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Improving Grain Quality and Yield in Heat-Stressed Wheat through Advanced Breeding Techniques- A Review

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Abstract

Heat stress poses a significant threat to global wheat production, particularly in light of climate change, which is increasing the frequency and intensity of extreme temperatures. Developing heat-tolerant wheat varieties is essential to sustain grain yield and quality under such conditions. This review highlights advancements in breeding strategies, including conventional approaches such as selection of heat-tolerant germplasm, hybridization, and backcrossing, and modern methods like marker-assisted selection (MAS), genomic selection (GS), and CRISPR-Cas9-based gene editing. The integration of omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, has facilitated the identification of key genes, proteins, and metabolites involved in heat stress tolerance. For example, traits such as canopy temperature depression (CTD), stay-green phenotype, and prolonged grain filling are being targeted using high-throughput phenotyping (HTP) tools in combination with genotyping data. Sustainable agronomic practices, including optimized irrigation, adjusted sowing dates, and nutrient management, play a pivotal role in mitigating heat stress and enhancing the performance of heat-tolerant varieties. Synergistic approaches that combine breeding with agronomy, such as the development of climate-resilient production systems, have shown promise in improving productivity under heat-stressed environments. Challenges remain, including the genetic complexity of heat tolerance, trade-offs with grain yield and quality, limited genetic diversity, and constraints in breeding infrastructure and resources. Emerging technologies, such as artificial intelligence (AI) and machine learning (ML), offer new opportunities to optimize breeding pipelines and accelerate the development of resilient varieties. The exploration of wild relatives and landraces presents untapped potential for introducing novel heat-tolerant traits into modern cultivars. Strengthening global collaboration and knowledge-sharing initiatives will be key to overcoming these challenges. The need for interdisciplinary approaches to achieve sustainable wheat production in a warming world and ensure global food security.

Key words : Heat-stress, Breeding, Wheat, Genomics, Phenotyping, Yield. Resilience.

A. Importance of Wheat as a Global Staple Crop : Wheat (*Triticum aestivum* L.) is one of the most important staple crops globally, providing approximately 20% of the world's dietary energy and protein intake. It is a primary food source for over 2.5 billion people, particularly in developing and middle-income countries where food security heavily relies on cereal crops. Due to its high adaptability, wheat is cultivated across a range of climatic zones, from temperate to tropical regions, covering over 220 million hectares worldwide (Shiferaw *et al*., 2013).The versatility of wheat stems from its use in diverse products such as bread, pasta, noodles, and pastries, making it a culturally and nutritionally indispensable food crop. Wheat is a key economic commodity, contributing significantly to agricultural GDPs and supporting rural livelihoods globally. With the growing global population projected to reach nearly 10 billion by 2050, the demand for wheat is expected to increase by approximately 60%, making its sustainable production a critical challenge.

B. Challenges Posed by Climate Change and Heat Stress to Wheat Production : Climate change poses an existential threat to wheat production worldwide. Among the various environmental stressors, heat stress, particularly during critical growth stages such as flowering and grain filling, is one of the most detrimental factors (Table 1) (Farooq *et al.*, 2017). It is estimated that for every 1°C rise in temperature, wheat yields could decline by 6%, leading to severe reductions in global wheat production. This is especially concerning in major wheat-producing regions such as South Asia, the Middle East, and Sub-Saharan Africa, where temperatures already approach or exceed optimal levels for wheat growth. Heat stress negatively impacts key physiological processes, including photosynthesis, pollen viability, and grain filling duration, resulting in reduced grain size, weight, and overall yield (Arshad *et al.*, 2017). Heat stress can compromise grain quality by altering protein composition and starch structure, directly affecting its suitability for processing and consumption. The frequency and intensity of heatwaves are projected to increase with ongoing global warming, further exacerbating the vulnerability of wheat production systems.Efforts to mitigate the effects of heat stress on wheat production face significant barriers, including limited availability of heat-tolerant cultivars, reduced genetic diversity in modern wheat varieties, and insufficient adoption of climate-resilient agricultural practices. Thus, there is an urgent need to develop innovative breeding strategies to enhance the resilience of wheat to heat stress while maintaining or improving yield and grain quality.

C. Significance of Grain Quality and Yield in Global Food Security : Grain quality and yield are central to ensuring global food security, particularly in a rapidly growing

Table 1. Challenges Posed by Climate Change and Heat Stress to Wheat Production (Sources: Arshad *et.al.*, 2017)

Aspect	Description	Impact on Wheat Production	Possible Solutions
Rising Temperatures	Increased global temperatures due to climate change	Shortened growth cycle, reduced grain filling, and lower yields	Development of heat-tolerant wheat varieties, adjusting sowing dates
Extreme Heat Events	More frequent and intense heatwaves	Spike in sterility rates, poor seed setting, and grain shriveling	Use of heat-resilient cultivars, improved irrigation techniques
Drought Stress	Reduced rainfall and soil moisture availability	Decline in biomass, reduced root growth, and premature senescence	Drought-tolerant varieties, water conservation techniques, mulching
Altered Phenology	Changes in wheat growth stages due to climate shifts	Early flowering and grain filling, yield instability	Precision farming, optimized planting time based on climate models
Soil Degradation	Increased soil erosion, loss of organic matter	Poor nutrient availability, lower water-holding capacity	Conservation agriculture, crop rotation, organic amendments
Heat-Induced Diseases & Pests	Rising temperatures favor pests and pathogens	Increased infestation rates, reduced grain quality	Integrated pest management (IPM), disease-resistant wheat varieties
Nutritional Decline	High CO_2 levels reduce nutrient uptake efficiency	Lower protein and micronutrient content in wheat grains	Biofortification, balanced fertilization strategies
Adaptation Strategies	Innovative breeding, climate-smart agriculture	Enhancing resilience against climate stressors	Genetic modification, policy support for sustainable wheat farming

population scenario. Wheat yield, defined as the total grain production per unit area, is critical for meeting global caloric needs (Hawkesford *et al.*, 2013). At the same time, grain quality, characterized by parameters such as protein content, gluten strength, and milling characteristics, determines its suitability for processing and consumption. The dual challenge of maintaining high yield and grain quality under heat stress has far-reaching implications for food availability, affordability, and accessibility.In heat-stressed environments, wheat plants prioritize survival over productivity, often at the expense of grain yield and quality. Reduced grain quality due to heat stress can lead to lower market value, increased food waste, and decreased nutritional value for consumers. Regions already facing food insecurity are disproportionately affected, as wheat often constitutes a significant portion of dietary intake in these areas (Grote *et al.*, 2021).The importance of addressing grain quality and yield in wheat breeding programs cannot be overstated. Improved heat-tolerant varieties with stable yields and high-quality grains have the potential to enhance both food security and farmer livelihoods. Achieving these goals aligns with the United Nations Sustainable Development Goals (SDGs), particularly SDG 2 (Zero Hunger) and SDG 13 (Climate Action).

2. Heat Stress in Wheat Production

A. Characterization of Heat Stress in Plants : Heat stress in plants is broadly defined as a condition where elevated temperatures surpass a plant's optimal threshold for growth, development, and reproduction, leading to irreversible physiological damage (Wahid *et al.*, 2007). In wheat, heat stress typically occurs when daytime temperatures exceed 30°C during critical growth stages, such as anthesis (flowering) and grain filling. It is classified as acute (short-term exposure to very high temperatures) or chronic (sustained exposure to moderately high temperatures over time), with both types severely affecting plant metabolism and productivity.The susceptibility of wheat to heat stress depends on the growth stage, with reproductive and grain-filling phases being the most vulnerable. High temperatures during these stages accelerate phenological development, shortening the grain-filling period and leading to yield and quality losses (Krishnan *et al.*, 2011). Heat stress is often exacerbated by concurrent abiotic stresses, such as drought, amplifying its negative effects on plant performance.

B. Physiological and Molecular Effects of Heat Stress on Wheat

1. Impact on Grain Quality (Protein Content, Starch Composition, etc.) : Heat stress during the grain-filling stage significantly affects wheat grain quality by altering the synthesis and deposition of storage proteins and starch, which are the two primary components of wheat grains. High temperatures have been shown to increase grain protein concentration due to the reduced synthesis of starch, which typically dilutes protein content in optimal conditions (Zahedi *et al.*, 2004). While protein concentration may increase, heat stress disrupts gluten protein composition, adversely affecting dough elasticity and bread-making quality. Starch composition is severely impacted, as heat stress inhibits the activity of starch-synthesizing enzymes such as starch synthase and granule-bound starch synthase. This results in reduced starch content, altered amylose-to-amylopectin ratios, and a smaller number of starch granules, directly affecting grain processing quality (Fasahat *et al.*, 2014). Heat stress can impair the accumulation of secondary metabolites, such as antioxidants and vitamins, further reducing the nutritional quality of wheat grains.

2. Impact on Yield (Grain Number, Size, and Weight) : Heat stress significantly reduces wheat yield by impacting three key yield components: grain number, grain size, and grain weight. During the reproductive stage, elevated temperatures disrupt meiosis and pollen viability, leading to reduced fertilization and grain set (Arshad *et al.*, 2017). This directly lowers the number of grains per spike, a major determinant of yield. Heat stress during grain filling accelerates the senescence of photosynthetic tissues, limiting the availability of assimilates for grain development. This results in smaller and lighter grains, as the duration of grain filling is drastically shortened under high temperatures. Studies have shown that a 1°C increase in mean temperature during the grain-filling period can reduce grain weight by up to 3%. Such reductions in grain size and weight collectively contribute to lower overall wheat yields, posing a significant threat to food security in heat-stressed regions (Sehgal *et al.*, 2018).

C. Current Global Distribution of Heat Stress in Wheat-Growing Regions : Heat stress is an increasingly pervasive challenge in major wheat-growing regions, particularly in areas where temperatures frequently exceed optimal thresholds for wheat growth. Regions such as South Asia, North Africa, the Middle East, and Sub-Saharan Africa are especially vulnerable to heat stress due to their warm climates and limited access to heat-tolerant cultivars.In South Asia, which accounts for nearly 20% of global wheat production, temperatures during the wheat-growing season are already at the upper limit of tolerance, with climate models predicting further increases in both average and extreme temperatures. Similar trends are observed in the Mediterranean and Middle East regions, where recurrent heatwaves have caused substantial yield losses in recent years (Zampieri *et al.*, 2017). Temperate regions such as Europe and North America, which have historically been less affected by heat stress, are now experiencing an increased frequency of extreme heat events during critical wheat growth periods. This expansion of heat stress into traditionally cooler wheat-growing regions highlights the global scale of the problem and underscores the need for widespread adoption of heat-resilient wheat varieties.

D. Socioeconomics of Heat-Stressed Wheat Production : The socioeconomic consequences of heat stress in wheat production are profound, particularly for smallholder farmers and resource-poor regions that rely heavily on wheat as both a food source and an economic commodity. Reduced wheat yields due to heat stress can lead to higher market prices, reducing the affordability of wheat-based products for low-income populations (Meng *et al.*, 2009). This can exacerbate food insecurity in vulnerable regions, where wheat constitutes a major component of daily caloric intake.Heat stress also affects the livelihoods of wheat farmers by reducing farm income and increasing production costs associated with adaptation strategies, such as supplemental irrigation or crop insurance. For smallholder farmers, who often lack access to advanced agricultural technologies, the inability to cope with heat stress can result in economic losses and increased poverty.On a global scale, the cumulative impact of heat stress on wheat production could disrupt international trade and exacerbate geopolitical tensions, particularly in regions that rely on wheat imports to meet domestic demand (Jia *et al.*, 2024). The development of heat-tolerant wheat varieties is therefore critical not only for safeguarding food security but also for promoting economic stability and social equity in a changing climate.

3. Breeding Techniques for Improving Grain Quality and Yield Under Heat Stress

A. Conventional Breeding Approaches

1. Selection of Heat-Tolerant Germplasm : The identification and selection of heat-tolerant germplasm are fundamental to conventional breeding efforts aimed at improving wheat's performance under heat stress (Table 2). Heat-tolerant genotypes are selected based on their ability to maintain grain yield and quality under high-temperature conditions (Chaudhary *et al.*, 2020). This approach typically involves screening genetic resources, including landraces, wild relatives, and existing cultivars, for traits such as canopy temperature depression (CTD), stay-green phenotype, and stability of grain weight.Wheat landraces and wild relatives, such as Aegilops tauschii and Triticum dicoccoides, are particularly valuable due to their genetic diversity and inherent adaptation to harsh environments. For instance, heat-tolerant wheat varieties such as 'Sitta' and 'Habaq' have been developed

Table 2. Breeding Techniques for Improving Grain Quality and Yield Under Heat Stress

Breeding Technique	Description	Impact on Grain Quality & Yield	Challenges & Limitations
Conventional Breeding	Selection and crossbreeding of heat-tolerant wheat varieties	Improved heat resilience, better grain filling, and yield stability	Time-consuming, limited by genetic variability in existing germplasm
Marker-Assisted Selection (MAS)	Use of molecular markers to identify heat-tolerant genes	Faster selection of desirable traits, improved efficiency in breeding programs	Requires well-mapped genetic markers, expensive technology
Genomic Selection (GS)	Whole-genome prediction models for selecting heat-resilient traits	Higher accuracy in breeding for complex traits like heat tolerance	Requires large datasets and computational resources
Genetic Engineering (GE)	Direct modification of wheat genes for heat stress tolerance	Faster development of stress-resilient varieties, enhanced grain quality	Regulatory hurdles, consumer acceptance issues
CRISPR-Cas9 Gene Editing	Precision genome editing to enhance stress tolerance and grain quality	Highly specific trait improvement, reduced breeding time	Ethical concerns, regulatory challenges
Hybrid Breeding	Development of hybrid wheat varieties with superior heat tolerance	Increased yield potential, better adaptation to heat stress	Hybrid seed production costs, seed viability issues
Mutation Breeding	Induced mutations to create new heat-tolerant wheat genotypes	Rapid trait development, potential for unique stress-resistant varieties	Random mutations may have undesirable effects
Speed Breeding	Accelerated plant growth cycles under controlled conditions	Faster development of heat-resilient wheat lines	Requires specialized infrastructure and controlled environments
Transgenic Approaches	Introduction of heat-tolerance genes from other species	Improved stress resistance, better grain filling under heat stress	Regulatory restrictions, potential environmental concerns
QTL Mapping for Heat Tolerance	Identification of quantitative trait loci (QTLs) linked to heat stress resilience	Helps in selecting key genes for breeding heat-tolerant wheat	Complex interactions of multiple genes, time-consuming validation

Source: Yadav *et al.*, 2022, Chaudhary *et al.*, 2020) through the selection of germplasm with enhanced thermal stability. This approach is labor-intensive and time-consuming, often requiring several years to identify and evaluate suitable germplasm.

2. Breeding for Heat Tolerance through Hybridization and Backcrossing : Hybridization and backcrossing are widely used traditional breeding methods for combining heat-tolerant traits from donor parents with high-yielding elite varieties (Bellundagi *et al*., 2022). Hybridization involves crossing two genetically diverse parents, followed by phenotypic selection for progeny exhibiting heat-tolerant traits such as delayed senescence, increased photosynthetic efficiency, and reduced floret abortion under heat stress.Backcrossing, on the other hand, involves repeatedly crossing hybrid progeny with the elite parent to recover desirable agronomic traits while introgressing heat-tolerance genes from the donor parent. This method has been used to transfer heat-tolerance traits from wild relatives into modern wheat cultivars, resulting in improved grain yield and stability under heat stress (Yadav *et al*., 2022).

3. Limitations of Traditional Breeding Methods : Despite their success, conventional breeding methods face several limitations in addressing heat stress challenges. First, the genetic complexity of heat tolerance, which involves multiple quantitative trait loci (QTLs) and gene-environment interactions, makes it difficult to achieve consistent progress through phenotypic selection alone. Second, the long breeding cycles associated with hybridization and backcrossing hinder the rapid development of new heat-tolerant varieties, especially in the face of accelerating climate change. Traditional methods often fail to fully exploit the genetic diversity present in wild relatives and exotic germplasm due to linkage drag and incompatibility issues (Kashyap *et al*., 2022).

B. Marker-Assisted Selection (MAS)

1. MAS in Wheat Breeding : Marker-assisted selection (MAS) represents a significant advancement over conventional breeding by enabling the indirect selection of desired traits through molecular markers linked to specific genes or QTLs. In wheat, MAS has been extensively employed to improve traits related to heat tolerance, such as CTD, early vigor, and spike fertility.MAS relies on identifying and tagging genetic regions associated with heat-tolerant traits using techniques such as quantitative trait locus (QTL) mapping and genome-wide association studies (GWAS). These markers are then used to screen large populations for the presence of favorable alleles, accelerating the breeding process and reducing dependence on phenotypic evaluations (Xu *et al*., 2012) (Song *et al*., 2023).

C. Genomic Selection (GS) : Genomic selection (GS) is a predictive breeding approach that uses genome-wide marker data to estimate the breeding values of individuals without directly measuring their phenotypes. In GS, genomic prediction models are trained on a reference population with known genotypic and phenotypic data, allowing the selection of superior individuals based on genomic estimated breeding values (GEBVs).Unlike MAS, which targets specific QTLs, GS captures the effects of all genome-wide markers, making it particularly effective for improving complex traits such as heat tolerance that are controlled by multiple small-effect genes (Kumar *et al*., 2024). GS also allows for the early selection of superior individuals, reducing breeding cycle time and increasing genetic gain per unit time.GS has been successfully implemented in wheat breeding programs to improve grain yield, CTD, and grain weight under heat-stress conditions. For example, CIMMYT (International Maize and Wheat Improvement Center) has integrated GS into its wheat breeding pipeline to accelerate the development of climate-resilient varieties.

D. Genetic Engineering and Gene Editing : CRISPR-Cas9 technology has revolutionized wheat breeding by enabling precise genome editing to improve heat tolerance. This method allows the targeted modification of heat-responsive genes, such as those encoding heat shock proteins (HSPs) and transcription factors (Kumar *et al.*, 2021).Heat-tolerant genes such as HSP101 and transcription factors like DREB2A and HSFA2 have been introduced into wheat using genetic engineering techniques. These genes enhance the plant's ability to maintain cellular homeostasis and mitigate heat-induced damage.Despite its potential, the adoption of genetically modified (GM) wheat faces regulatory and consumer acceptance challenges. Public perception and strict biosafety regulations have limited the commercialization of GM wheat, particularly in Europe and Asia.

E. Speed Breeding and Rapid Generation Advancement : Speed breeding techniques, which involve controlled environments with extended photoperiods, enable the production of up to 6 generations of wheat per year, significantly accelerating breeding cycles (Samantara*et al.*, 2022).Speed breeding, when combined with high-throughput phenotyping tools such as remote sensing and imaging, allows for the rapid evaluation of heat-tolerant traits, such as canopy temperature and stay-green phenotype.Speed breeding has been successfully applied in wheat improvement programs to develop heat-tolerant varieties. For example, CIMMYT and the University of Queensland have used speed breeding to accelerate the selection of wheat lines with improved performance under heat stress.

4. Phenotyping for Heat Stress Tolerance

A. High-Throughput Phenotyping (HTP)

1. HTP Technologies (e.g., Drones, Imaging, Sensors) : High-throughput phenotyping (HTP) technologies have emerged as powerful tools for screening large populations of plants for stress tolerance traits under field and controlled conditions. These technologies use advanced imaging systems, sensors, and platforms such as drones, ground-based vehicles, and fixed-position setups to rapidly measure plant traits related to heat stress tolerance (Atefi *et al.*, 2021). HTP technologies can monitor phenotypes such as canopy temperature, vegetation indices, chlorophyll fluorescence, and plant architecture in a non-destructive, efficient, and accurate manner. For example, thermal imaging cameras are used to measure canopy temperature, an indirect indicator of transpiration and heat stress tolerance. Hyperspectral imaging provides insights into changes in leaf pigment composition, water content, and photosynthetic capacity under heat stress (Melandri *et al.*, 2021). Drones equipped with multispectral and thermal cameras have revolutionized field-based phenotyping by enabling rapid data collection across large breeding trials, reducing the labor and time required for manual observations. Other ground-based platforms, such as the Field Scanalyzer, use fixed sensors and robotic arms to collect time-series data on plant growth, stress responses, and phenotypic variation (Ayeneh *et al.*, 2002).

B. Physiological Traits as Selection Criteria

1. Canopy Temperature Depression (CTD) : Canopy temperature depression (CTD) is one of the most widely used traits for assessing heat tolerance in wheat. It measures the difference between canopy temperature and ambient temperature, with lower canopy temperatures indicating better cooling capacity through transpiration (Rahman *et al.*, 2017). CTD is strongly correlated with grain yield under heat stress, making it a valuable selection criterion in wheat breeding programs. Wheat genotypes with higher CTD under heat stress tend to maintain stomatal conductance, which helps sustain photosynthesis and assimilate production during periods of elevated temperatures. Thermal imaging technologies have enabled the rapid and accurate measurement of CTD across large breeding populations, significantly enhancing the selection process.

2. Photosynthetic Efficiency and Chlorophyll Stability : Photosynthetic efficiency, often measured as the maximum quantum yield of photosystem II (Fv/Fm), is a critical determinant of wheat's ability to tolerate heat stress (Sommer *et al.*, 2023). Heat stress damages photosynthetic machinery, leading to a decline in energy conversion efficiency and a reduction in biomass and grain yield.Chlorophyll stability is another important physiological trait under heat stress. Heat-tolerant wheat genotypes are able to maintain chlorophyll content and integrity during stress, which is essential for sustaining photosynthesis and delaying senescence. Non-invasive techniques, such as chlorophyll fluorescence imaging and hyperspectral reflectance, have been successfully employed to quantify photosynthetic performance and chlorophyll stability in wheat (Zhang *et al.*, 2024).

3. Grain Filling Duration Under Heat Stress : Grain filling duration is the period during which wheat grains accumulate starch, proteins, and other storage compounds. Heat stress accelerates the senescence of flag leaves and reduces grain filling duration, leading to smaller and lighter grains.Heat-tolerant wheat genotypes exhibit a longer grain filling duration, allowing for greater assimilation and translocation of photoassimilates to the developing grains. Phenotyping tools, such as NDVI (Normalized Difference Vegetation Index) sensors and time-lapse imaging, have been used to monitor the progression of grain filling and identify genotypes with stable performance under heat stress (Bhardwaj *et al.*, 2024).

C. Integration of Phenotyping with Genotyping Data : The integration of phenotyping and genotyping data represents a transformative approach to wheat breeding for heat stress tolerance. This integration, often referred to as phenomics-genomics integration, combines high-resolution phenotypic data with genetic information to identify marker-trait associations, develop genomic prediction models, and facilitate precision breeding. Phenotyping platforms provide quantitative data on traits such as CTD, photosynthetic efficiency, and grain filling duration, which are then linked to genotypic information obtained from high-throughput sequencing or SNP genotyping (Bhat *et al.*, 2020). Genome-wide association studies (GWAS) and genomic selection (GS) models leverage this integrated data to identify QTLs and predict the breeding values of individuals for heat tolerance.For example, CIMMYT has successfully combined HTP data and genotyping-by-sequencing (GBS) to identify heat-tolerant wheat lines and validate markers for traits such as grain yield and CTD under heat stress. This approach accelerates the development of heat-tolerant wheat varieties by enabling the selection of superior genotypes at earlier breeding stages.

5. Role of Omics Technologies in Heat-Stress Tolerant Wheat Breeding : Omics technologies have revolutionized wheat breeding by providing deep insights into the molecular mechanisms underlying heat stress tolerance (Singh *et al.*, 2024). These tools enable the identification of genes, proteins, and metabolites associated with stress responses, offering breeders novel targets for the development of heat-tolerant wheat varieties.

A. Genomics :

1. Sequencing of Wheat Genomes and Identification of Heat-Tolerant Loci : The sequencing of wheat genomes has been a milestone in advancing our understanding of its genetic architecture and improving breeding for heat stress tolerance. The release of the Triticum aestivum genome by the International Wheat Genome Sequencing Consortium (IWGSC) has provided breeders with a complete reference genome, facilitating the identification of genes and loci associated with heat tolerance (Mourad *et al*., 2019).Genomic studies have identified quantitative trait loci (QTLs) linked to heat tolerance traits such as grain filling duration, canopy temperature depression (CTD), and chlorophyll retention. For example, QTLs on chromosomes 2B, 3B, and 7D have been associated with heat tolerance in wheat, offering breeders valuable targets for marker-assisted selection. High-throughput genotyping technologies, such as SNP arrays and genotyping-by-sequencing (GBS), have further accelerated the discovery of heat-tolerant loci. These advancements allow the rapid identification of genetic markers that can be used to track heat tolerance traits in breeding programs (Driedonks *et al*., 2016).

2. Genome-Wide Association Studies (GWAS) for Heat Stress Tolerance : GWAS is a powerful genomic tool that identifies genetic variants associated with heat tolerance by linking phenotypic data to genome-wide markers. GWAS has successfully identified single nucleotide polymorphisms (SNPs) associated with key heat stress traits, such as CTD, grain yield, and spike fertility under high-temperature conditions. A GWAS study in spring wheat identified SNPs linked to heat tolerance on chromosomes 3B and 7A, which are associated with increased grain filling duration and cooler canopies under heat stress. Integrating GWAS with advanced phenotyping techniques has further improved the resolution and accuracy of detecting heat-tolerant loci (Kayess *et al*., 2024).

B. Transcriptomics

1. Identifying Heat-Responsive Genes and Pathways : Transcriptomics, the study of RNA transcripts, has been instrumental in uncovering the molecular pathways involved in heat stress tolerance in wheat. Heat-responsive genes, including those encoding heat shock proteins (HSPs), transcription factors (TFs), and enzymes involved in antioxidant production, play key roles in protecting cells under heat stress.For example, the DREB2A (Dehydration-Responsive Element-Binding Protein 2A) gene has been identified as a critical regulator of heat and drought tolerance in wheat, activating downstream genes involved in stress adaptation. Similarly, genes encoding heat shock transcription factors (HSFs), such as HSFA2 and HSFA6, are upregulated during heat stress, enhancing cellular protection and repair mechanisms (Scharf *et al*., 2012).

2. RNA-Seq Applications in Wheat Under Heat Stress : RNA sequencing (RNA-Seq) has enabled the identification of differentially expressed genes (DEGs) under heat stress, providing a comprehensive view of wheat's transcriptional response to high temperatures. For instance, RNA-Seq studies have revealed the upregulation of HSPs, antioxidant enzymes (e.g., superoxide dismutase and catalase), and osmoprotectants during heat stress. RNA-Seq has also been used to study the temporal dynamics of gene expression during heat stress, identifying early and late stress-responsive pathways. This information helps breeders target specific genes and regulatory networks to enhance wheat's resilience to high temperatures (Ober *et al*., 2021).

C. Proteomics

1. Role of Heat Shock Proteins (HSPs) in Stress Adaptation : Heat shock proteins (HSPs) are molecular chaperones that play a crucial role in protecting cellular proteins from heat-induced denaturation and aggregation. HSPs, such as HSP70, HSP90, and small HSPs, are rapidly upregulated under heat stress and are essential for maintaining protein homeostasis.In wheat, HSPs have been shown to improve heat tolerance by stabilizing the photosynthetic apparatus, protecting membrane integrity, and enhancing enzymatic activity during stress. For instance, HSP70 assists in refolding denatured proteins, while small HSPs stabilize heat-sensitive proteins, preventing irreversible damage (Langer *et al*., 1990).

2. Proteomic Profiling of Heat-Stressed Wheat Plants : Proteomic studies provide insights into the changes in protein abundance and modifications under heat stress, revealing key proteins involved in stress adaptation. Techniques such as two-dimensional gel electrophoresis (2D-GE) and mass spectrometry have been used to identify stress-responsive proteins in wheat, including enzymes involved in carbon metabolism, photosynthesis, and antioxidant defense (Bhati *et al*., 2024).Proteomic profiling has identified candidate proteins that can serve as biomarkers for heat tolerance, aiding in the selection of heat-tolerant genotypes in breeding programs. For example, increases in antioxidant enzymes such as superoxide dismutase and glutathione peroxidase have been correlated with improved stress tolerance in wheat.

D. Metabolomics

1. Key Metabolites Involved in Heat Tolerance (e.g., Osmolytes, Antioxidants): Metabolomics, the study of small molecules (metabolites), has uncovered key metabolites that enhance wheat's resilience to heat stress. These include:

- **Osmolytes:** Compounds such as proline, glycine betaine, and trehalose accumulate under heat stress, protecting cellular structures and maintaining osmotic balance (Singh *et al*., 2015).
- **Antioxidants:** Metabolites such as ascorbate, glutathione, and carotenoids play crucial roles in scavenging reactive oxygen species (ROS) generated during heat stress, protecting cells from oxidative damage.
- **Sugars:** Soluble sugars such as sucrose and raffinose act as osmoprotectants and energy reserves, supporting cellular metabolism under stress.

2. Metabolic Engineering for Heat Stress Resilience : Metabolic engineering aims to enhance the production of protective metabolites in wheat to improve heat tolerance. For instance, overexpression of genes involved in proline biosynthesis (P5CS) has been shown to increase heat tolerance in wheat by enhancing osmoprotection (Amini *et al*., 2015). Similarly, manipulating antioxidant pathways through the overexpression of genes such as APX (ascorbate peroxidase) and GR (glutathione reductase) has improved oxidative stress tolerance in wheat.Advancements in metabolomics and gene editing technologies, such as CRISPR-Cas9, offer new opportunities to engineer wheat plants with enhanced heat stress resilience by precisely modulating metabolic pathways.

6. Challenges and Limitations in Breeding Heat-Stress Tolerant Wheat

A. Genetic Complexity of Heat

Tolerance in Wheat : Heat tolerance in wheat is a complex quantitative trait controlled by multiple genes, gene-environment interactions, and regulatory networks (Munkvold *et al.*, 2013). This complexity makes it challenging to identify, validate, and manipulate heat tolerance-related traits through traditional or molecular breeding methods.For example, traits like CTD, grain filling duration, and membrane stability are influenced by multiple QTLs, each with small effects, requiring advanced genomics tools such as genomic selection (GS) and genome-wide association studies (GWAS) to capture their combined effects. The polyploid nature of wheat complicates gene editing and marker-assisted selection (MAS) for heat tolerance due to redundancy in the wheat genome (Uauy*et al.*, 2017).

B. Trade-Offs Between Heat Tolerance, Yield, and Grain Quality : Breeding for heat tolerance often involves trade-offs with other key traits such as yield potential and grain quality. For instance, heat-tolerant varieties may prioritize stress survival mechanisms (e.g., osmotic adjustment or reduced leaf area) at the expense of maximum yield potential under optimal conditions. Maintaining grain quality under heat stress is a significant challenge, as elevated temperatures often lead to increased protein content but reduced gluten strength and starch quality, affecting processing and end-use quality. Balancing these trade-offs remains a major limitation in developing commercially viable heat-tolerant wheat varieties (Reynolds *et al.*, 2016).

C. Limited Genetic Diversity in Wheat Germplasm for Heat Tolerance : Modern wheat breeding programs rely heavily on a narrow genetic base, limiting the availability of alleles for heat tolerance. This bottleneck is partly due to the domestication and selection processes that have favored high-yielding but genetically uniform wheat varieties.Wild relatives and landraces of wheat possess valuable traits for heat tolerance, such as efficient water use, prolonged photosynthetic activity, and superior membrane stability under heat stress (Yadav *et al.*, 2022). The transfer of these traits into modern wheat varieties is constrained by linkage drag, genetic incompatibilities, and the lack of efficient introgression techniques.

D. Constraints in Resources and Infrastructure for Breeding Programs : Developing heat-tolerant wheat varieties requires significant investments in resources, infrastructure, and technical expertise, which are often lacking in resource-limited regions. For example: High-throughput phenotyping (HTP) facilities for heat stress traits, such as canopy temperature or stay-green phenotype, are expensive and require technical expertise. Advanced molecular breeding tools, such as GS and CRISPR-Cas9, demand substantial investments in laboratory infrastructure and bioinformatics capabilities.Conducting multi-location field trials under controlled heat stress conditions is resource-intensive and logistically challenging, particularly in developing countries (Occelli *et al.*, 2024).

E. Policy and Regulatory Challenges for Adoption of Novel Techniques : The adoption of advanced breeding technologies, such as genetic engineering and gene editing, is hindered by strict regulatory frameworks and public perception issues, particularly in regions with strong anti-GMOsentiment.The approval process for genetically modified (GM) wheat varieties is often lengthy and uncertain, discouraging investment in genetic engineering approaches.Public resistance to GM crops, driven by misinformation and concerns about food safety, remains a significant barrier to the adoption of heat-tolerant GM wheat varieties. The high cost of patented technologies, such as CRISPR-Cas9, restricts access for public-sector breeding programs and small-scale farmers (Molinari *et al.*, 2024).

7. Future and Opportunities : Emerging technologies such as artificial intelligence (AI) and machine learning (ML) are transforming wheat breeding by enabling rapid data analysis and predictive modeling. AI and ML algorithms can analyze large datasets from genomics, phenomics, and environmental factors to identify key traits and predict heat-tolerant genotypes. Additionally, AI-powered decision support tools can optimize breeding strategies and accelerate the development of climate-resilient wheat varieties.Wild relatives and landraces of wheat harbor untapped genetic diversity for heat tolerance traits, including enhanced root systems, prolonged photosynthesis, and membrane stability under stress (Jamil *et al.*, 2024). Advances in genome editing and introgression techniques, such as CRISPR-Cas9 and genomic selection, provide opportunities to efficiently transfer these traits into modern wheat cultivars. This exploration is critical to overcoming the genetic bottlenecks in current wheat breeding programs.Integrated climate-resilient systems, combining heat-tolerant wheat varieties with sustainable agronomic practices such as conservation agriculture, precision irrigation, and nutrient management, offer a holistic approach to mitigate heat stress impacts. These systems enhance soil health, optimize water use, and create microclimates conducive to wheat growth, ensuring stable yields under variable and extreme temperatures.Global collaboration among research organizations, policymakers, and farmers is essential to tackle heat stress in wheat. Initiatives such as the International Wheat Yield Partnership (IWYP) and the Heat and Drought Wheat Improvement Consortium (HeDWIC) foster knowledge exchange, resource sharing, and coordinated efforts to develop heat-resilient wheat varieties. Strengthening such networks will accelerate the adoption of innovative solutions and improve global food security.

Conclusion

Addressing the challenge of heat stress in wheat production is critical for ensuring global food security in the face of climate change. Advanced breeding techniques, such as marker-assisted selection, genomic selection, and gene editing, have significantly enhanced the development of heat-tolerant wheat varieties, while omics technologies have provided insights into the physiological and molecular mechanisms of heat stress tolerance. Integrating these genetic improvements with sustainable agronomic practices, such as optimized irrigation, sowing adjustments, and soil management, can amplify their impact on grain yield and quality under high-temperature conditions. Challenges such as the genetic complexity of heat tolerance, limited genetic diversity, and resource constraints must be addressed through global collaboration, knowledge-sharing initiatives, and innovative technologies like AI and ML. Together, these efforts can pave the way for climate-resilient wheat production systems and sustainable agriculture.

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