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Case Study **Open Access**

Research in Wheat Heat Tolerance Breeding

Shuping Lang, Yanxin Ma, Shuo Yang
Jiaxing Academy of Agricultural Sciences, Jiaxing, 314016, Zhejiang, China
Corresponding email: littlelsp@163.com

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Abstract With the global warming, heat stress has become one of the primary factors limiting wheat yield and quality. Developing heat-tolerant wheat varieties is crucial for stabilizing wheat production and adapting to climate change. This study summarizes current progress in wheat heat tolerance breeding, analyzing the effectiveness of traditional and modern breeding technologies such as marker-assisted selection (MAS), genomic selection (GS), and gene editing. It also explores the role of omics technologies in improving wheat heat tolerance, integrating case analyses, and proposing future directions to address challenges in wheat heat tolerance breeding. The research indicates that the complexity of heat tolerance traits in wheat and their polygenic regulatory nature make it difficult for traditional breeding methods alone to effectively counteract the effects of heat stress. MAS and GS have significantly enhanced breeding efficiency, while gene editing technology provides a new pathway for precise improvement of heat tolerance genes. Additionally, the integrated application of transcriptomics, metabolomics, and proteomics has facilitated a deep understanding of heat tolerance mechanisms in wheat, promoting the identification and precise selection of candidate genes. This study provides a systematic reference for wheat heat tolerance breeding, revealing the potential of multi-technology integration in improving heat tolerance and accelerating the development of wheat varieties that can adapt to climate change, thereby offering crucial support for global food security.

Keywords Wheat; Heat tolerance; Marker-assisted selection; Genomic selection; Omics integration

1 Introduction

Wheat (*Triticum aestivum* L.) is a staple crop that plays a crucial role in global food security, providing a significant portion of the daily caloric intake for millions of people worldwide. However, wheat production is increasingly threatened by global climate change, particularly the rising temperatures that lead to heat stress (Wang and Li, 2024). The impact of heat stress on wheat is multifaceted, affecting all stages of plant development and leading to a significant decline in yield. Heat stress during the reproductive and grain-filling phases is particularly detrimental, causing reductions in grain number, grain weight, and overall grain quality (Farooq et al., 2011; Farhad et al., 2023). The physiological and biochemical disruptions induced by heat stress include impaired photosynthesis, accelerated leaf senescence, and oxidative damage to cellular structures (Gourdji et al., 2013; Yadav et al., 2022). These changes not only reduce the plant’s ability to produce and store carbohydrates but also affect the stability and functionality of essential proteins and enzymes (Farooq et al., 2011; Gourdji et al., 2013).

At the physiological level, heat stress disrupts key processes such as photosynthesis and respiration, leading to reduced biomass accumulation and grain yield (Farooq et al., 2011; Gourdji et al., 2013). The generation of reactive oxygen species (ROS) under heat stress conditions causes oxidative damage to cellular components, including chloroplasts and membranes, further impairing plant growth and productivity (Gourdji et al., 2013; Lal et al., 2021). Molecular responses to heat stress involve the activation of heat shock proteins (HSPs) and other stress-responsive genes that help protect cellular structures and maintain metabolic functions (Farooq et al., 2011; Lal et al., 2021). Advances in omics technologies, such as genomics, transcriptomics, proteomics, and metabolomics, have provided deeper insights into the complex regulatory networks underlying heat stress tolerance in wheat (Lal et al., 2021; Yadav et al., 2022).

Given the significant impact of heat stress on wheat production, breeding heat-tolerant wheat varieties has become a critical priority for ensuring food security in a warming climate. Traditional breeding methods, combined with modern biotechnological approaches, have been employed to develop wheat genotypes with enhanced heat tolerance (Kamara et al., 2021; Langridge and Reynolds, 2021; Al-ashkar et al., 2023). These efforts include the identification and selection of key physiological traits, such as membrane stability and photosynthetic efficiency, as well as the incorporation of heat tolerance genes through genetic engineering and marker-assisted selection (MAS) (Farooq et al., 2011; Kamara et al., 2021; Al-ashkar et al., 2023). The development of heat-tolerant wheat varieties not only helps mitigate the adverse effects of climate change but also contributes to the stability and resilience of wheat production systems (Langridge and Reynolds, 2021; Al-ashkar et al., 2023).

This study will summarize the current status and methods of breeding heat-tolerant wheat varieties, providing an overview of the physiological, molecular, and genetic strategies applied in heat tolerance breeding. It will highlight the most promising approaches and identify key areas for future research. This study serves as a valuable resource for researchers, breeders, and policymakers, promoting the development of heat-tolerant wheat varieties to ensure sustainable wheat production in the context of global climate change.

2 Effects of Heat Stress on Wheat Physiology and Yield

2.1 Impact on photosynthesis

Heat stress significantly impairs the photosynthetic efficiency of wheat, primarily by causing metabolic limitations and oxidative damage to chloroplasts, which in turn reduces dry matter accumulation and grain yield (Farooq et al., 2011). High temperatures inhibit photosynthesis by damaging the photosystem II (PSII), a critical component of the photosynthetic machinery. The critical temperature at which PSII begins to incur damage varies among genotypes, suggesting that genetic variation can be exploited to improve photosynthetic heat tolerance (Coast et al., 2022). Additionally, heat stress leads to the deactivation of Rubisco, a key enzyme in the photosynthetic process, further reducing the production of photoassimilates necessary for grain filling and yield (Tao and Han, 2024). Enhanced photosynthesis under heat stress conditions has been observed in genotypes that exhibit delayed senescence and improved assimilate remobilization, indicating that these traits could be targeted in breeding programs to improve heat tolerance (Kumar et al., 2023).

2.2 Sensitivity during flowering and grain filling

The reproductive and grain-filling phases of wheat are particularly sensitive to heat stress, which can lead to significant yield reductions. High temperatures during these stages can shorten the grain filling duration, limit resource allocation to grains, and induce early senescence, resulting in lower productivity (Bergkamp et al., 2018). Terminal heat stress, which occurs towards the end of the growing season, is especially detrimental as it affects phenological traits such as biomass and crop duration, both of which are positively correlated with seed yield (Kumar et al., 2023). The grain filling stage is also critical, as heat stress during this period can decrease single seed weight and overall grain yield. Genetic improvements in heat tolerance have shown that certain genotypes can maintain higher chlorophyll content and shoot dry weight under heat stress, which are indicative of better heat tolerance mechanisms (Fu et al., 2023). Moreover, breeding efforts have demonstrated that selecting for traits such as membrane stability, photosynthetic rate, and grain weight under heat stress can lead to the development of more heat-tolerant wheat varieties (Farooq et al., 2011).

2.3 Impact on grain quality

Heat stress not only affects the yield but also the quality of wheat grains. Elevated temperatures can alter the composition of starch and protein in the grains, which are critical determinants of grain quality. For instance, heat stress can accelerate the conversion of soluble sugars to starch in wheat grains, resulting in faster grain filling but potentially compromising the quality (Zhang et al., 2022). The biochemical activity of enzymes such as superoxide dismutase (SOD), peroxidase (POX), and ascorbate peroxidase (APX) is induced in heat-tolerant genotypes, which helps mitigate oxidative damage and maintain grain quality under heat stress (Kumar et al., 2023). Additionally, the interplay of various systems comprising antioxidants and hormones plays a crucial role in maintaining cellular homeostasis and grain quality under heat stress conditions (Lal et al., 2021). Therefore, breeding programs that focus on improving both yield and quality under heat stress conditions are essential for developing wheat varieties that can withstand the challenges posed by global warming (Yadav et al., 2022).

3 Genetic Basis of Heat Tolerance in Wheat

3.1 Quantitative trait loci (QTL) associated with heat tolerance

QTL mapping has been instrumental in identifying genomic regions associated with heat tolerance in wheat. Several studies have pinpointed key QTLs that contribute to heat tolerance by influencing various phenotypic traits. For instance, a significant QTL hotspot on chromosome 4D was identified, which includes six major QTLs associated with traits such as shoot length, root length, and whole plant length under heat stress conditions (Lu et al., 2022). Another study identified a major QTL on chromosome 7AL, which was linked to heat tolerance traits such as SPAD chlorophyll content and grain yield (Lu et al., 2020). Additionally, QTLs on chromosomes 2B, 7B, and 7D were found to be associated with heat tolerance traits like heat susceptibility index and canopy temperature depression, explaining up to 20.34% of phenotypic variation (Paliwal et al., 2012). These QTLs are crucial for marker-assisted selection and breeding programs aimed at improving heat tolerance in wheat.

3.2 Identification of candidate genes for heat tolerance

The identification of candidate genes within QTL regions has provided deeper insights into the genetic mechanisms underlying heat tolerance. For example, seven candidate genes linked to a major QTL on chromosome 7AL were identified, which are involved in critical processes and pathways in response to heat stress (Lu et al., 2020). Another study identified 12 potential candidate genes associated with Fv/Fm, a measure of photosynthetic efficiency under heat stress, located on chromosomes 1D and 3B (Sharma et al., 2017). These genes are involved in photosynthesis and heat stress response, making them valuable targets for genetic improvement. The integration of molecular markers and candidate gene discovery has facilitated the development of near-isogenic lines (NILs) and other genetic resources that are essential for fine-mapping and cloning of major heat tolerance genes (Sharma et al., 2017; Lu et al., 2020).

3.3 Gene-environment interaction and heat tolerance

The expression of heat-tolerant genes in wheat is significantly affected by environmental factors, which determine the phenotypic outcomes. Studies have shown that QTLs for heat tolerance can exhibit varying degrees of expression depending on environmental conditions such as temperature and sowing dates. For instance, QTLs identified for traits like normalized difference vegetation index(NDVI) and grain yield showed different levels of expression under late and very late sown conditions, highlighting the importance of gene-environment interactions (Raveendran et al., 2020). Additionally, the stability of QTLs across different environments is crucial for their effective utilization in breeding programs. Some QTLs, such as those on chromosomes 2B and 7B, have been shown to be stable across multiple trials, indicating their robustness in different environmental contexts (Paliwal et al., 2012). Understanding these interactions is essential for developing wheat varieties that can maintain high levels of heat tolerance across diverse growing conditions.

4 Application of Traditional Breeding Methods in Wheat Heat Tolerance Improvement

4.1 Phenotypic selection

Phenotypic selection remains a cornerstone in traditional breeding methods for improving heat tolerance in wheat. This approach involves selecting plants that exhibit desirable traits under high-temperature conditions. For instance, traits such as delayed leaf senescence, increased photosynthetic capacity, and extended grain filling periods have been identified as critical for heat tolerance. These traits were effectively utilized in a three-tiered phenotyping strategy to select heat-tolerant wheat genotypes derived from emmer wheat, demonstrating the potential of phenotypic selection in identifying and developing heat-tolerant varieties (Ullah et al., 2021). Additionally, the use of agro-physiological indices and multidimensional analyses has been shown to enhance the accuracy and credibility of phenotypic selection, allowing breeders to classify wheat genotypes based on their heat tolerance levels (Al-ashkar et al., 2023).

4.2 Hybrid breeding and trait improvement

Hybrid breeding is another traditional method that has been effectively used to introduce heat tolerance genes into wheat. This method involves crossing genetically diverse parents to produce hybrids with superior traits. For example, the genetic distance between wheat genotypes has been correlated with heterosis, which can be exploited to improve hybrid performance under heat stress. In a study evaluating 16 wheat genotypes, hybrids with greater genetic diversity showed significant improvements in grain yield and other heat tolerance traits, such as grain filling duration and canopy temperature (Al-ashkar et al., 2020). Marker-assisted backcross breeding (MABB) is another strategy that has been employed to introgress specific QTLs associated with heat tolerance into popular wheat varieties. This method has successfully improved traits like early anthesis and high kernel weight, leading to the development of heat-tolerant lines with higher grain yields (Bellundagi et al., 2022).

4.3 Successful cases of classical breeding

Several successful cases of classical breeding for heat tolerance in wheat have been documented. For instance, recurrent selection has been shown to be an effective strategy for improving heat tolerance. Studies conducted in different growing seasons demonstrated significant genetic gains and variability, indicating the potential for successful recurrent selection in developing heat-tolerant wheat varieties (Machado et al., 2010). Another notable example is the identification of heat-tolerant genotypes based on pollen viability under heat stress. Genotypes such as Chenab-70, Pari-73, and Pak-81 have been found to maintain high pollen viability under elevated temperatures, making them valuable genetic resources for breeding heat-tolerant cultivars. Khan et al. (2022b) found that the heat-tolerant line (Chenab-70) maintained better pollen morphology under heat stress, with even distribution and good staining, demonstrating a higher level of heat tolerance. In contrast, the susceptible lines (Meraj-08 and Gomal-08) showed significantly damaged pollen under heat stress, with poor staining and reduced quantity, indicating decreased pollen viability (Figure 1). Additionally, the use of QTL mapping has identified significant genomic regions associated with heat tolerance, which can be utilized in marker-assisted selection to develop heat-tolerant wheat varieties (Paliwal et al., 2012).

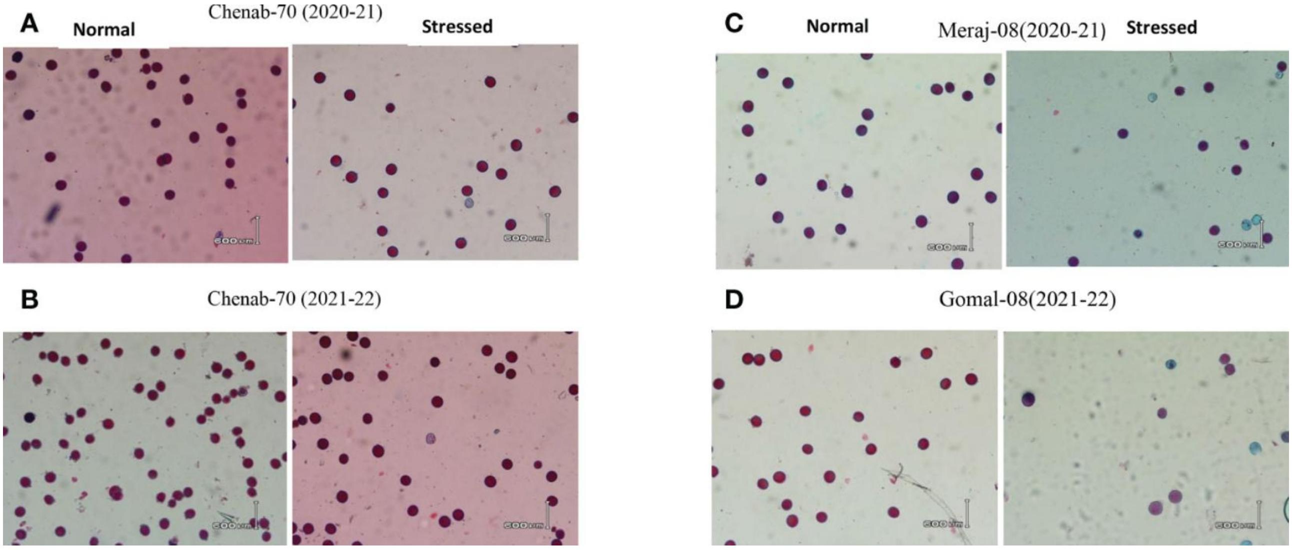

Figure 1 Microscopic observation of pollen from heat-tolerant and susceptible wheat lines under normal and heat stress conditions (Adapted from Khan et al., 2022b)

Image caption: Microscopic images (10x magnification) of pollen from heat-tolerant wheat line (A, B: Chenab-70) and heat-susceptible wheat lines (C: Meraj-08, D: Gomal-08) under normal (left) and heat stress conditions (right). The images display pollen conditions for the two types of wheat lines over two consecutive years (2020-2021 and 2021-2022) (Adapted from Khan et al., 2022b)

5 Application of Molecular Breeding Techniques in Wheat Heat Tolerance Improvement

5.1 Marker-assisted selection (MAS)

MAS has become a pivotal tool in accelerating the breeding of heat-tolerant wheat varieties. MAS leverages molecular markers linked to desirable traits, enabling breeders to select plants with these traits more efficiently than traditional phenotypic selection methods. For instance, the introgression of QTLs associated with early anthesis and high kernel weight into the heat-sensitive wheat variety HD2877 through marker-assisted backcross breeding (MABB) has shown promising results (Figure 2). This approach utilized markers Xbarc186 and

Xgwm190 to fix the alleles in successive generations, resulting in lines with improved heat tolerance and higher grain yield (Bellundagi et al., 2022). Additionally, the development of heat-responsive gene-based SSRs and miRNA-SSR markers has facilitated the genetic diversity analysis of wheat genotypes, further enhancing the MAS-based breeding programs for heat tolerance (Sharma et al., 2021). The efficiency of MAS in improving quantitative traits has been demonstrated through various strategies, including marker-assisted backcrossing, forward breeding, and the use of high-throughput genotyping technologies (Gupta et al., 2010; Song et al., 2023).

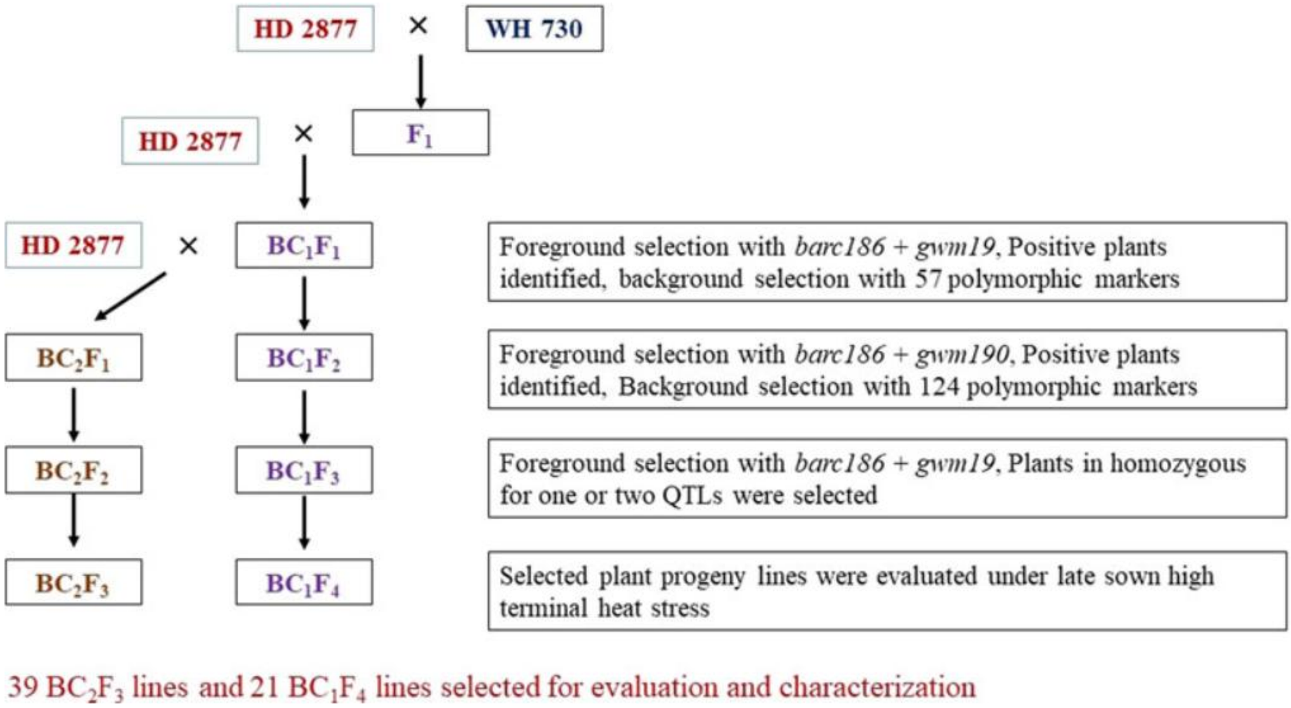

Figure 2 Marker-assisted backcross breeding process for improving HD2877 with heat tolerance QTLs using WH730 as the donor (Adapted from Bellundagi et al., 2022)

Image caption: WH730 is used as the donor to introduce heat tolerance QTLs into the HD2877 background. The backcross breeding process involved multiple generations of selection and background selection to ensure the integration of donor QTLs and the elimination of excess donor genes. Finally, in the BC_2F_3 and BC_1F_4generations, a total of 39 BC_2F_3 and 21 BC_1F_4lines were selected for evaluation and trait characterization under late-sown heat stress conditions (Adapted from Bellundagi et al., 2022)

5.2 Genomic selection (GS)

Genomic selection (GS) represents a significant advancement in the breeding of heat-tolerant wheat varieties by utilizing genomic data to predict and select for desirable traits. Unlike MAS, which focuses on specific markers, GS incorporates genome-wide marker information to estimate the breeding values of individuals. This approach has been particularly effective in improving complex polygenic traits, such as heat tolerance, which are controlled by multiple genes with small effects. GS has been widely adopted in animal breeding and is now being explored for crop improvement due to its potential to enhance selection accuracy, reduce phenotyping efforts, and accelerate breeding cycles (Budhlakoti et al., 2022; Paux et al., 2022). The integration of GS in wheat breeding programs has shown promising results in improving yield, biotic and abiotic stress tolerance, and overall genetic gains (He et al., 2014). The use of high-density molecular marker maps and full genome sequences has further facilitated the implementation of GS, enabling breeders to develop climate-resilient wheat varieties more efficiently (Paux et al., 2022).

5.3 Gene editing technology

Gene editing technologies, particularly CRISPR/Cas9, have revolutionized the field of plant breeding by allowing precise modifications of specific genes associated with heat tolerance. This technology enables the targeted editing of heat-related genes, thereby enhancing the heat tolerance of wheat varieties. While the provided data does not include specific studies on the application of CRISPR/Cas9 in wheat heat tolerance, the potential of this technology is well-recognized in the scientific community. Gene editing can complement traditional breeding and molecular techniques by providing a rapid and precise method to introduce beneficial traits into wheat genomes. The integration of CRISPR/Cas9 with other molecular breeding techniques, such as MAS and GS, holds great promise for developing wheat varieties that can withstand the increasing temperatures associated with climate change.

6 Application of Multi-Omics Integration in Wheat Heat Tolerance Research

6.1 Transcriptomics

Transcriptomics has been instrumental in understanding the gene expression changes in wheat under heat stress. Studies have shown that heat stress induces significant alterations in the expression of a wide array of genes, including those encoding heat shock proteins (HSPs), transcription factors, and proteins involved in phytohormone biosynthesis and signaling pathways. For instance, a genome-wide gene expression analysis using the Wheat Genome Array revealed that approximately 10.7% of probe sets displayed more than a two-fold change in expression under heat stress conditions. This includes genes related to primary and secondary metabolism, RNA metabolism, and other stress-related proteins. Additionally, the differential expression of 313 probe sets between heat-tolerant and heat-susceptible genotypes suggests that these genes could be crucial for heat tolerance (Qin et al., 2008). The integration of transcriptomic data with other omics approaches can further elucidate the complex regulatory networks involved in heat stress responses (Chatterjee et al., 2023).

6.2 Metabolomics

Metabolomics provides a comprehensive overview of the metabolic changes in wheat under heat stress, identifying key metabolites and metabolic pathways that contribute to heat tolerance. Metabolomic profiling has revealed that heat stress significantly affects amino acid, carbohydrate, and nitrogen metabolism, which are critical for plant stress responses. For example, the accumulation of specific metabolites such as osmoprotectants and antioxidants helps in mitigating the adverse effects of heat stress by stabilizing cellular structures and scavenging reactive oxygen species (Raza, 2020). The integration of metabolomics with transcriptomics has been particularly effective in linking metabolic changes to gene expression, thereby identifying potential biomarkers for heat tolerance (Abdelrahman et al., 2020; Raza, 2020). This approach has facilitated the development of metabolomics-assisted breeding (MAB) strategies, which aim to enhance heat tolerance by selecting for favorable metabolic traits (Raza, 2020).

6.3 Proteomics and epigenetics

Proteomics and epigenetics play crucial roles in regulating heat tolerance traits in wheat. Proteomic studies have identified several heat-responsive proteins, including HSPs, which are essential for protein folding and protection under stress conditions (Chatterjee et al., 2023). These proteins help maintain cellular homeostasis and protect against heat-induced damage. Additionally, epigenetic modifications such as DNA methylation and histone modifications have been shown to influence gene expression in response to heat stress. These modifications can lead to the activation or repression of stress-responsive genes, thereby modulating the plant's ability to cope with high temperatures (Ni et al., 2017). The integration of proteomic and epigenetic data with other omics approaches provides a holistic understanding of the molecular mechanisms underlying heat tolerance and can guide the development of heat-tolerant wheat cultivars (Ni et al., 2017; Chatterjee et al., 2023).

7 Success Stories in Wheat Heat Tolerance Breeding

7.1 Wheat varieties with high heat adaptability

Several wheat varieties have been developed and promoted for their high heat tolerance, demonstrating significant resistance effects. For instance, the study by Al-ashkar et al. (2023) identified new wheat lines such as DHL25, DHL05, DHL23, and DHL08, along with the cultivar Pavone-76, as promising genetic sources for heat-tolerant breeding programs. These varieties were classified based on agro-physiological indices and multidimensional analyses, showing high heritability and genetic gain under heat stress conditions. Additionally, the research by Khan et al. (2022a) characterized 194 historical wheat cultivars of Pakistan, identifying loci associated with heat tolerance at the seedling stage. The study highlighted the potential of these cultivars to sustain high temperatures, with specific haplotypes (Hap-20 and Hap-21) showing strong heat tolerance (Table 1). These findings highlight the success of breeding heat-tolerant wheat varieties, enabling wheat to maintain a stable yield under high temperature stress conditions.

Table 1 Variation in seedling traits among 24 haplotypes of the wheat TaHST1 QTL under heat stress (HS) conditions (Adapted from Khan et al., 2022a)

Haplotype	Xhau-1	Xhau-2	Xhau-3	Xhau-4	Xhau-5	Deleted sites	Number of lines	Frequency (%)	RL (cm) in HS	RW (g) in HS	SL (cm) in HS	SW (g) in HS
Hap1	−	−	+	127	−	3	34	19.4	14.3	0.14	36.4	0.8
Hap2	−	−	−	−	−	5	23	13.1	14.3	0.11	37.4	0.78
Hap3	−	−	+	127	+	2	20	11.4	13.7	0.1	37.6	0.84
Hap4	−	−	−	195	−	4	17	9.7	14.1	0.12	38.8	0.75
Hap5	+	+	+	127	+	0	16	9.1	15	0.15	37.3	0.83
Hap6	−	−	−	127	+	3	11	6.3	15.3	0.17	38	0.83
Hap7	−	−	−	127	−	4	9	5.1	9.4	0.09	35.3	0.87
Hap8	−	−	−	127	−	4	9	5.1	13.6	0.09	37	0.72
Hap9	+	−	+	127	+	1	8	4.6	12.8	0.09	36.4	0.73
Hap10	+	+	+	127	−	1	7	4	15	0.13	41.1	0.85
Hap11	−	+	+	127	−	2	5	2.9	13.8	0.13	35	0.67
Hap12	−	−	−	195	+	3	5	2.9	15	0.11	36	0.82
Hap13	−	−	+	−	−	4	4	2.3	13.2	0.07	37.2	0.73
Hap14	−	−	−	−	+	4	3	1.7	12.7	0.07	31.2	0.66
Hap15	+	+	+	−	+	1	3	1.7	15.6	0.17	39.7	0.82
Hap16	+	+	−	127	−	2	2	1.1	14.7	0.13	35.6	0.71
Hap17	−	+	−	−	−	4	1	0.6	20.2	0.17	40	0.88
Hap18	+	+	+	−	−	2	1	0.6	14.3	0.26	42	0.59
Hap19	+	−	+	−	+	2	1	0.6	13.2	0.14	43	0.76
Hap20	+	+	+	195	+	0	1	0.6	14	0.11	40.6	1.03
Hap21	−	+	−	127	−	3	1	0.6	14	0.22	41.3	1
Hap22	−	+	−	127	+	2	1	0.6	13.4	0.07	32	0.7
Hap23	−	−	+	195	−	3	1	0.6	12.5	0.09	36.3	0.7
Hap24	−	−	+	195	+	2	1	0.6	14.3	0.07	36	0.8
Total							175	100				

Note: + and − shows positive and negative amplifications; Xhau-4 is a co-dominant marker showing amplifications of 127 bp or 195 bp depending on the genotype; RL: root lenght; RW: root wenght; SL: shoot lenght; SW: shoot wenght

7.2 Performance of heat-tolerant wheat varieties in different regions

The performance of heat-tolerant wheat varieties has been evaluated across various regions, demonstrating their adaptability to different climatic conditions. For example, the research by Gourdji et al. (2013) utilized data from 25 years of wheat trials in 76 countries to assess genetic gains in heat tolerance. The study found that the Semi-Arid Wheat Yield Trial (SAWYT) showed the strongest genetic gains at the hottest temperatures, indicating the effectiveness of targeted breeding efforts in hot environments. Similarly, Fu et al. (2023) evaluated 304 elite winter wheat lines from the US, Australia, and Serbia, identifying significant genetic variation for chlorophyll retention and seed weight under heat stress. The study proposed two mechanisms of heat tolerance during grain filling, represented by wheat lines OK05723W and TX04M410164, which could be useful for breeding programs. These case studies highlight the successful application and performance of heat-tolerant wheat varieties in diverse regions, contributing to global food security.

7.3 Implementation experiences in heat-tolerant wheat breeding programs

Practical strategies and operations in heat-tolerant wheat breeding programs have been crucial in achieving success. The study by Langridge and Reynolds, (2021) emphasized the importance of combining genetic analysis, phenotyping, and screening techniques to enhance heat tolerance. This comprehensive approach has expanded the understanding of factors influencing yield under stress and identified promising strategies for breeding. Additionally, Ni et al., (2017) reviewed recent progress in understanding the molecular mechanisms of heat tolerance, including phytohormone signaling and epigenetic regulation. These insights have informed integrative strategies to improve heat tolerance by utilizing existing germplasm, modern cultivars, landraces, and related species. Furthermore, Driedonks et al., (2016) highlighted the need for a multidisciplinary approach involving governmental agencies, private companies, and academic institutions to address the complex nature of plant heat tolerance. These implementation experiences demonstrate the effectiveness of collaborative and integrative strategies in breeding heat-tolerant wheat varieties, ensuring their success in mitigating the impacts of global warming on wheat production.

8 Challenges and Future Directions in Wheat Heat Tolerance Breeding

8.1 Phenotypic complexity and environmental adaptability

The diversity and complexity of heat tolerance traits in wheat under high temperatures present significant challenges for breeders. Heat tolerance in wheat is influenced by a multitude of phenological, physiological, and biochemical traits, which exhibit substantial genotypic and environmental variations. For instance, traits such as grain yield, grain-filling duration, spike length, and canopy temperature have been identified as critical indicators of heat tolerance, but their expression can vary widely depending on environmental conditions (Al-ashkar et al., 2023; Kumar et al., 2023). Additionally, the interaction between genotype and environment (G x E) complicates the selection process, as traits that confer heat tolerance in one environment may not be as effective in another (Reynolds et al., 2004). This phenotypic complexity necessitates the use of multidimensional analyses and comprehensive indices to accurately classify and select heat-tolerant genotypes (Al-ashkar et al., 2023).

8.2 Data integration and multidisciplinary collaboration

The integration of omics data (genomics, transcriptomics, proteomics, and metabolomics) with phenotypic and environmental data is crucial for advancing heat tolerance breeding in wheat. Multidisciplinary collaboration is essential to harness the full potential of these diverse data sources. For example, genome-wide association studies (GWAS) have identified numerous QTLs associated with heat tolerance, which can be used for marker-assisted selection (Paliwal et al., 2012; Khan et al., 2022a). However, the successful application of these findings requires collaboration between geneticists, physiologists, and breeders to ensure that the identified markers are effectively integrated into breeding programs. Additionally, the development of advanced phenotyping techniques and the use of high-throughput screening methods can enhance the accuracy and efficiency of selecting heat-tolerant genotypes (Yang et al., 2002; Langridge and Reynolds, 2021).

8.3 Heat tolerance breeding strategies in the context of climate change

As global temperatures continue to rise, breeding strategies must adapt to ensure that wheat varieties can cope with future climate conditions. One approach is to focus on the genetic improvement of key physiological traits that confer heat tolerance, such as canopy temperature depression, membrane thermostability, and photosynthetic efficiency (Reynolds et al., 2004; Kamara et al., 2021). Another strategy involves the use of genetic resources from heat-tolerant wheat species, such as emmer wheat, to introduce valuable alleles into modern bread wheat cultivars (Ullah et al., 2021). Additionally, breeding programs should prioritize the development of genotypes with stable yield performance across a range of stress scenarios, including combined drought and heat stress, which are likely to become more prevalent with climate change (Tricker et al., 2018). By adopting these adaptive strategies, breeders can enhance the resilience of wheat to high temperatures and ensure food security in the face of a changing climate.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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