
Review Article

Molecular basis of heat stress tolerance in wheat

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Abstract

The rise in Earth's temperature is one of the most alarming climatic issues in the field of agriculture and food production, in the present context. The increase in temperature leads to heat stress, major abiotic stress responsible for a huge decline in the production of crops. Wheat (*Triticum aestivum*), among many crops, also experiences a significant decline in yield and overall productivity due to extreme heat stress. But Wheat has also developed natural tolerance mechanisms to defend itself from heat damage. The selection of cultivars with a higher degree of tolerance mechanism protects against thermal stress, which minimizes the risk of poor productivity to a greater extent. In this review, we discuss the current works of literature concerning the heat stress tolerance mechanism in wheat plants and also highlight the strategic approaches that improve their heat stress tolerance at the molecular level. The success of these approaches depends on a better understanding of heat tolerance traits, their genomic composition, and molecular responses.

Introduction

Global warming is one of the most serious environmental threats in the present scenario, which is growing unprecedentedly day by day due to the ever-increasing temperature (Moore et al., 2021). The 2018 summary by IPCC has indicated that a rise in temperature of 1.5 degrees Celsius may occur between 2030 and 2052 if this trend is continued (Intergovernmental Panel on Climate Change, 2018). This rise, especially during heat-sensitive crop stages is likely to result in a significant decline in crop productivity (Farooq et al., 2017). This

decline is caused mainly due to the inhibition in crop growth, physiology, and yield and yield attributing characters resulting from heat stress (Hemantaranjan et al., 2018). Terminal heat stress is defined as an increase in temperature between the heading and maturity phases of a plant (Sarkar et al., 2021). The loss is more pronounced in reproductive and grain-filling stages as temperature plays a very crucial role at these times (Farooq et al., 2017). Respiration rate gets higher during heat-stressed environments, whereas the rate of photosynthesis reduces (Li et al., 2021).

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Likewise, the root system is severely disturbed, which leads to poor water and nutrient absorption failing to sustain basic physiological plant processes (Janni et al., 2020). The combination of higher temperature and moisture stress results in crop production losses and lowers grain quality (Qin et al., 2008). This shows heat stress has emerged as an alarming issue against global agricultural production.

Wheat (*Triticum aestivum*) is an important staple crop in the world. It is ranked 2nd worldwide in terms of grain production with a total production of 776.7 million tons at the year 2020/21 (Food Agricultural Organization, 2022). It belongs to one of the most consumed food grains in the world as 35% of the global population consume the crop daily in various forms (Grote et al., 2021). The ever-increasing population has signified the growing demand of wheat crop (Erenstein et al., 2022). But recent data has suggested that global wheat production has reached an all-time plateau (Savadi et al., 2018). A contributing factor behind this is the heat stress experienced by wheat plants that result in lower productivity (Riaz et al., 2021; Wang et al., 2018). With a rise in temperature of 1 degree Celsius, wheat production reduces by 6% in the world. Like many crops, wheat also exhibits poor performance at the molecular level as they are not very tolerant to heat stress (Lu et al., 2022). Climate change due to elevated CO₂ concentration in the atmosphere would stimulate biomass production in crops particularly C3 crops like wheat. But simultaneously increasing heat stress due to elevated temperature and resulting moisture stress will reduce yield of crops (Dubey et al., 2020). To enhance crop productivity under harsh environment, drought or heat stress tolerant cultivars can be selected or breeding practices can be done to improve the tolerance level (El Sabagh et al., 2019). Hence, researchers are prioritizing on development of tolerant genotypes, as well as tolerating techniques that would allow maximum yield even during extreme abiotic stress, such as heat stress (Munaweera et al., 2022). This review article discusses the molecular response of wheat in tolerating heat stress. Heat shock proteins and

Reactive Oxygen Species provide natural tolerance mechanism against heat stress (Devireddy et al., 2021). Molecular breeding approaches that focus on improving the tolerance mechanism can help wheat plants to survive in extreme heat-stressed environment without experiencing decline in yield and productivity (Li et al., 2022). This paper also discusses such strategic methods that improve the tolerance level of wheat plants at molecular level.

Influence of heat stress in wheat

The increase in temperature during grain filling stage is due to shorter time span between anthesis and physiological maturity that leads to reduction in grain yield (Uddin et al., 2010). Heat stress has a wide range of consequences on plants as shown in Figure 1, such as reduced growth and development, disruptions in physiological and biochemical activities, and lower grain yield and productivity (Munaweera et al., 2022).

Heat stress alters the responsiveness of the pigmentation in wheat and maize, and it also has an impact on Photosystem II, which has a detrimental influence on sprouting and leaf growth (Qadir et al., 2018). Along with burning of the twigs and leaves, high temperatures can also cause sunburn-like symptoms, leaves to age prematurely, growth to be inhibited, and discoloration of the fruits and leaves. The germination potential of the seeds decreases due to high temperatures, which leads to poor germination and stand establishment (Fahad et al., 2017). A significant impact of heat stress is observed during reproductive stage. The effects of heat stress on seed filling, yield and seed composition could be the result of the combination's effects on overall biomass through inhibition of photosynthesis on plant reproductive mechanisms like fertilization and/or abortion (Cohen et al., 2021). In the case of wheat, hormonal phenomenon, metabolic functions, and plant water relations are severely affected (Barnabás et al., 2008). Wheat starch accumulation is significantly reduces by heat stress during grain filling stage (Sehgal et al., 2018). Reduction in photosynthetic capacity and pol-

len tube growth is also observed, while production of oxidative reactive species, is promoted due to heat stress (Akter & Islam, 2017). These

responses to heat stress require a thorough understanding in order to develop solutions against heat stress.

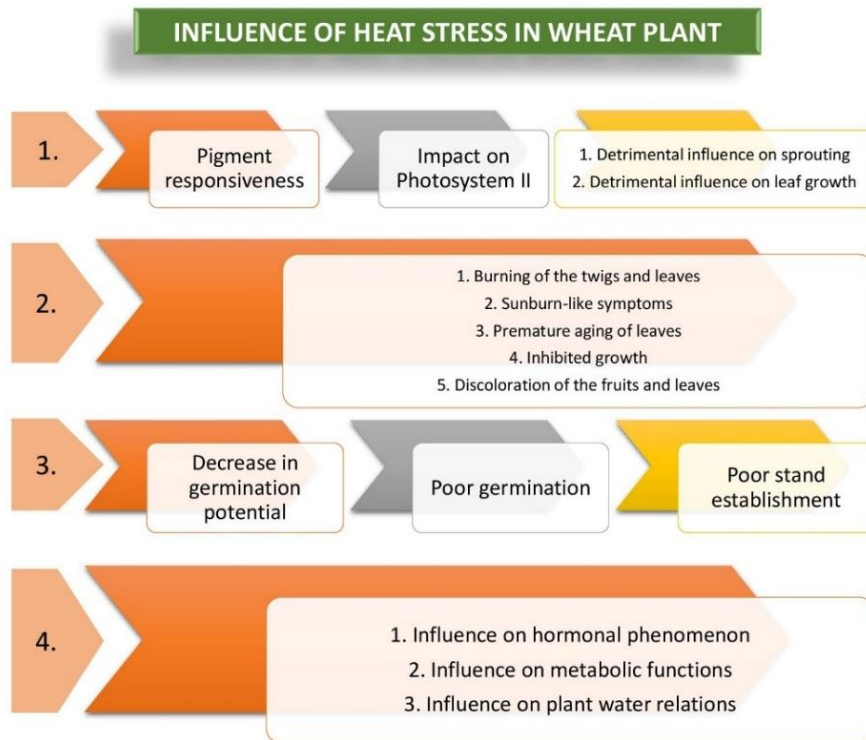


Figure 1 Schematic diagram showing influence of heat stress in wheat plant

Tolerance mechanism against heat stress in wheat: heat shock proteins

Naturally, plants have their own tolerating or avoiding response mechanisms at the molecular level against extreme heat conditions as listed in Table 1. Heat stress tolerance is an adaptation mechanism that involves a brief acclimatization phase at warmer temperature or by exposure to other harmless stressor before following heat stress (Talukder et al., 2014). With the help of the iTRAQ method, Kumar et al. (2019) have detected around 4272 Stress Associated Active Proteins (SAAPs) that get activated under heat stress. These SAAPs include heat shock protein (HSP), Heat shock cognate protein, Rubisco, Photosystem I P700, ATP synthase subunit beta, chloroplastic, and monomeric alpha-amylase inhibitor, etc. HSP has

been quite intensively studied by researchers as they act as molecular chaperones to discourage the misfolded protein from aggregating permanently which promotes thermal tolerance (Comastri et al., 2018). These HSPs also act as adhesive for binding glutenins, gliadins, and starch required for gluten production in wheat (Janni et al., 2020). Also, wheat contains about 56 HSF, among which A2 and A6 HSF showed activation during the stressed condition (Sun et al., 2022). The discovery of these proteins with their location provides accurate data to conduct breeding programs that allow modifying the protein structures or altering its function (Kumar et al., 2019). Manipulation of the genes of HSP helps in improving the tolerance level of wheat crop against heat stress.

Table 1. A list of various activities occurring in wheat in order to tolerate the heat stress and minimize the adverse effects due to heat stress

S. N.	Tolerance mechanisms of wheat	References
1.	Activation of 4272 Stress Associated Active Proteins (SAAPs) such as a) Heat shock protein (HSP) b) Heat shock cognate protein c) Rubisco d) Photosystem I P700 e) ATP synthase subunit beta f) Chloroplastic, and monomeric alpha-amylase inhibitor,	Kumar et al. (2019)
2.	Activation of A2 and A6 HSF	Sun et al. (2022)

Response of reactive oxygen species

During extreme heat stress, a large number of Reactive Oxygen Species (ROS) are also produced due to resultant oxidative stress ([Qu et al., 2013](#)). This production encourages protein oxidation, nucleic acid degradation, obstruction during enzyme performance, alters cell membrane permeability, and hence leading to necroptosis ([Poudel & Poudel, 2020](#)). ROS also contributes to activating the HSF proteins under heat stress, by acting as chemical messengers for cellular impulses related to the stress tolerance system ([Janni et al., 2020](#)). This shows the accumulation of reactive oxygen species under heat stress. Heat stress tolerance is also linked with a rise in activity by antioxidant enzyme ([Almeselmani et al., 2009](#)). Plants with higher heat stress tolerance possess higher chance of combating heat stress.

Strategies to improve heat stress tolerance in molecular level

Screening genetic resources for the discovery of heat-tolerant crops is part of the process to generate new crops that can withstand future climates with high-temperature occurrences ([Bita & Gerats, 2013](#)). [Akter & Islam \(2017\)](#) has supported the use of heat sensitivity index, susceptibility index, QTL mapping index, thylakoid membrane stability index, and mass screening using the stay-green character to study yield attributing characters that would aid in discovering heat stress-tolerant varieties. Stay-green genotypes are able to retain photosynthesis due to slow expression of alleles related to senescence ([Cossani & Reynolds, 2012](#)). Such strategies that improve heat stress tolerance in molecular level are summarized in [Table 2](#) and explained below as well.

Table 2. A summarized table showing various approaches at molecular level to locate and manipulate the genes related to heat stress tolerance

S. N.	Strategies to improve heat stress tolerance in molecular level	Activity	References
1.	QTL mapping	Detection of wheat genes related to yield under heat stress condition such as 1A, 1BL, 1D, 2BS, 3A, 3BS, 3BL, 3D, 4A, 4B, 4DL, 5A, 5B, 6A, 6B, 6D, 7AS, 7AL, 7BS, and 7BL	Tricker et al. (2018)

Continued Table 2

S. N.	Strategies to improve heat stress tolerance in molecular level	Activity	References
2.	Transgenic approach	a) Use of transgene PEPC in wheat cultivar PC27 and PC51	Qi et al. (2017)
		b) Use of transgene EF-Tu	Fu et al. (2008) , Akter & Islam (2017)
		c) Use of transgene ZmEFTu1	Kaur et al. (2019)
3	Omics approach		
	a) Transcriptomics	Use of iTRAQ method to locate heat stress related protein	Zhang et al. (2017)
	b) Proteomics	Identifying and studying anti-oxidant enzymes, MAPKs and CDPKs, and Heat Shock Proteins	Yadav et al. (2022) , Shah et al. (2018) , Nadeem et al. (2018)
	c) Metabolomics	Study of metabolites such as L-tryptophan, Pipecolate, Drummondol, and Anthranilate	Yadav et al. (2022)

a. Marker assisted selection: QTL mapping

Quantitative trait Locus (QTL) mapping is an effective tool for discovering the wheat genes related to heat stress ([Bhusal et al., 2017](#)). A study conducted by [Hassouni et al. \(2019\)](#) showed that 12 such QTL were in control of major heat-tolerant characters. Three of them were stimulated in a stressed environment, making them suitable breeding sites. As mentioned by [Tricker et al. \(2018\)](#), QTL related to grain yield has been identified in chromosomes of 1A, 1BL, 1D, 2BS, 3A, 3BS, 3BL, 3D, 4A, 4B, 4DL, 5A, 5B, 6A, 6B, 6D, 7AS, 7AL, 7BS, and 7BL under heat stress condition. QTLs for other yield influencing characters during heat stress such as grain weight per spike, grain number per spike, spike weight, plant height, spike length, test weight, and many others have been discovered through various studies ([Touzy et al., 2022](#)). Detection of these QTLs allows to conduct the marker-assisted selection of chromosomes of yield and yield attributes that are affected under extreme heat-stressed environment.

b. Transgenic approach

Transgenesis is another suitable option used to enhance heat stress tolerance in wheat plants by replacing their genes with superior ones ([Ni et al., 2018](#)). The study by [Qi et al. \(2017\)](#) indicated that even in a heat-stressed environment, the transgenic wheat cultivar PC27 and PC51, which contained the PEPC gene from maize showed higher heat tolerance. [Tian et al. \(2018\)](#) reported that transgenic approach also led to increase in thousand kernel weight by 21-34% in wheat plants. The transgenesis in wheat due to EF-Tu gene helped from the thermal aggregation of leaf proteins ([Fu et al., 2008](#)). It also minimized rupturing of thylakoid membrane caused due to heat stress. Another such transgene is ZmEFTu1, found in heat stress tolerant plants, that resulted higher CO₂ fixation rate ([Kaur et al., 2019](#)). Hence, transgenesis is another viable option for gene manipulation in improving heat stress tolerance.

c. Omics approach: transcriptomics, metabolomics and proteomics

Few transcription and translation-based methods are also gaining popularity for identifying and locating the genes involved in heat stress response (Wu et al., 2021). By using microarray analysis, it has been found that 10.7% of probe sets showed a response to heat stress at 40 degrees Celsius, whereas RNA-seq analysis has discovered 1525 genes in response to heat stress environment (Sun et al., 2022). An analytical study by Zhang et al. (2017) revealed the presence of 256 proteins through the iTRAQ method that showed stress tolerance response among others. Another omics approach for improving heat tolerance includes Proteomics approach (Shah et al., 2018). Study of signaling protein molecules like antioxidant enzymes, MAPKs and CDPKs, and Heat Shock Proteins can help to explore novel ways in tolerating thermal stress (Yadav et al., 2022). Proteomics screening also aids in identifying key proteins contributing the activity of heat shock, glycolysis, photosynthesis, and stress resistance (Nadeem et al., 2018). Along with proteomics, metabolomics analysis also provides crucial insights in studying the effect of metabolites in heat stress tolerance in wheat. Abdelrahman et al. (2020) have mentioned the importance of studying lipid metabolism in breeding bread wheat that can withstand heat stress. Under heat stress, metabolites such as L-tryptophan and Pipecolate were found to be increased, whereas the level of Drummondol and Anthranilate reduced to a significant extent (Yadav et al., 2022). These omics approaches help to locate the genes related to heat stress tolerance with higher precision that allows accurate manipulation of the genes.

Conclusion

A primary issue in the wheat farming system is heat stress. Heat stress is responsible for changes in numerous molecular level processes such as respiration, photosynthesis, nutrient-water relationship, membrane stability, grain filling, and development in the wheat plant. Comprehensive scientific studies of the responses of these processes under heat stress should be conducted at the molecular level to

assess their effect on the yield of wheat. These responses also aid in discovering the best breeding varieties in terms of heat-stress tolerance. The tolerance mechanisms of the wheat plants can be identified and improved with the help of methods such as QTL mapping, and transgenic and omics approaches. This article is aimed at summarizing the molecular modifications achieved via these strategies that can help improve heat stress tolerance. While these efforts are expected to lead to more advancements in the world of wheat breeding, there is still room for more research to help the end-users, mainly farmers to benefit from these methods in combating the issue of heat stress.

Author's declaration and contribution

The authors show no conflict of interest. All the authors have provided equal contribution.

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