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Breeding for heat tolerance in wheat

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Abstract

Wheat is one of the major cereals grown worldwide. Wheat is sensitive to heat stress. Slight increase in temperature can adversely affect the global wheat production. For every 1 °Celsius increase in temperature, global wheat production is reduced by 4.1% to 6%. With regards to global estimates, 20% of yield losses occurred due to heat stress. Terminal heat occurs at the grain filling stage. This review paper gives a detailed overview of the heat tolerance mechanism which includes heat shock proteins and an antioxidative enzyme is essential to formulate appropriate breeding strategies to develop varieties tolerant to the heat stress. Heat stress influences various morphological factors, for instance, hinders seed germination, reduces dry mass and shoots and root length. Heat stress increases the production of sterile spikelets, declines the number of grains per ear, number of grains per spikelet, grain weight and mean grain weight per spikelets. Heat stress affects physiological factors such as photosynthesis and respiration and biochemical factors such as starch and amylose content. The integration of conventional breeding with the genetic engineering further enhances the development of novel heat tolerant varieties.

Keywords: Heat stress, heat shock proteins, antioxidative enzymes, QTL mapping, transcriptome profiling, proteomics, metabolomics, genetic engineering and speed breeding

Introduction

Wheat (*Triticum aestivum* L.) is one of the most widely cultivated cereal crop. It belongs to the order *Poales*, family *Poaceae* and botanical tribe *Triticeae*. Wheat is an allohexaploid species ($2n = 6x = 42$) that originated in the Fertile Crescent area in the early Neolithic period (Kilian *et al.*, 2010). It is a staple food for about 35% of the world population accounting for an annual global production of 775.87 million metric tonnes (USDA, 2020-21). Wheat is cultivated in tropical and subtropical regions that are subjected to various abiotic stresses. Stress is defined as a phenomenon that affects crop productivity or destroys plant biomass (Vijayalakshmi, 1999) [37]. Abiotic stress is caused by non-living factors which includes heat stress, water logging, drought, salinity, mineral deficiency, heavy metal toxicity and ultraviolet radiation (B). Heat stress is a phenomenon of increase in temperature above threshold level for a sufficient period of time to cause damage to plant growth and development. Heat tolerance is described as potential of a plant to produce grain yield under heat stress (Wahid *et al.*, 2007) [38]. According to global climate models for every 1 °C increase in temperature, global wheat production decreases by 4.1% to 6% which indicates sensitivity of wheat to heat stress (Liu *et al.*, 2016) [21]. As per global estimates, about 20% of yield losses occurs due to heat stress (Karki *et al.*, 2021). In wheat, terminal heat stress occurs when the mean temperature during the grain filling stage exceeds 31 °C (Dubey *et al.*, 2020) [7]. Terminal heat stress at reproductive stage showed higher severity at booting and heading stages than anthesis and grain filling stage. This resulted in yield reduction of 41.4-88.4%, 22.1-66.8, 7-31.1% respectively than control that grown under well irrigated and ambient temperature conditions. Under heat stress, the wheat cultivar Mairaj-2008 had taken more duration for grain filling. While, heat sensitive cultivars such as BARS-2009 and Shafaq-2006 showed declined grain filling duration (Nawab *et al.*, 2013).

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Table 1: List of heat tolerant varieties of wheat released in India (Gupta *et al.*, 2018 ^[12] and Indian Institute of Wheat and Barley Research).

S. No	Name of variety	Developed by	Notification number and date	Yield(t/ha)	
				Av.	Pot.
1.	A-9-30-1	AAU ARS, Arnej	566(E) 21.09.1974	1.54	2.02
2.	HD4502 (MALVIKA)	IARI, N. Delhi	786(E) 02.02.1976	2.63	2.71
3.	GW2	JAU, Junagadh	295(E) 09.04.1985	1.60	2.40
4.	GW 173	RARS, Vijapur	636(E) 02.09.1994	4.10	4.9
5.	AKW 1071 (PURNA)	PDKV, Akola	408(E) 04.05.1995	3.70	4.74
6.	PBN 51 (PARBHANI 51)	MKV, Parbhani	1(E) 01.01.1996	3.93	4.04
7.	K 9644 (ATAL)	CSAUA&T, Kanpur	340(E) 03.04.2000	1.5	1.74
8.	K 7903 (HALNA)	CSAUA&T, Kanpur	92(E) 02.02.2001	2.5	3.5
9.	WH 711	CCS HAU, Hisar	937(E) 04.09.2002	4.80	5.95
10.	GW 322	RARS, Vijapur	937(E) 04.09.2002	4.47	6.63
11.	RAJ 3777	RARI, Durgapura	283(E) 12.03.2003	4.2	4.8
12.	MP 4010	RVSKVV, Gwalior	283(E) 12.03.2003	4.01	5.36
13.	K 9423 (UNNAT HALNA)	CSAUA&T, Kanpur	1566(E) 5.11.2005	3.66	4.07
14.	UP 2565	GBPUA & T, Pantnagar	599(E) 25.04.2006	4.18	4.44
15.	MP 1142	JNKVV RS, Powarkheda	1178(E) 20.07.2007	4.70	5.00
16.	DDK 1029 (dicoccum)	UAS, Dharwad	1703(E) 05.10.2007	4.09	5.99
17.	MP 1202	JNKVV, Jabalpur	211(E) 29.01.2010	4.2	5.39
18.	RAJ 4079	RARI, Durgapura	283(E) 07.02.2011	4.37	5.6
19.	K0402	CSAU & T, Kanpur	2817(E) 19.09.2013	4.31	6.74
20.	DBW 107	IIWBR	268(E) 28-01-2015	4.13	6.87
21.	DBW 173	IIWBR	1979(E) 27-05-2018	4.72	5.7

Some of the heat stress tolerant varieties of wheat released till 2018 were listed in the Table1 and further wheat genetic stocks such as RWP-2017-21, DBW166 and RW5were

registered in the year 2020 by ICAR-IIWBR, Karnal.

Heat Tolerance Mechanism

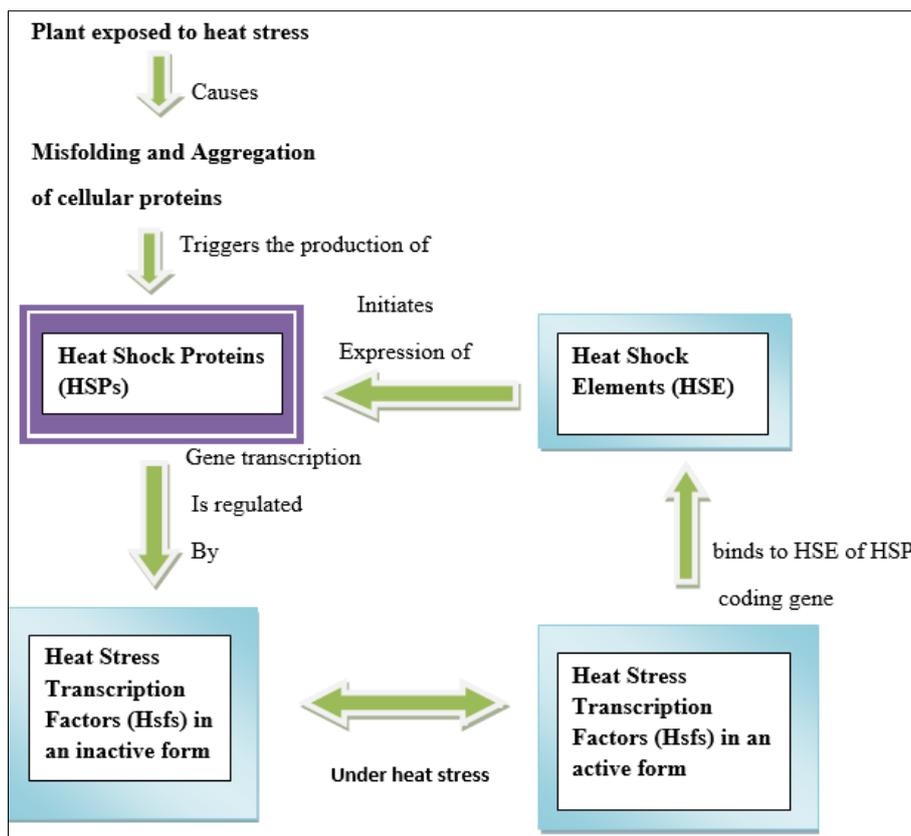


Fig 1: Schematic representation of mechanism of HSPs

Major heat tolerance mechanisms in wheat include Heat Shock Proteins (HSPs), antioxidant defense and stay green.

Heat Shock Proteins

Under heat stress condition, protein synthesis and folding are affected. These results in the production of stressing agents in

cell which disrupts DNA replication, under heat stress transcription, mRNA transport and translation till the cell recover (Bahadur Poudel and Ram Poudel, 2020). To overcome this damage, Plant develops a defense mechanism by increasing production of group of proteins known as Heat shock proteins (HSPs). Heat Stress Transcription Factors

(Hsfs) are regulatory proteins that control transcription of Heat Shock Proteins (HSPs) but these Hsfs are present in an inactive form in the cytoplasm. Under heat stress condition, these Hsfs act as transcriptional activators for HSPs. Hsfs binds to cis-regulatory motifs, heat shock element (HSE) which leads to the expression of HSPs. Heat Shock Proteins prevents misfolding and aggregation of essential cellular proteins and further involves in the refolding of proteins (Goswami *et al.*, 2021).

Antioxidant defense mechanism

Reactive Oxygen Species (ROS) includes unnecessary byproducts generated from oxygen which includes¹ O₂ (Singlet oxygen), H₂O₂ (hydrogenperoxide), O₂⁻ (Superoxide radical) and OH[•] (hydroxyl radical). In general, a balance exists between continuous generation and scavenging of ROS in cell but this balanced is disrupted under heat stress conditions (Das *et al.*, and Choudhury *et al.*, 2014). This overproduction of ROS leads to oxidative damage of biomolecules which includes product of protein oxidation, enzymes inactivation, lipid peroxidation, change membrane fluidity, degradation of chlorophyll, damage to nucleic acid and activates apoptosis (Sachdev *et al.*, 2021). The pre-anthesis high temperature regulates the expression of the antioxidant enzyme-related genes such as catalase (CAT), chloroplastic Cu/Zn superoxide dismutase (Cu/Zn-SOD) and mitochondrial manganese superoxide dismutase (Mn-SOD) and improves antioxidant enzyme activities at the transcription level. This pre-anthesis high-temperature adaptation could reduce the photosynthetic and oxidative damage caused to the flag leaf during post-anthesis thermal stress and enhances the heat tolerance in wheat at grain setting and filling stages (Wang *et al.*, 2011) [40].

Impact of heat stress on wheat morphological factors

Heat stress hinders seed germination and results in poor stand establishment (Johkan *et al.*, 2011; Hossain *et al.*, 2013) [15, 14]. The exposure of wheat to high temperature around 45 °C damages seed germination and emergence (Essemine *et al.*, 2010) [9]. The experimental studies on ten aseptically grown wheat genotypes revealed that heat stress reduced dry mass and length of root and shoot. The short term heat treatment at 45 °C for 2 h declined cell membrane stability index and chlorophyll content in all the genotypes (Gupta *et al.*, 2013) [13]. Thermal stress accelerated the grain filling rate, reduced the post-heading duration, grain number, m⁻² and harvest index (Talukder *et al.*, 2014) [33]. Heat stress immediate to the pre-anthesis or during post-anthesis stages decreased grain weight (Savin *et al.*, 1999) [32]. High temperature increased the production of sterile wheat spikelets but decreased the number of kernels per spike (Modarresi *et al.*, 2010) [25]. Drought along with heat stress declined the number of grain per ear, number of grains per spikelet, grain weight and mean grain weight per spikelet (Amin, 2011) [11].

Impact of heat stress on wheat physiological factors

Chloroplast and Photosynthesis

Heat stress for three days changed chloroplast shape to round, damaged envelope, swollen thylakoid membrane and loosen grana arrangement. Heat stress reduced the chlorophyll a+b content which resulted in loss of chlorophyll pigment in flag leaves that caused leaf senescence. It declined the activity of ribulose-1, 5-bisphosphate enzyme. Heat stress caused closure of PSII reaction centre that ceased the electron transport

between electron donor and acceptor of PSII that lead to the downregulation of PSII (Feng *et al.*, 2014) [10].

Water Potential

The interaction of heat stress with drought decreased Relative Water Content (RWC) and increased Osmotic Potential (OP) (Sattar *et al.*, 2020) [31]. The combination of heat stress with drought declined daily water uptake of wheat plants. They altered transpiration response to Vapour Pressure Deficit (Habti *et al.*, 2020) [8].

Impact of heat stress on biochemical factors

Antioxidant enzymes

The enzymatic activity of glutathione-S transferase (GSH-S-Tr.) increases significantly in the genotype, Plainsman V and Mv Magma. This neutralizes the damaging effect of ROS and free radicals produced under heat stress. The guaiacol peroxidase (GPx) enzyme is not affected by high temperature whereas enzymes such as catalase and ascorbate peroxidase (APx) shows significant increase in the genotype, Plainsman V but the activity of the enzyme catalase gradually decreased in the genotype Mv Magm but APx enzymatic activity is unaltered (Balla *et al.*, 2009) [4].

Starch Accumulation

Heat stress reduced starch accumulation up to 35% in endospermic tissues during grain filling stage (Asthir *et al.*, 2014; Kumar *et al.*, 2015) [3, 18]. Starch synthase enzymes are thermo labile which severely affects starch synthase activity (Yang *et al.*, 2018) [41].

Amylose and Amylopectin

Amylose content was unaltered during heat stress but amylopectin content was significantly reduced. High temperature enhanced α-amylase activity which makes starch granules susceptible to heat stress (Kumari *et al.*, 2020) [20].

Breeding strategies to overcome heat stress in wheat

Screening wheat germplasm for heat tolerance

Three wheat entries CB-367, CB-333 and CB-335 showed maximum grain yield even under heat stress at terminal growth stage. These varieties can be utilized as parents in hybridization programs to develop heat tolerant wheat varieties (Rehman *et al.*, 2009) [35]. The screening of wheat germplasm can be done using temperature indices such as Heat Tolerance Index (HTI). Heat Tolerance Index is used as a measure to estimate plant potential to tolerate heat stress. It is a mathematical equation which considers temperature and duration to measure heat stress and to differentiate between heat tolerant and heat escaped genotypes. This index is used to identify varieties tolerant to heat stress (Rane and Nagarajan, 2004) [29]. The conventional breeding method such as recurrent selection can be used to enhance heat tolerance in wheat (Machado *et al.*, 2009) [22].

QTL mapping

QTL mapping of each yield trait as a heat susceptibility index and their aggregate contribution to heat tolerance and grain yield stability. Thylakoid membrane stability is strongly linked to heat tolerance capacity in wheat. The stay green trait can be used as selection criteria to perform mass screening of wheat varieties tolerant to heat (Mason *et al.*, 2010) [23]. The trait stay green is correlated with the grain development and heat tolerance in wheat. The researchers found 3 QTLs on the

chromosome 1AS, 3BS and 7DS for stay green trait using recombinant inbred lines (RILs) (Kumar *et al.*, 2010) ^[19]. The polygenic character of wheat tolerance makes it complex to perform a conventional phenotypic selection. Therefore, Marker Assisted Selection (MAS) was regarded as an efficient approach to screen heat tolerance varieties by linking SSR markers with grain filling duration and Heat Susceptibility Index (Heat Susceptibility Index) kernel weight (Sadat *et al.*, 2013) ^[30]. Heat stress QTLs were discovered on wheat chromosomes 1B, 2B, 3B, 4A, 4B and 7A (Pinto *et al.*, 2010) ^[28].

Biotechnological approach

An over accumulation of glycinebetaine (GB) is an efficient biotechnological approach to mitigate the decrease of photosynthesis caused by heat stress by improving the activity of antioxidative enzymes (Wang *et al.*, 2010) ^[39]. Genetic engineering is a process of introgression of gene of interest into desirable to enhance heat tolerance (Zheng *et al.*, 2012) ^[42]. The SSR markers integrated with bulk segregant analysis could be used to discover markers linked to the grain filling rate as an indicator for heat stress tolerant genes (Barakat *et al.*, 2011) ^[26]. A biotechnological approach of increasing OPR3 expression leads to the Jasmonic Acid biosynthesis and accumulation to increase heat tolerance (Tian *et al.*, 2020) ^[34]. The rapid phenotyping in combination with speed breeding was used to improve stay-green trait in wheat grown under high temperature and drought conditions (Christopher *et al.*, 2015) ^[6]. The speed breeding is a rapid generation advancement technology that can be combined with biotechnology to develop more heat tolerant wheat genotypes in less time.

Transcriptome profiling

In the investigation of gene expression in wheat, expressed sequence tag databases show that homologous genes can disclose expression in one but stay silent in one or both of the genomes. Deepgenome sequencing technology (RNA-Seq), which has been shown to be successful tool for identifying definitive alterations in the genome (Mochida *et al.*, 2004) ^[24]. is enabling high-throughput gene expression analysis. Although next-generation sequencing technology is still in its early stages in plant research, it has the potential to replace microarray technology due to its precision. The lack of a full sequenced genome in hexaploid wheat makes OMICS investigations problematic.

Proteomics

Proteins play a significant role in plant stress response, therefore studying proteome changes under heat stress conditions is essential. The cellular mechanisms of stress sensing and signaling are the antecedents to the plant response under heat stress conditions.

Metabolomics

Metabolites, as basic components of various structural and enzymatic compounds, provide the energy required for protoplasm metabolism and growth. Metabolites not only act as a link between phenotypic and genotypic information, but they also aid in determining a physiological state of organism (Bino *et al.*, 2004) ^[5]. The availability of whole genome sequence, genome wide variations and cost-effective genotyping assays are useful to combine metabolomics with crop breeding programmes. Certain technologies such as mass

spectrometry (MS) and nuclear magnetic resonance (NMR) spectrometry are found to be successful (Fernie and Schauer, 2009) ^[11].

Conclusion

The complexity of wheat genome has created a barrier to biotechnological application, however combining traditional breeding with biotechnology will result in the efficient production of heat-tolerant wheat varieties. To cope with anticipated climate changes, a detailed understanding of the underlying mechanisms of heat tolerance in wheat is essential. Inter-specific genome diversity could be a source of novel genes involved in adaptation to climate change. The process driving heat tolerance can be discovered using various omic methodologies, while germplasm banks must be explored for the candidate genetic stocks. Enzymes involved in oxidative stress scavenging, carbon fixation, their activation factors, transcription factors and heat shock proteins could be potential targets for diagnostic markers in marker-assisted breeding. Despite the complexity of wheat heat tolerance mechanisms, the improvement of wheat genotypes is possible through genome wide selection and marker-assisted recurrent selection.

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