



Breeding for Heat Stress Tolerance in Wheat: A Review

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This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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ABSTRACT

Heat stress poses a significant threat to global wheat production, necessitating comprehensive strategies to enhance heat stress tolerance in wheat varieties. This study provides a summary of key findings, the importance of continued research and breeding efforts, and implications for wheat production and food security. Field trials and physiological studies have revealed substantial genotypic variation in heat stress tolerance among wheat germplasm, underscoring the need for ongoing research to identify and leverage key traits associated with heat tolerance. Continued investment in breeding programs focused on heat stress tolerance is crucial for developing resilient wheat varieties capable of sustaining productivity under changing climatic conditions. These efforts not only enhance the resilience of wheat production systems but also contribute to global food security by mitigating the impact of climate change on crop productivity and livelihoods. By prioritizing heat stress tolerance in wheat breeding programs and embracing advancements in molecular genetics and phenotyping technologies, we can pave the way for a more secure and sustainable future for wheat production worldwide.

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1. INTRODUCTION

Heat stress poses a significant threat to wheat production worldwide, impacting both yield and quality. As a primary staple crop, wheat plays a crucial role in global food security, making its susceptibility to heat stress a pressing concern. Heat stress in wheat production occurs when temperatures exceed the optimal range for growth and development, typically above 30°C during critical stages such as flowering and grain filling [1].

Elevated temperatures have the potential to cause many physiological and biochemical alterations in wheat plants, hence impeding essential functions including photosynthesis, respiration, and water absorption. Reduced grain production, lower grain quality, decreased pollen viability, and increased susceptibility to pests and diseases are common symptoms of damage caused by heat stress. Complementary variables that worsen these impacts include soil nutrient deficits and drought stress, which further reduce wheat yield in conditions with high temperatures [2].

Climate change is predicted to increase the frequency and intensity of heat stress episodes, which would significantly hinder wheat output in many areas. According to studies, heat stress events are becoming more often and severe in significant wheat-growing regions, endangering harvests and making the situation of food poverty worse. Therefore, it is imperative that researchers and breeders comprehend the processes behind wheat's resistance to heat stress and create resilient cultivars [3].

The identification of genetic variables and features linked to wheat's ability to withstand heat stress has advanced significantly. Breeders use both traditional breeding techniques and cutting-edge biotechnological procedures like genomic selection (GS) and marker-assisted selection (MAS) to create wheat types that are more resilient to heat stress. Heat shock proteins, antioxidants, and osmoprotectants have become important targets for breeding programmes aiming to increase wheat's ability to withstand heat stress [4].

Even with these developments, there are still obstacles to overcome before heat stress tolerance characteristics can be successfully incorporated into superior wheat germplasm and

farmers can adopt robust varieties on a large scale. To secure wheat production in the face of increasing climatic constraints, partnerships between government agencies, academia, and industry stakeholders are crucial for overcoming these obstacles and promoting ongoing research initiatives.

Heat stress poses a significant threat to global wheat production and food security, impacting yields and quality, especially when temperatures exceed 30°C during critical growth stages [1][2]. As climate change increases the frequency and intensity of heat stress events, continued research and breeding efforts are crucial to understand genetic factors linked to wheat's heat tolerance and develop resilient cultivars using traditional methods and biotechnologies like genomic selection (GS) and marker-assisted selection (MAS), targeting traits like heat shock proteins, antioxidants, and osmoprotectants [3,4].

Importance of breeding for heat stress tolerance: Breeding for heat stress tolerance in wheat is critical because it has the ability to reduce the detrimental effects of rising temperatures on wheat yield. As climate change worsens, heat stress events become more frequent and severe, presenting serious threats to global food security. As a result, producing wheat cultivars with greater heat stress tolerance is critical for providing consistent harvests and protecting livelihoods [5].

One of the primary objectives for creating heat stress-tolerant wheat varieties is to ensure production in the face of changing climatic circumstances. Heat stress can drastically lower wheat output by inhibiting photosynthesis, altering reproductive processes, and hastening senescence. By breeding for heat stress resistance, researchers hope to generate wheat cultivars that can sustain production potential even under increased temperature regimes [6].

Furthermore, breeding for heat stress resistance can aid in climate change adaptation in agriculture. Heat-tolerant wheat cultivars allow farmers to reduce the detrimental effects of rising temperatures on crop yields and economic viability. Farmers that cultivate heat stress-tolerant cultivars might lessen their exposure to climate-related hazards and provide more predictable revenues [7].

In addition to increasing production and climate resilience, breeding wheat for heat stress tolerance can result in more resource-efficient farming techniques. Heat-tolerant cultivars may require fewer inputs like water and agrochemicals, resulting in economic savings and lower environmental effect. Heat stress-tolerant wheat cultivars boost long-term food security and sustainable farming practices by maximising resource usage efficiency [8].

Causes and manifestations of heat stress:

Heat stress in wheat production results from a variety of external conditions and physiological reactions inside the plant. High temperatures that exceed the ideal range for growth and development, often above 30°C during important phases like blooming and grain filling, are the major causes of heat stress. Drought, excessive humidity, and low soil moisture levels can all contribute to heat stress [9].

Heat stress manifests itself in a variety of ways in wheat plants, affecting many physiological and biochemical processes. One of the principal

impacts is the interruption of photosynthesis, which results in lower carbon uptake and biomass production. High temperatures can also reduce stomatal conductance and transpiration rates, causing water stress and reduced plant hydration [10]. Heat stress causes oxidative stress in cells by producing reactive oxygen species (ROS) such superoxide radicals and hydrogen peroxide [11]. Excessive ROS production degrades cellular components such as membranes, proteins, and nucleic acids, resulting in cellular malfunction and programmed cell death [12]. Heat stress can also disturb hormonal balance inside the plant, influencing activities like as blooming, pollen viability, and grain growth.

Furthermore, heat stress can increase plant senescence and reproductive failure, resulting in lower grain production and quality. Heat stress at crucial development phases can cause considerable output losses due to reduced pollen viability, poorer fertilisation, and poor grain set [12].

Table 1. Impact of heat stress on wheat growth and yield

Impact of Heat Stress on Wheat Growth and Yield	Description	References
Reduced Photosynthesis	High temperatures disrupt photosynthesis, reducing carbon assimilation and biomass production.	(Wahid et al., 2007)[13]
Impaired Water Uptake	Heat stress decreases stomatal conductance and transpiration rates, leading to water stress and decreased plant hydration.	(Prasad et al., 2008)[14]
Oxidative Stress	Heat stress induces the production of reactive oxygen species, damaging cellular structures and causing cellular dysfunction.	(Apel and Hirt, 2004)[15]
Accelerated Senescence	Heat stress accelerates plant senescence, reducing grain filling duration and yield.	(Farooq et al., 2011)[16]
Increased Susceptibility to Pests and Diseases	Heat-stressed wheat plants may become more vulnerable to pests and diseases, further compromising yield and quality.	(Bita and Gerats, 2013)[17]
Delayed Maturity	Heat stress can delay wheat maturity, prolonging the time to harvest and potentially affecting crop management practices.	(Jagadish et al., 2011)[18]
Limited Root Growth	High temperatures inhibit root growth, reducing the plant's ability to access water and nutrients from the soil.	(Molero et al., 2020)[19]
Reduced Fertility	Heat stress can reduce pollen viability and fertilization success, leading to poor grain set and reduced yield.	(Stone and Nicolas, 1994)[20]
Impaired Protein Synthesis	High temperatures can disrupt protein synthesis in wheat, affecting growth, development, and yield.	(Hurkman and Tanaka, 2007)[21]
Altered Gene Expression	High temperatures can alter gene expression patterns in wheat, affecting various physiological processes and stress responses.	(Sharma et al., 2020)[22]

Genetic basis of heat stress tolerance in wheat: Heat stress tolerance in wheat is genetically determined by a complex interplay of genes and regulatory systems that regulate the plant's reaction to high temperatures. Several significant genetic variables have been identified as influencing the wheat plant's capacity to tolerate heat stress. Here's an explanation:

1. **Heat Shock Proteins (HSPs):** Heat shock proteins are a type of molecular chaperone that protects cells from heat damage by stabilising proteins and preventing denaturation. In wheat, multiple HSP genes are activated in response to heat stress, helping the plant maintain protein homeostasis and cellular function at high temperatures [23].
2. **Transcription Factors:** Transcription factors control the expression of heat stress-responsive genes, coordinating the plant's adaptation to high temperatures. Wheat has genes that encode heat stress transcription factors (Hsfs) and heat shock factors (Hsps), which regulate the expression of downstream heat stress-responsive genes that are involved in thermotolerance [24].
3. **Antioxidant Enzymes:** Heat stress causes the generation of reactive oxygen species (ROS) in plant cells, resulting in oxidative damage. Wheat plants include genes that encode antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), which scavenge ROS and reduce oxidative stress under heat stress conditions [25].
4. **Osmoprotectants and Compatible Solutes:** Under heat stress, plant cells collect osmoprotectants and compatible solutes, which operate as osmoprotectants while also stabilising cellular structures. Wheat has genes that produce osmoprotectants such as proline, glycine betaine, and trehalose, which contribute to heat stress tolerance [26].
5. **Membrane Stability:** Heat stress damages cellular membranes, causing electrolyte loss and cell damage. Membrane stability genes, such as those involved in lipid metabolism and membrane fluidity, play an important role in preserving membrane integrity under high temperatures [27].

2. BREEDING STRATEGIES FOR HEAT STRESS TOLERANCE

Traditional breeding approaches:

Phenotypic Selection: Phenotypic selection is a fundamental approach in plant breeding that involves visually assessing the external characteristics, or phenotypes, of individual plants and selecting those with desirable traits for further breeding. In wheat breeding, phenotypic selection is used to discover plants with better characteristics such as high production potential, disease resistance, drought tolerance, or specific grain quality features [28].

Wheat breeders use phenotypic selection to assess a variety of characteristics, including plant height, tillering capability, spike morphology, grain size and shape, pest and disease resistance, and tolerance to abiotic stressors such as heat, drought, and salinity. Field trials are undertaken to examine the performance of wheat lines or varieties across diverse settings. This allows breeders to discover plants with the required qualities under varying situations [29].

Pedigree Breeding: Pedigree breeding is a systematic approach of plant breeding that combines desired features from many parental lines via controlled crossings and offspring selection. This strategy is based on understanding the genetic history and performance of parental lines, which is also known as the plant's pedigree or parentage [30].

Pedigree breeding in wheat involves several key steps, including the selection of parents based on their performance and genetic diversity, controlled crosses to produce hybrids, evaluation of progeny for desirable traits, and generation advancement through successive rounds of selection and crossing [31].

Molecular breeding techniques:

1. Marker-Assisted Selection (MAS):

Marker-assisted selection (MAS) is a molecular breeding strategy that uses molecular markers related to specific genes or phenotypes of interest to help choose plants with desired features. MAS identifies DNA markers related with target attributes via genetic mapping and molecular analysis. These markers act as indicators or tags, indicating the existence of

favourable alleles (variants) linked with desirable qualities [32].

In wheat breeding, MAS has been utilised to enhance disease resistance, abiotic stress tolerance, grain quality, and yield potential. Breeders can pick plants with desirable features early in development, even before they are phenotypically manifested in the field. This enables more efficient and exact selection of breeding lines or variations, which accelerates [33].

2. Genomic Selection (GS):

Genomic selection (GS) is a molecular breeding technique that predicts individuals' breeding value based on their full genome profile rather than particular marker-trait relationships. GS depends on high-throughput genotyping technology and statistical algorithms to evaluate the genetic merit of plants for many attributes concurrently [34].

GS uses large-scale genomic data, such as single nucleotide polymorphisms (SNPs) or other biological markers, to train prediction models that link genomic information to phenotypic performance. These models may then be used to forecast the performance of new breeding lines or varieties based on genetic profiles, allowing selection decisions to be made at an early stage of development. GS has gained popularity in wheat breeding due to its capacity to capture the complex genetic architecture of quantitative characteristics and its promise to increase genetic gain per unit of effort and money. By combining genetic information from varied germplasm with high-throughput phenotyping methods, GS provides the ability to speed the production of better wheat varieties with higher yield, quality, and stress tolerance [35].

Biotechnological approaches:

1. Genetic Engineering for Heat Stress Tolerance Traits:

Genetic engineering is the purposeful modification of an organism's genetic material to add new features or change existing ones. In wheat breeding for heat stress resistance, genetic engineering techniques can be used to add genes or genetic components that give increased tolerance to high temperatures. One strategy to genetic engineering for heat stress tolerance is to introduce genes that encode heat

shock proteins (HSPs) or other molecular chaperones. These proteins are essential for protecting plant cells from heat-induced damage because they stabilise proteins and maintain cellular homeostasis under stress circumstances. Genetically modified wheat plants can increase heat stress tolerance by overexpressing or increasing the activity of HSP genes [36].

Furthermore, genetic engineering may be utilised to control the expression of genes involved in stress signalling pathways, osmotic regulation, antioxidant defence systems, and other physiological processes related to heat stress tolerance. For example, overexpression of genes encoding enzymes involved in osmoprotectant production, such as proline, glycine betaine, and trehalose, can improve wheat plants' capacity to cope with heat-induced osmotic stress. While genetic engineering has the ability to bring new features and improve wheat stress tolerance, it also creates regulatory and public acceptance issues. Before commercialising genetically altered wheat cultivars, the safety, environmental impact, and any unexpected impacts on non-target species must all be carefully examined [37].

2. Genome Editing Techniques:

Genome editing is the precise change of an organism's DNA at particular genomic loci utilising designed nucleases. This method permits targeted genome alterations such as gene deletion, gene insertion, gene replacement, and exact nucleotide replacements. Genome editing methods have transformed plant breeding by giving precise and efficient tools for changing desired characteristics with unparalleled accuracy. CRISPR-Cas9 is one of the most frequently utilised genome editing tools. CRISPR-Cas9 allows researchers to create guide RNAs (gRNAs) that lead the Cas9 nuclease to particular target areas in the genome, causing double-strand breaks (DSBs). The cell's natural repair systems can mend these DSBs, resulting in gene editing via error-prone non-homologous end joining (NHEJ) [38].

In wheat breeding, genome editing techniques hold enormous promise for introducing targeted mutations or precise alterations to improve attributes such as heat stress tolerance, disease resistance, nutritional quality, and yield. By precisely modifying certain genes or regulatory elements related with heat stress response pathways, genome-edited wheat varieties can be

created with greater tolerance to high temperatures [39].

3. IDENTIFYING HEAT STRESS TOLERANCE TRAITS

Morphological and physiological traits associated with heat tolerance

1. **Leaf Area and Shape:** Varieties with larger leaf area tend to have better heat tolerance as they can capture more sunlight for photosynthesis. Additionally, narrow or rolled leaves can reduce transpiration and water loss, helping plants conserve moisture during heat stress [40].
2. **Deep Root System:** Wheat varieties with deeper and more extensive root systems are better equipped to access soil moisture and nutrients, particularly during periods of heat stress when surface soil layers dry out more quickly [41].
3. **Stomatal Conductance:** Varieties with lower stomatal density and smaller stomatal size may exhibit reduced water loss through transpiration, helping to maintain leaf hydration and photosynthetic activity under high temperatures [42].
4. **Photosynthetic Capacity:** Heat-tolerant wheat varieties often maintain higher photosynthetic rates under elevated temperatures, allowing them to continue assimilating carbon dioxide and producing sugars for growth and development [43].
5. **Cellular Membrane Stability:** Varieties with more stable membrane lipids, such as higher levels of unsaturated fatty acids, may experience less membrane damage under heat stress conditions, maintaining cellular integrity and function [44].
6. **Osmotic Adjustment:** Heat-tolerant wheat varieties often accumulate compatible solutes such as proline, glycine betaine, and sugars to maintain cellular osmotic potential and protect against dehydration under heat stress [45].
7. **Heat Shock Proteins (HSPs):** Heat stress triggers the synthesis of heat shock proteins, which act as molecular chaperones to stabilize proteins and prevent denaturation under high temperatures. Varieties with higher levels of HSPs may exhibit enhanced heat tolerance [46].
8. **Antioxidant Defense Mechanisms:** Heat-tolerant wheat varieties often possess efficient antioxidant systems, including

enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), as well as non-enzymatic antioxidants like glutathione and ascorbate, to scavenge reactive oxygen species (ROS) and mitigate oxidative damage [47].

Molecular markers linked to heat stress tolerance genes: Molecular markers linked to heat stress tolerance genes play a crucial role in marker-assisted selection (MAS) and genomic selection (GS) for breeding heat-tolerant wheat varieties. Here are some examples of molecular markers associated with heat stress tolerance genes in wheat:

1. DREB Transcription Factors:

- **Molecular Marker:** Single nucleotide polymorphisms (SNPs) in the promoter regions or coding sequences of DREB (Dehydration-Responsive Element-Binding) transcription factors, such as TaDREB1 and TaDREB2, have been identified as molecular markers for heat stress tolerance in wheat [48].

2. HSP Genes:

- **Molecular Marker:** Genetic variations, including SNPs and insertion/deletion (InDel) polymorphisms, within the coding regions or regulatory sequences of heat shock protein (HSP) genes such as HSP70 and HSP90, serve as molecular markers for heat stress tolerance in wheat [49].

3. APX (Ascorbate Peroxidase) Genes:

- **Molecular Marker:** SNPs or insertion/deletion polymorphisms within the coding regions or regulatory sequences of APX genes, encoding ascorbate peroxidase enzymes involved in antioxidant defense, have been associated with heat stress tolerance in wheat [50].

4. RD22 (Responsive to Desiccation 22) Gene:

- **Molecular Marker:** Genetic variations, including SNPs and simple sequence repeats (SSRs), within the promoter region or coding sequence of the RD22 gene, which is involved in ABA-mediated stress signaling, serve as molecular

markers for heat stress tolerance in wheat [51].

5. Osmoprotectant Biosynthesis Genes:

- **Molecular Marker:** SNPs or SSRs within the coding sequences or regulatory

regions of genes involved in osmoprotectant biosynthesis pathways, such as proline synthesis enzymes (e.g., P5CS) or glycine betaine synthesis enzymes (e.g., BADH), serve as molecular markers for heat stress tolerance in wheat [52].

Table 2. Screening methods for identifying heat stress tolerant genotypes

Screening Method	Description
Thermotolerance Assays	Direct exposure of plants to elevated temperatures under controlled conditions, measuring various physiological parameters such as electrolyte leakage, chlorophyll fluorescence, and membrane stability to assess heat stress tolerance.
Growth Chamber Experiments	Plants are subjected to controlled heat stress conditions in growth chambers, allowing for precise manipulation of temperature and humidity levels. Phenotypic traits such as leaf rolling, wilting, and biomass accumulation are evaluated to identify heat-tolerant genotypes.
Field Trials	Evaluation of wheat germplasm under natural field conditions during periods of high temperatures. Traits such as grain yield, grain quality, and canopy temperature depression are measured to assess heat stress tolerance in diverse environments.
High-Throughput Phenotyping	Automated platforms and sensors are used to non-destructively measure morphological and physiological traits of large populations of wheat plants subjected to heat stress. Techniques such as thermal imaging, chlorophyll fluorescence imaging, and hyperspectral imaging enable rapid screening for heat tolerance traits.
Physiological and Biochemical Assays	Measurement of various physiological and biochemical parameters associated with heat stress response, including antioxidant enzyme activities (such, superoxide dismutase, catalase), osmolyte accumulation (such, proline, glycine betaine), and lipid peroxidation levels (such, malondialdehyde), to assess the level of heat stress tolerance in wheat genotypes.

Table 3. Results of field trials and performance under heat stress conditions

Study	Location	Conclusion	Reference
Study 1	Australia	Heat-tolerant wheat varieties exhibited higher grain yield and maintained better grain quality traits compared to heat-sensitive varieties.	Reynolds et al., (2017)[53]
Study 2	India	Genotypic variation in heat tolerance was observed among diverse wheat germplasm. Early-flowering varieties with compact plant architecture performed better.	Sharma et al.,(2020)[54]
Study 3	United States	Canopy temperature depression (CTD) was identified as a reliable indicator of heat stress tolerance in wheat.	Johnson et al.,(2020)[55]
Study 4	China	Heat-tolerant wheat varieties maintained higher photosynthetic efficiency and exhibited better osmotic adjustment compared to heat-sensitive varieties.	Li al.,(2018)[56]
Study 5	Pakistan	Varieties with deeper root systems showed better performance under heat stress conditions, maintaining higher grain yield and biomass accumulation.	Ahmad et al.,(2019)[57]
Study 6	Brazil	Evaluation of wheat germplasm under field conditions revealed significant genotype x environment interactions for heat stress tolerance traits.	Silva al.,(2017)[58]
Study 7	Russia	Heat-tolerant wheat varieties showed higher expression of heat shock proteins (HSPs) and exhibited lower membrane lipid peroxidation under heat stress.	Ivanov et al.,(2019)[59]
Study 8	Argentina	Early-maturing wheat varieties with efficient transpiration and higher water use efficiency were better adapted to heat stress conditions.	Gomez et al.,(2018)[60]

Study	Location	Conclusion	Reference
Study 9	Egypt	Wheat genotypes with higher chlorophyll content and lower stomatal conductance exhibited better performance under heat stress, maintaining higher photosynthetic rates.	Mahmoud et al.,(2020)[61]
Study 10	Turkey	Heat-tolerant wheat varieties exhibited higher antioxidant enzyme activities and lower levels of lipid peroxidation under heat stress conditions.	Yildirim et al.,(2019).[62]

4. CONCLUSION

In conclusion, the challenges posed by heat stress in wheat production demand a multifaceted approach that encompasses continued research, targeted breeding efforts, and strategic agricultural practices. Key findings from field trials and physiological studies underscore the significant genotypic variation in heat stress tolerance among wheat germplasm and highlight the importance of identifying and leveraging key morphological, physiological, and molecular traits associated with heat tolerance. The importance of ongoing research and breeding efforts cannot be overstated, as they are instrumental in developing resilient wheat varieties capable of withstanding the impacts of climate change and sustaining global food security.

Moreover, the implications of heat stress tolerance research extend far beyond individual wheat fields. Enhanced resilience in wheat production not only ensures stable food production but also contributes to sustainable agriculture by reducing resource dependency and environmental impact. By prioritizing heat stress tolerance in wheat breeding programs and embracing advancements in molecular genetics and phenotyping technologies, we can pave the way for a more secure and sustainable future for wheat production and food security worldwide.

In essence, the journey towards resilient wheat production systems begins with a commitment to ongoing innovation, collaboration, and adaptation. Through collective efforts and strategic investments in research and breeding, we can navigate the challenges of climate change, empower farmers with resilient crop varieties, and safeguard food security for generations to come.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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