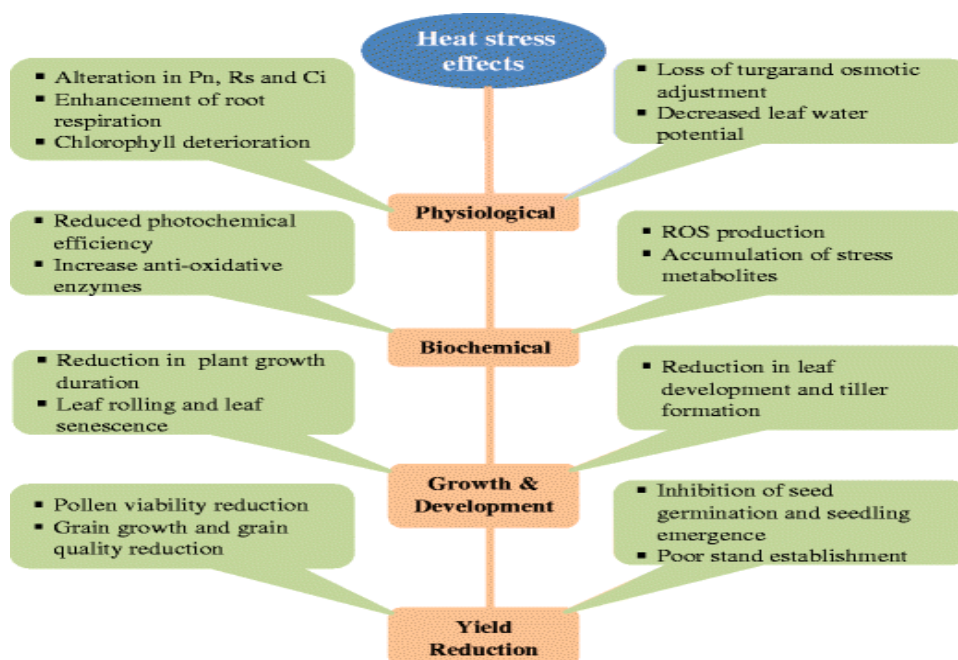
2015) [18]. Generally, many morphological symptoms like leaf scorching, sun burning of stems and leaves, leaf senescence can be observed in plant under heat stress.

**Table 1:** Threshold temperature at different developmental stages of major cereal crops

Sr. No.	Crop	Threshold temp. (°C)	Developmental Stage
1	Rice	15-35	Germination
		33	Biomass
		25	Grain formation and yield
2	Wheat	24	Grain yield and quality
		10-35	Germination
		20-30	Vegetative
		15	Reproductive
		35	Post anthesis
3	Maize	35	Protein accumulation
		15-40	Germination
		33-38	Photosynthesis
		38	Vegetative
		36-40	Pollen viability and fertilization
4	Pearlmillet	10-34	Germination
5	Sorghum	20-40	Germination
		26-34	Vegetative
		25-28	Reproductive

(Source: Govindaraj *et al.*, 2018)

**Effect of heat stress on wheat:** The phenological development of wheat (total crop growth duration/days to maturity) significantly affected by the heat stress. The pre-reproductive and reproductive stages are more prone to heat stress as compared to post reproductive stages (Yang *et al.*, 2013) [48]. Specifically twenty day prior to the anthesis and ten days after anthesis are considered as sensitive stages to heat stress (Balla *et al.*, 2019) [6]. It reduces the green leaf area, reduces the pollen fertility from 86.6 % to 80.0 % and reduces the germination percentage from 97.9 % to 84.1 % (Joshi *et al.*, 2016) [22].



**Fig 1:** Effect of heat stress (Pn, Rs, and Ci indicate photosynthesis, stomatal conductance, and intercellular CO<sub>2</sub> concentration, respectively) (Source: Heat stress effects and management in wheat: a review, Aktar and Islam, 2017)

The leaf development and productive tillers formation is severely affected by the day and night temperature (30 °C and 25 °C respectively) (Rahman *et al.*, 2009) [31]. At cellular level, heat stress results in increased cell membrane permeability by denaturation of proteins and increases the level of fatty acids results in inhibition of cellular function (Cossani *et al.*, 2012) [10]. In wheat, starch synthesis is more sensitive to heat stress than protein synthesis (Bhullar and Jenner 2005) [8], the temperature between 30-40 °C can reduce the activity of soluble starch synthase enzyme thus decreases the starch accumulation by 30 % in developing wheat kernels (Stone *et al.*, 1995) [59]. The temperature above 30 °C sharply declines the rate of photosynthesis (Wardlaw *et al.*, 1974) [45]. Decrease in photosynthesis can be due to the damage to thylakoid membrane, changed lipid composition, production of more reactive oxygen species, stomatal and non-stomatal limitations (Djanaguiraman *et al.*, 2018) [14, 15]. Heat stress at the time of reproductive phase also retards the root growth, reason behind decreased carbon partitioning in roots (Porter and Gawmuth, 1999) [30].

**Effect of heat stress in rice:** The stress induced by high temperature significantly negatively affects the rice crop from germination to ripening led to low or no harvest when high temperature climate occurs at anthesis (Shah *et al.*, 2011 and Fu *et al.*, 2016) [54, 16]. The optimum temperature for rice germination is between 28 °C to 30 °C. The most sensitive stage to heat stress in rice production is the flowering, and continuous exposure to high temperature (>35 °C for 4-5 days) induces pollen sterility, failed germination of pollen on stigma with no seed produced (Satake *et al.*, 1978) [35]. The production and quality of rice deteriorated with the occurrence of high temperature at flowering and grain filling stage. The critical temperature for spikelet fertility has been reported to be 35 °C, above this temperature spikelet fertility decreases due to inhibition in anther dehiscence and reduced pollen activity (Coast *et al.*, 2016) [15]. The auxin level plays a critical role in pollen tube elongation inside the pistil, and decreased auxin level under heat stress increases the spikelet sterility (Zhang *et al.*, 2018) [49]. Heat stress blocks the sucrose transport and metabolism in phloem of leaf, sheath-stem and grains by the deposition of callose onto the plasmodesmata of leaf and sheath cells thus decreases the kernel weight (Zhang *et al.*, 2018) [49]. During rice ripening period high temperature may produce chalky grains that decrease the appearance of rice kernels (Mitsui *et al.*, 2013) [27]. The grain chalkiness is the result of increased activity of alpha amylase which hydrolysis the starch when plant is exposed to high temperature at grain filling stage (Suriyasak *et al.*, 2017) [40]. The high temperature >32 °C results in excessive production of ethylene which leads to male sterility.

**Effect of heat stress in maize:** Maize is one the prime three cereal crop across the globe having wider adaptability under diverse agro-climatic conditions. However, variable climatic condition leads to abrupt rice in temperature poses a serious threat on the quality and yield of grain in maize. The temperature above 25-30 °C (optimum daytime range) affects both the vegetative and reproductive stages of maize. The highly sensitive stages to heat stress in maize are anthesis, silking and grain filling which shows pronounced decline in grain production (Shah *et al.*, 2011) [54]. The high temperature perturbrates metabolic rate which shortens the life cycle. The 35/27 °C temperature at reproductive stage results in reduced

ear expansion, suppression of cob extensibility by impairing hemicelluloses and cellulose synthesis through reduction of photosynthate supply (Yin *et al.*, 2010) [72]. The heat stress negatively affects the pollen dehiscence, pollen fertility, silk emergence and stigma receptivity, seed setting and grain filling leads to reduction in grain yield (Xiao *et al.*, 2011) [47]. Higher temperature induces the oxidative damage by framing imbalance between antioxidant activity and production of reactive oxygen species. Further, it leads to alternation of membrane fluidity and ultimately has negative impact on photosynthesis and respiration (Bita *et al.*, 2013) [9]. Heat stress may induce specific injuries in maize plant namely leaf firing, tassel blast and senescence and affects the photosynthetic efficiency. These tissue injuries could be associated with reduced chlorophyll content, oxidative damage and eventually with the low grain yield (Alam *et al.*, 2017) [4]. At molecular level, temperature above 45 °C results in inactivation of Rubisco and substantial reduction in photosynthesis and malate-inhibited PEPC activity (Crafts-Brander and Salvucci, 2002) [11].

**Effect of heat stress in Pearlmillet:** Pearlmillet is an important nutritional crop in arid and semi-arid regions. It requires 26 °C for vegetative growth and 22-25 °C for reproductive growth. The temperature beyond this range may induce heat stress in plant and can cause negative impact on grain yield. In pearlmillet, two periods 10-12 days before anthesis (gametogenesis) and 2-0 days before anthesis (anthesis, fertilization and embryo formation) during reproductive stage are most sensitive period to heat stress results in decreased pollen germination and seed set, temperature 36/26 °C led to floret sterility (Djanaguiraman *et al.*, 2017) [23]. Growth reduces under heat stress due to reduction in cell size and water status (Ashraf and Hafeez, 2004) [5]. Reactive oxygen species (ROS) contribute largely to the heat stress sensitivity, in pearlmillet ROS are more than the ROS scavenging enzymes in pistil compared with the pollen, thus pistil are more heat sensitive (Djanaguiraman *et al.*, 2018) [14, 15].

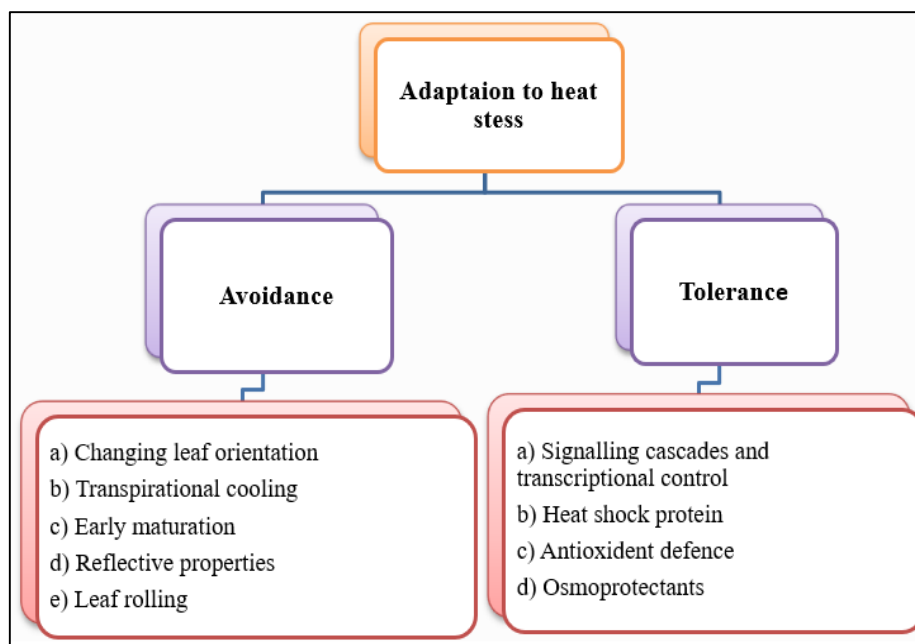
**Effect of heat stress in Sorghum:** Sorghum is more tolerant to heat stress than other crops due to its floret morphology. In sorghum, period of sporogenesis when confront high temperature stress leads to abnormal development of pollen exine wall, damages the membrane and degradation of tapetal cells and eventually leads to the pollen sterility. High temperature affects both the vegetative and reproductive stages of development. It increases the developmental rate, leaf number, leaf appearance rate. The most sensitive period to heat stress is head emergence through flowering (Bean, 2017) [8]. The temperature 40/30 °C at 65 days to maturity lead to decreased chlorophyll content, chl a fluorescence, decreased PS II activity, decreased antioxidant activity damage thylakoid membrane and end result will be reduced yield. In case of sorghum due to its high tolerance to heat stress, most tolerant genotype showed small reduction in seed set at 38 °C and most sensitive genotype showed significant reduction in seed set at 36 °C of temperature, could be due to the exposure to high temperature during the period of pollination or pollen formation (Hammer *et al.*, 2015) [19].

#### Mechanism of adaptation to heat stress

Plant adopts morphological, physiological and molecular mechanism to survive under stress conditions because they

cannot move out from the unfavorable condition and are compelled to grow there. In case of high temperature stress caused multifarious conditions like increased soil temperature, increased ambient air temperature and water scarcity, plant responds accordingly to reduce its effect and to maintain its survival and retain its growth, development,

physiological processes and ultimately less reduction in yield. The plant reprogram its metabolic activities and alter its morphology to reduce the effect of heat stress and to decrease the surface area that come in direct contact with high temperature.



**Fig 2:** Flow chart deciphering mechanism of heat tolerance adopted by plant

Two types of mechanism adopted by plant to survive under high temperature: 1) Avoidance 2) Tolerance

### 1. Avoidance mechanism

- a) **Escape mechanism:** In escape mechanism, plant tries to complete its growth duration or heat stress sensitive phenological stages before the arrival of high temperature stress conditions. Escape from heat stress is only possible in areas where natural heat stress occurs at particular time and is predictable (Ahmed *et al.*, 2012) <sup>[1]</sup>. In cereal crops, early flowering in maize and rice decreases the pollen sterility percentage by moving the peak flower opening time to the cooler timing of day under dry conditions. The opening of flower during cooler hours reduces 71 % sterility in rice. In wheat, anthesis may occur either in morning hours or cooler evening hours to combat the heat stress effect on reproductive organs, and shows no seed set reduction (Aiqui *et al.*, 2018) <sup>[2]</sup>. It involves increased rate of phenological development (early onset of reproductive phase and early maturity) (Dalal *et al.*, 2012) <sup>[12]</sup>.
- b) **Leaf orientation and leaf rolling:** Some plant growing in hot climatic condition adopt a mechanism called as paraheliotropism, in which leaf orient themselves parallel to sun rays to reduce solar radiation absorption (Hasanuzzaman *et al.*, 2013) <sup>[20]</sup>. They often rolled their leaf blades in order to minimize their exposure to direct sun rays and also under water stress condition. In wheat, leaf rolling increases the water use efficiency in flag leaf under heat stress by decreasing the transpirational surface area by other leaves (Sarieva *et al.*, 2010) <sup>[34]</sup>. This strategy will extend the leaf area duration, delays leaf senescence and improve grain size (Sirault *et al.*, 2015) <sup>[38]</sup>. The transverse rolling of lamina along the mid axis or

leaf rolling can be seen in wheat, maize, rice and sorghum. Depending upon stress condition, under mild heat stress condition, delayed leaf rolling will be beneficial to sustain plant growth and yield production whereas, under severe condition leaf rolling provide better chances to regain plant's normal metabolism when stress is relieved (Blum *et al.*, 1998) <sup>[13]</sup>.

- c) **Transpirational cooling:** It is very important for a plant to regulate its leaf temperature to prevent the deterioration of protein structure, electrolyte leakage by the cell due to loss of membrane integrity, production of reactive oxygen species by intra-cellular organelles i.e. mitochondria, chloroplast and peroxisomes, degradation of photosystem I and II, abnormal chloroplast structure formation and enzyme activities which may end up with leaf senescence under high temperature stress. It is an effective strategy for maintaining cooler canopy temperature under heat stress. It helps in achieving high rate of photosynthesis under stress condition and is the most active as well as common method of heat dissipation in wheat as, tolerant genotypes maintains high stomatal conductance. In pearl millet, it has been reported that heat tolerant genotypes record high temperature up to the middle of the plant and after that internal temperature of plant start decreasing due to the transpirational cooling effect (Shankar *et al.*, 2020) <sup>[37]</sup>. This method is also beneficial for rice and maize.
- d) **Reflective properties:** The leaf surface traits like glaucousness and pubescence are components for heat avoidance. These two traits help in lowering the water loss and maintain lower leaf temperature under high irradiance. They may contribute to increase water use efficiency under stress condition by increasing leaf boundary layer resistance.

## 2. Tolerance mechanism:

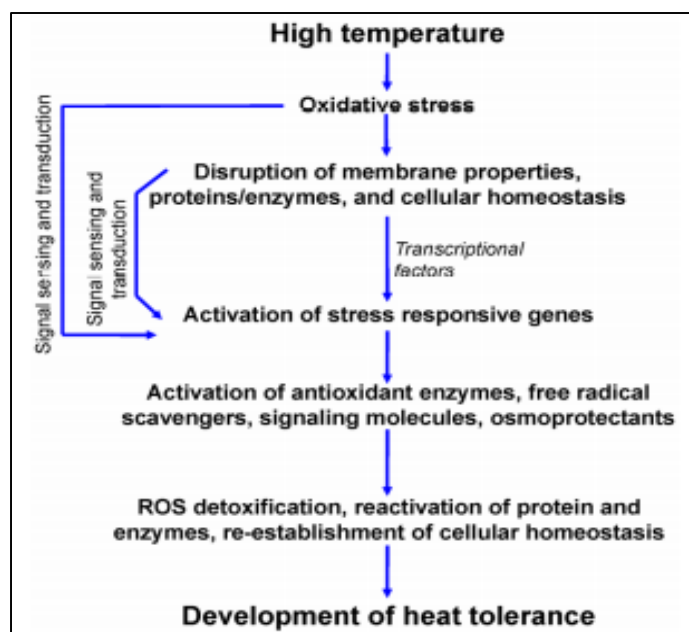
a) Antioxidant defense mechanism: Heat stress is responsible for the over production of reactive oxygen species by the intra-cellular organelles which disturbs the homeostasis inside the cell, this can be overcome by the modification of antioxidant system which will re-establish the redox potential and homeostasis. The high temperature increases the monoaldehyde (MDA) content in leaves by decreasing the activity of antioxidant enzymes in rice. The MDA content react with protein and amino acids, results in aging and seed damage (Weber *et al.*, 2004). The balance between production and detoxification of ROS is maintained by the activity of antioxidants. This can be of two types:

- 1.) Enzymatic antioxidants: it comprises of superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), guaiacol peroxidase (POX) peroxidoxins (Prxs), and enzymes of the ascorbate-glutathione (AsAGSH) cycle, such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR).
- 2.) Non-enzymatic antioxidants: it includes cellular redox buffers such as ascorbate (AsA) and glutathione (GSH), tocopherol, carotenoids and phenolic compounds (Scandalios, 2005) [36].

In case of wheat, under heat stress conditions activity of SOD, CAT, POX and GR increases to detoxify the toxic levels of ROS (Wang *et al.*, 2014) [43]. The SOD catalysis the dismutation of superoxide radical to hydrogen peroxides and thus acts as frontlines defense mechanisms under abiotic stresses. By comparing antioxidants active between rice and maize, it has been found out that the activity of enzymatic antioxidants such as CAT, APX and GR was found to be higher in *Z. mays* plants compared to *O. sativa* plants and also

non- enzymatic antioxidants like AsA and GSH were maintained significantly greater levels at 45/40 °C in maize than in *O. sativa* genotype. This suggests that *Zea mays* is more tolerant under high temperature stress than the *Oryza sativa*. In pearl millet, under heat stress conditions the activity of CAT and GR increases for scavenging the ROS, whereas the level of GPX and APX were almost similar in all types of abiotic stresses ranging between 54–68.9 and 50–59%, respectively (Lakshmi *et al.*, 2017) [42]. While in case of sorghum, the up regulation of antioxidant enzyme activity of SOD, POD and CAT under heat stress, their concentration may vary according to the genotypes (Gosavi *et al.*, 2014) [17].

b) Osmoprotectants: Osmoprotectants or compatible solutes are small organic molecules, which don't carry any charge and thus are neutral and remain low toxic at high concentration, help the plants to survive under extreme osmotic stress conditions (Riaz *et al.*, 2019) [33]. They help the plant to regulate the gene expression in response to environmental osmolarity. They may include amino acids (proline, ectoine, pipercolic acid, etc), polyamines, betaines (glycine betaine, choline-O-sulfate, β-alanine betaine, etc.) quaternary ammonium compounds, sugar alcohols and non reducing sugar (trehalose, sorbitol, inositol, mannitol, etc.) (Slama *et al.*, 2015) [39]. They may acts as metabolic signals, stabilize the cellular structures and structure of enzymes and also helps in scavenging of ROS produced under stress conditions. In sorghum, under high temperature stress glycine betain plays the crucial role of osmoprotectant in leaves. For such crops, application of genetic engineering brought solutions by making them transgenic so that they can synthesis osmolytes under stress conditions for the maintenance of cell structure by acting as membrane stabilizer.



**Fig 3:** Schematic illustration of heat induced signal transduction mechanism and development of heat tolerance in plant (Source: Hasanuzzaman *et al.*, 2013) [20]

c) Signaling cascades and transcriptional control: The initial stress signals like change in membrane integrity, change in osmotic balance, and change in temperature may triggers the downstream signaling processes and

transcriptional control to re-establish the homeostasis and protect and repair the denatured protein structure and membrane. Signalling molecules like calcium dependent protein kinases (CDPKs), mitogen-activated protein

kinases (MAPKs), nitous oxide (NO), sugar and phytohormones (Ahmad *et al.*, 2012 <sup>[1]</sup>). These are the secondary messengers which are involved in protein phosphorylation cascades accumulation of regulatory molecules like stress related hormones (abscisic acid, ethylene and salicylic acid), involved in activation of stress responsive genes so that activated genes reprogram the cellular metabolism and main the production of ROS (Chen *et al.*, 2020) <sup>[14]</sup>. In wheat and pearl millet calcium iron dependent heat signaling pathway are generated to activate the heat responsive genes (Liu *et al.*, 2016) <sup>[36]</sup>. In case of maize, calcium ion act as secondary messenger and abscisic acid activates the heat shock protein genes under high temperature stress conditions (Zhi-quiang *et al.*, 2015) <sup>[76]</sup>. In case of rice, ethylene work as signaling molecule enhanced heat shock factors and activate ethylene related gene expression under heat stress, this pathway also regulate scavengers enzymes to enable rice seedling adaptation under oxidative stress (Yu-Sian Wu and Yang, 2019) <sup>[73]</sup>. In sorghum, CDPKs and MAPKs work as signaling molecule when both the heat and draught stress occurs together.

Heat shock proteins: Heat shock proteins are molecular chaperones that regulate the folding, localization,

accumulation, and degradation of protein molecules in plants and impart tolerance to high temperature stress. These molecular mass ranges between 10 to 200 kDa, helps in maintaining normal protein conformation and are involved in signal transduction under heat stress. A total of 753 HSP genes were identified in the wheat genome which includes 169 SHSP, 273 HSP40, 95 HSP60, 114 HSP70, 18 HSP90 and 84 HSP100 and in rice 15 HSP gene were identified which includes 3 HSP60, 6 HSP70, 3 HSP 90 and 3 HSP 100 have been reported by using genome wide identification for the heat shock protein family. In maize, by using proteomic analysis the expression of four heat shock protein were detected which play significant role in thermo-tolerance, it includes ATPase beta subunit, HSP26, HSP16.9, and unknown HSP. In pearl millet, accumulation of heat shock protein under heat stress play a crucial role in its heat stress response and thermo-tolerance. There are 30 differentially expressed genes associated with heat shock protein were reported when plant is exposed to 48 hours of heat stress. In this 3 genes codes for HSP100, 14 genes code for HSP90, 12 genes code for HSP 70 and 1 gene encode sHSP (Sun *et al.*, 2020) <sup>[60]</sup>.

**Table 2:** Basic function of major classes of heat shock proteins in plant system for heat stress tolerance.

Major classes of heat shock protein	Functions
HSP100	ATP dependent dissociation and degradation of aggregate protein
HSP90	Co-regulator of heat stress linked signal transduction complexes and manages protein folding. It requires ATP for its function
HSP70, HSP40	Primary stabilization of newly formed proteins, ATP dependent binding and release
HSP60, HSP10	ATP dependent specialized folding machinery
HSP20 or small HSP (sHSP)	Formation of high molecular weight oligomeric complexes which serve as cellular matrix for stabilization of unfolded proteins. HSP100, HSP70 and HSP40 are needed for its release

Source: Physiological, Biochemical, and Molecular mechanism of Heat Stress Tolerance in Plants (Hasanuzzaman *et al.*, 2013) <sup>[20]</sup>

## Conclusion

Heat stress is an important constraint limiting the crop productivity worldwide. Plant shows a wide range of responses to high temperature stress conditions prevailing in their micro and macro environment. Each degree rise in average seasonal temperature can decrease the crop yield by 4.1 % to 10.0 % depending upon the species and stage at which they occur. There is varying degree of threshold temperature for each crop species above which crop losses can be seen. The most effective way to reduce or prevent the yield losses due to stress is to develop abiotic stress tolerant varieties. For initiating any breeding programme, one should know the physiology of crop plant, degree of damage cause by heat stress, manner in which they response to heat stress conditions, mechanism they adopt to tolerate the heat stress and biomolecules responsible for heat stress tolerance. Heat shock proteins are molecular chaperones that regulate the folding, localization, accumulation, and degradation of protein molecules in plants and impart tolerance to high temperature stress. Although not all species and varieties show similar responses to heat stress, monitoring the response of the available germplasm through physiological, biochemical and molecular indicators will allow to identify possible progenitors for genetic improvement, and to recommend tolerant genotypes to regionalize varieties.

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