

Review Article

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Heat and Combined Heat-Drought Stress in Wheat: Physiological Responses, Molecular Mechanisms, and Climate-Resilient Breeding and Management Strategies

Manisha Kumari^{1*} and Amit Godara²

¹Department of Horticulture Sciences, University of Georgia, 4604 Research Way, Tifton, GA 31793

²Department of Crop and Soil Sciences, University of Georgia, 2360 Rainwater Road, Tifton, GA 31793

*Corresponding author

ABSTRACT

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Wheat (*Triticum aestivum* L.) is among the most strategically important cereal crops on earth. Supplying approximately one-fifth of total human caloric intake and serving as a primary protein source for billions of people across all continents. However, the escalating frequency and intensity of heat and drought stress events driven by anthropogenic climate change now represent one of the most severe and immediate threats to global wheat production and food security. Temperatures exceeding the optimal range for wheat growth during the critical reproductive stage trigger cascading physiological, biochemical, and molecular disruptions that culminate in yield and quality losses. This review synthesizes the current understanding of the impacts of heat and drought stress on wheat. This review is organized across four major dimensions: (1) physiological and morphological responses to heat and drought stress, including photosynthetic impairment, membrane thermostability disruption, stomatal behavior, reproductive organ damage, and altered source-sink dynamics; (2) molecular mechanisms underpinning heat tolerance, encompassing the heat shock protein (HSP) chaperone network, heat shock transcription factors (HSFs), dehydration-responsive element binding (DREB) proteins, reactive oxygen species (ROS) signaling, and epigenetic regulation; (3) the interactive and often synergistic impacts of combined heat and drought stress, a condition increasingly prevalent in major wheat-growing regions, including its effects on gametophyte development, endosperm formation, starch biosynthesis, and grain protein composition; and (4) breeding and management strategies for improving heat stress tolerance, encompassing conventional breeding, marker-assisted selection, quantitative trait loci (QTL) mapping, genomic selection, transgenic approaches, CRISPR-based genome editing, and agronomic management practices. Selected research findings synthesized from field and controlled environment trials conducted across contrasting environments demonstrate that genotype, environment, and their interaction all substantially influence the expression of heat tolerance traits, underscoring the need for multi-environment evaluation frameworks. Research tables summarize findings from 30+ studies, covering yield losses, grain quality, gene expression, QTL loci, and management outcomes. The review concludes by identifying critical knowledge gaps and highlighting priority research directions, including the urgent need to develop climate-resilient wheat cultivars capable of sustaining productivity under increasingly higher temperature environments.

Introduction

Wheat is cultivated on approximately 220 million hectares with an annual production of 778 million metric tons. It ranks among the three most critical staple crops for global food security, alongside rice and maize (Nyaupane *et al.*, 2024). Wheat contributes approximately 20% of the calories and protein consumed by humans globally (Langridge & Reynolds, 2021). Each kilogram delivers approximately 9.4% protein, 69% carbohydrates, 2.5% fat, and 1.8% dietary fiber to human diets at the global scale (Nyaupane *et al.*, 2024). The crop has historically been the cornerstone of agricultural civilizations across the temperate zones of Asia, Europe, North Africa, and the Americas. Its central role in human nutrition and food systems has only deepened as the global population has grown.

The accelerating pace of anthropogenic climate change, however, now places wheat production under severe and growing threat. Global mean surface temperatures have been rising at a rate of approximately 0.06°C per year, accompanied by a parallel decline in mean annual precipitation of approximately 16.09 mm per year (Paudel *et al.*, 2020; Nyaupane *et al.*, 2024). These trends are projected to intensify, with more frequent and severe heatwaves expected in major wheat-producing regions including South Asia, the Mediterranean basin, sub-Saharan Africa, and parts of North America (Yadav *et al.*, 2022). In many of these regions, critical phenological stages of wheat, particularly anthesis and grain filling, increasingly coincide with episodes of elevated temperature that exceed the crop's thermal tolerance thresholds.

Heat stress in wheat is broadly defined as the exposure of plants to temperatures above a threshold, generally considered to be above 30°C during the day, for a duration sufficient to cause irreversible damage to plant function and productivity (Akter & Rafiqul Islam, 2017). Heat damages cells by denaturing enzymes and proteins, destabilizing membranes, and triggering oxidative stress. This causes harm to DNA, lipids, and proteins (Yadav *et al.*, 2022). Heat stress disrupts chloroplast architecture, impairs thylakoid membranes, and reduces photosynthetic efficiency. It also compromises pollen viability and interferes with stigma receptivity and fertilization (Zahra *et al.*, 2021). These disruptions cause accelerated leaf senescence, shortened grain filling, and reduced grain weight and number. The result is altered grain composition and substantial yield losses.

The economic consequences are already substantial. Heat stress has been estimated to reduce global wheat yields by between 1% and 2% per decade (Tack *et al.*, 2014). In semi-arid conditions representative of major wheat-producing zones in Pakistan, combined heat and drought stress reduced wheat yields by as much as 56.47% (Qaseem *et al.*, 2019). Wheat yield fluctuations of up to 40% attributable to combined heat and drought stress have been documented at the global scale (Zampieri *et al.*, 2017). Climate models project a 1.9% global wheat production decline by mid-century under RCP 8.5, with Africa and South Asia facing 15% and 16% losses respectively. Historical data show wheat yields fell 5.5% during 1980-2010 due to rising temperatures (Pequeno *et al.*, 2021). A landmark multi-model analysis using 30 wheat crop models confirmed that global wheat production declines by approximately 6% for each degree Celsius increase in temperature, equivalent to one-quarter of the annual global wheat trade (Asseng *et al.*, 2015). These figures underscore the urgency of developing comprehensive, scientifically grounded strategies to protect wheat productivity against thermal stress.

Heat stress rarely occurs alone in agricultural fields. Elevated temperatures are usually accompanied by soil water deficits, creating combined heat-drought stress with synergistic rather than simply additive negative effects. Rampino *et al.*, (2012) cDNA-AFLP transcriptomic analysis showed wheat's molecular response to combined heat and drought stress is qualitatively distinct from individual stressors. Substantially more genes are differentially expressed under combined conditions, particularly those involved in transport, transcription regulation, and novel stress-response pathways. This has profound implications for breeding strategies. Tolerance to individual stresses may not translate into tolerance to the combined stress regime plants encounter in the field.

Despite four decades of research, significant knowledge gaps remain: reproductive-stage thermotolerance mechanisms, genetic architecture of combined stress tolerance, and field-level translation of laboratory findings. The emergence of powerful new tools, including high-throughput genomics, transcriptomics, metabolomics, CRISPR editing, and phenotyping platforms, offer unprecedented opportunities for progress. Agronomic practices, optimized sowing, irrigation management, nutrient supplementation, and biostimulants offer practical near-term mitigation options

The present review synthesizes current knowledge across four major areas: (1) the physiological and morphological consequences of heat stress in wheat; (2) the molecular and biochemical mechanisms underlying heat stress perception, signaling, and tolerance; (3) the interactive effects of combined heat and drought stress on grain development and quality; and (4) breeding and management strategies for developing and deploying heat-tolerant wheat. Special attention is given to genotype-by-environment interactions on stress responses and the contrasting effects of heat versus drought on grain quality parameters. The focus includes practical requirements for translating mechanistic understanding into genetic improvement of wheat for a warming world.

Physiological Impacts of Heat Stress on Wheat

Morphological and Phenological Effects

Heat stress disrupts developmental, physiological, and reproductive processes across all growth stages. This leads to substantial yield penalties. The magnitude of damage is strongly dependent on the timing of stress exposure, with reproductive stages being particularly vulnerable (Yadav *et al.*, 2022). Elevated temperatures accelerate development, compressing vegetative growth, internode elongation, and spike formation. This shortens the critical pre-anthesis period, during which yield potential is determined by spikelet and floret numbers. Heat stress during the double-ridge stage and early reproductive development reduces the number of spikelets per spike and florets per spikelet, directly constraining the maximum attainable grain number per unit area (Li *et al.*, 2022; Yadav *et al.*, 2022).

Terminal heat stress, defined as elevated temperature occurring during grain filling, is particularly damaging. It curtails filling duration and reduces assimilate transport to grains. Grain size and weight are the primary yield components affected, with numerous studies documenting substantial reductions in thousand-kernel weight (TKW) under heat stress (Zahra *et al.*, 2021).

The reproductive stage is especially vulnerable; temperatures above 32°C during anthesis and early grain filling are sufficient to cause irreversible damage to pollen, reduce seed set, and shorten grain-filling duration, resulting in shriveled, low-weight grains (Stone & Nicolas, 1995; Kumar *et al.*, 2023).

Photosynthesis and Carbon Assimilation

Tyagi and Pandey (2022) identified overlapping and stress-specific response pathways in wheat. They confirmed three shared physiological challenges: photosynthetic impairment, osmotic stress, and oxidative damage. Membrane thermostability disruption and protein denaturation are more specifically associated with heat stress. Understanding shared and distinct physiological mechanisms is essential for designing breeding strategies that confer tolerance to multiple stresses simultaneously. This aligns with the consensus that field-relevant heat tolerance must be evaluated and selected under combined stress conditions.

Photosynthesis is among the most temperature-sensitive processes in wheat physiology (Lv *et al.*, 2022). Lal *et al.*, (2022) confirmed that photosynthetic disruption is among the earliest heat stress effects. Three mechanisms operate simultaneously: PSII destabilization, Rubisco inactivation, and reduced electron transport. Heat stress reduces photosynthetic efficiency through multiple interconnected pathways (Yadav *et al.*, 2022). High temperatures destabilize thylakoid membranes and disrupt PSII architecture. The D1 protein, PSII's central reaction center component, is especially targeted for degradation. The destabilization of PSII under heat stress leads to reduced quantum yield of photochemistry, impaired electron transport, and decreased ATP and NADPH production available for carbon fixation through the Calvin cycle.

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the primary enzyme of photosynthetic carbon fixation, is highly sensitive to elevated temperatures. Heat directly inactivates Rubisco by disrupting its subunits and denaturing RCA. It also favors oxygenase over carboxylation, increasing photorespiratory loss and reducing net photosynthesis (Kumar *et al.*, 2016). Research has confirmed that RCA (TaRCA1) is a critical catalytic chaperone that regulates Rubisco activity in wheat under heat stress. Simultaneously, total chlorophyll content declines under heat stress due to the activation of chlorophyllase, ROS-mediated chloroplast damage, and accelerated leaf senescence (Nyaupane *et al.*, 2024).

These photosynthetic impairments reduce photosynthate supply for grain filling. This exacerbates yield losses due to shorter filling duration. Shah and Paulsen (2003)

demonstrated that drought stress combined with high temperatures (35/30°C Day/Night) had the most severe effects on grain filling, restricting grain growth at both moisture regimes and highlighting the compound impact of simultaneous stresses on carbon assimilation and allocation.

Membrane Stability and Reactive Oxygen Species

Cell membrane thermostability (CMT) is a well-established physiological indicator of heat stress tolerance in wheat. Membranes depend on precise lipid bilayer properties. Elevated temperatures alter saturated-to-unsaturated fatty acid ratios, increasing fluidity and disrupting ion channels, transporters, and receptors (Yadav *et al.*, 2022). The thylakoid membrane of chloroplasts is particularly vulnerable, as its structural integrity is directly coupled to the efficiency of the photosynthetic light reactions. Heat stress rigidification of thylakoid membranes and associated disruption of electron transport chains trigger a burst of reactive oxygen species (ROS) production, including superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\bullet OH$).

ROS accumulation causes oxidative damage through peroxidation. This compromises membrane integrity, inactivates enzymes, and triggers cell death in severely stressed tissues (Yadav *et al.*, 2022). However, ROS also functions as an important secondary messenger in heat stress signaling cascades, activating downstream transcriptional and biochemical responses, including the induction of antioxidant enzyme systems.

Tolerant wheat genotypes consistently exhibit higher activities of key ROS-scavenging enzymes, superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and peroxidases (POX), compared to susceptible genotypes, enabling them to maintain cellular redox homeostasis under heat stress conditions (Kumar *et al.*, 2023).

Reproductive Development under Heat Stress

Farooq *et al.*, (2014) conducted a comprehensive review of heat stress during reproductive and grain-filling phases in wheat, establishing that the critical temperature threshold for reproductive damage in wheat is approximately 30°C, above which pollen viability and

tube germination begin to decline significantly. They found that the window between meiosis in microspore mother cells and anthesis is the most thermosensitive developmental period, and that even brief heat episodes of 1 to 2 days during this window can cause yield losses comparable to those from prolonged moderate heat stress. Their review also highlighted that genotypic variation in heat sensitivity during reproductive stages is substantial and exploitable in breeding programs.

The reproductive stage of wheat development, encompassing gametogenesis, anthesis, fertilization, and early grain development, represents the period of maximum heat sensitivity. Brief heat episodes above 30°C during meiosis and microspore development damage pollen mother cells.

This disrupts tetrad separation, microspore development, and pollen maturation (Jäger *et al.*, 2008). Heat stress at the mid-uninucleate stage of microspore development, a particularly critical developmental checkpoint, has been shown to produce pollen grains stuck together, multinucleated pollen, and equal rather than asymmetric microspore division in sensitive wheat genotypes (Zahra *et al.*, 2021).

Heat stress dramatically reduces pollen viability. Cappelle Desprez (drought-sensitive) shows 65-84% reductions, while Plainsman V (heat-tolerant) shows only 2.6-3.9% reductions under the same conditions (Fábián *et al.*, 2019). Female reproductive structures are also affected: Fábián *et al.*, (2019) reported that heat and drought stress reduced stylodia length, degenerated transmitting tissues, and reduced the overall functionality of pistils, with damage to female reproductive organs accounting for approximately 34% of total generative fertility loss, while male organs accounted for approximately 66%.

The combined effect of reduced pollen viability, impaired stigma receptivity, and ovule abortion under heat stress results in dramatically reduced seed set. Under experimental combined heat and drought stress conditions at anthesis, spikelet fertility reductions of 70.97-90.91% have been documented across winter and spring wheat cultivars (Mahrookashani *et al.*, 2017). Such extreme fertility losses translate directly into catastrophic grain yield reductions, underscoring the critical importance of the reproductive stage as the primary target for improving heat stress tolerance.

Grain Filling, Starch, and Protein Accumulation

Grain filling, when endosperm accumulates starch and storage proteins, is highly sensitive to elevated temperatures. Heat stress during grain filling accelerates grain maturation while shortening its duration, resulting in smaller, lighter, and often shriveled grains (Shah & Paulsen, 2003). Schmidt *et al.*, (2020) evaluated 203 accessions using X-ray tomography. Combined stress severely deformed seeds with large cavities, indicating arrested endosperm development and incomplete starch deposition.

Starch biosynthesis is vulnerable because key enzymes (AGPase, GBSS, SS, SBE) are heat-labile with low thermostability (Lu *et al.*, 2019). Under combined heat and drought stress, Lu *et al.*, (2019) found that 11 of 23 genes encoding starch-biosynthesis enzymes were downregulated, with only ISA2 (isoamylase 2) upregulated. Combined heat and drought stress significantly decreased total starch content by approximately 25.78% and amylopectin content by approximately 31.83% relative to unstressed controls (Lu *et al.*, 2014).

Paradoxically, heat stress increases grain protein percentage despite lower overall grain mass. This occurs because starch accumulation declines more than protein accumulation. However, the increased protein percentage does not translate into improved end-use quality: heat stress alters the composition and polymer size distribution of storage proteins, reducing the proportion of very large glutenin polymers and the glutenin-to-gliadin ratio, which are the key determinants of dough rheological properties and bread-making quality (Balla *et al.*, 2011).

Source-Sink Relationships and Assimilate Partitioning

Heat stress disrupts source-sink balance by reducing photosynthetic supply (source limitation) and impairing grain capacity to receive assimilates (sink limitation). The source-sink relationship governs the partitioning of fixed carbon between vegetative storage tissues and the grain, and its disruption under heat stress is a primary driver of reduced harvest index and grain yield (Akter & Islam, 2017). Heat stress reduces photosynthesis and accelerates leaf senescence, decreasing sucrose production in flag leaves. Simultaneously, it reduces

endosperm enzyme activity, limiting the sink's capacity to convert and accumulate assimilates.

The mobilization of stem-reserve carbohydrates and water-soluble carbohydrates (WSC) stored in internodes prior to anthesis becomes more important under heat-stress conditions, partially compensating for reduced flag-leaf photosynthesis during grain filling. Genotypes with high stem WSC and efficient remobilization maintain grain filling better under heat. Stem reserve capacity is thus an important breeding target (Tricker *et al.*, 2018). Heat stress also shortens the grain-filling period by accelerating the transition to physiological maturity, reducing the total time available for assimilate deposition and resulting in smaller, lighter grains even when the rate of grain filling is maintained.

Molecular Mechanisms of Heat Stress Tolerance

Heat Shock Proteins and the Chaperone Network

Heat shock proteins (HSPs) are the most evolutionarily conserved and extensively characterized components of the molecular heat stress response in wheat and other organisms. HSPs function as molecular chaperones that facilitate protein folding, prevent aggregation under stress, and assist refolding during recovery (Yadav *et al.*, 2022). In wheat, HSPs are classified into five major families based on molecular weight: HSP110, HSP90, HSP70, HSP60, and small HSPs (sHSPs, typically 15-30 kDa), each with distinct subcellular localizations and functional specificities (Li *et al.*, 2022).

HSP70 is among the most studied and functionally important HSPs in wheat heat stress responses. The Blumenthal *et al.*, (1998) study documented increased accumulation of HSP70 under heat stress during grain filling in wheat, and subsequent research has confirmed that HSP70 proteins are critical for maintaining protein homeostasis, supporting protein translocation across membranes, and regulating the activity of heat shock transcription factors (HSFs) through direct protein-protein interactions. It maintains master HSF regulators such as HSF1 in an inactive state under non-stress conditions (Li & Howell, 2021). HSP101 (ClpB-class) disaggregates protein aggregates formed under acute heat stress. This function is essential for acquired thermotolerance. Grigorova *et al.*, (2011) studied two cultivars (drought-tolerant cv. Katya and susceptible Sadovo). Combined stress induced higher HSP

expression than either stress alone. Immunoblotting confirmed that high-molecular-weight HSPs (>100 kDa) showed the greatest expression under combined stress. Katya showed higher expression than susceptible cultivars, suggesting HSPs as stress resistance markers. Rampino *et al.*, (2012) demonstrated through RT-PCR analysis that TdHSP101 expression in durum wheat begins to increase at 34°C (Heat Stress 1 condition) and reaches its maximum at 42°C (heat stress 3), while TdHSP17.6 (a small HSP) shows a similar but slightly delayed induction profile.

Small HSPs (sHSPs) are particularly abundant in plant heat stress responses, with wheat possessing numerous members distributed across the cytoplasm, chloroplasts, mitochondria, endoplasmic reticulum, and nucleus. The chloroplastic sHSP26 in wheat has been specifically implicated in protecting the photosynthetic apparatus from heat damage and maintaining seed maturation and germination capacity under elevated temperatures (Chauhan *et al.*, 2012; Li *et al.*, 2022). The coordinate expression of multiple HSP families under heat stress conditions, spanning all major cellular compartments, reflects the requirement for comprehensive protein quality control systems across all sub-cellular environments when thermal stress is imposed.

Heat Shock Transcription Factors

The transcriptional induction of HSPs and other heat-responsive genes is orchestrated primarily by heat shock transcription factors (HSFs). Which constitute a large gene family in plants with 21 members in Arabidopsis and substantially more in the hexaploid wheat genome (Guo *et al.*, 2016). Plant HSFs are classified into three classes (HSFA, HSFb, HSFC) based on the architecture of their oligomerization domains. HSFA acts as a transcriptional activator; HSFb acts as a repressor (Feng *et al.*, 2025).

HSFA1 proteins occupy the apex of the HSF regulatory hierarchy and function as master activators of the heat stress response. Under normal conditions, HSFA1 is bound to HSP70/HSP90 chaperones. Heat stress releases these chaperones, allowing HSFA1 to trimerize, enter the nucleus, and bind HSEs in the promoters of target genes (Feng *et al.*, 2025). In wheat, TaHSFA2-10 overexpression in transgenic Arabidopsis has been shown to enhance thermotolerance by upregulating multiple AtHSPs, and TaHsfC2a-B overexpression upregulates HSP genes in leaves and during grain filling under water

stress (Zahra *et al.*, 2021). These findings demonstrate that manipulating wheat HSF genes represents a viable strategy for engineering improved thermotolerance.

DREB2A links heat and drought response pathways by regulating HSFA3 transcription. This creates a bridge between drought-responsive genes and HSP genes (Guo *et al.*, 2016). This regulatory crosstalk helps explain why combined heat and drought stress elicits a qualitatively distinct transcriptional response compared to either stressor applied individually. Morran *et al.*, (2011), suggested that the combined induction of DREB and heat shock factors could improve wheat tolerance under combined heat and drought stress conditions.

Gene Expression Under Combined Heat and Drought Stress

Rampino *et al.*, (2012) used cDNA-AFLP to analyze durum wheat flag leaves. From 2,000 detectable fragments, they identified 380 stress-responsive genes, of which 242 were upregulated. Combined stress uniquely upregulated 90 genes not induced by individual stresses. This confirms combined stress elicits a distinct response. Among the 37 novel durum wheat genes identified, those induced specifically by combined stress included genes encoding transcription factors (Td2ITG3, Td3ITG3), ABC transporters (Td3ITM2, Td15ITM6), receptor protein kinases (Td1ITF1), and a chaperone homologous to t-complex protein 1 theta chain (Td4TF1).

ABC transporter genes upregulated by combined stress are significant because they regulate ion balance and protect cells under heat stress (Li *et al.*, 2011; Rampino *et al.*, 2012). The upregulation of receptor protein kinase genes (Td1ITF1, Td6TM1) under combined stress conditions is consistent with a role in activating cellular defense and adaptation responses to environmental perturbation (Lehti-Shiu *et al.*, 2009). Importantly, Rampino *et al.*, (2012) also identified 8 cDNA sequences showing no significant similarity to annotated sequences in any public database, representing entirely novel genes whose functions in combined stress tolerance in wheat remain to be characterized.

Antioxidant Defense Systems

Antioxidant enzyme systems mitigate heat stress by scavenging ROS in chloroplasts, mitochondria, and cytoplasm. The primary antioxidant enzymes in wheat include superoxide dismutase (SOD), which catalyzes the

dismutation of superoxide radicals to H₂O₂ and O₂; ascorbate peroxidase (APX), which reduces H₂O₂ using ascorbate as the electron donor in the ascorbate-glutathione cycle; catalase (CAT), which decomposes H₂O₂ to water and oxygen; and guaiacol peroxidase (GPX), which also scavenges H₂O₂ (Kumar *et al.*, 2023).

Heat-tolerant genotypes show higher antioxidant enzyme activity and stress-induced upregulation. This prevents damaging ROS accumulation (Kumar *et al.*, 2023). Overexpression of SOD and APX genes has been documented as a key mechanism of enhanced antioxidative defense in heat-tolerant genotypes (Kumar *et al.*, 2023). Non-enzymatic antioxidants including proline, glycine betaine, and various compatible solutes also contribute substantially to thermotolerance by directly scavenging ROS, stabilizing cell membranes, and maintaining protein structure under heat stress (Yadav *et al.*, 2022). Proline, in particular, has attracted attention as both an osmoprotectant and a ROS scavenger, and as a signaling molecule influencing redox homeostasis; heat-tolerant wheat genotypes typically exhibit moderately elevated proline accumulation under stress compared to susceptible genotypes (Kumar *et al.*, 2023).

Osmolyte Accumulation and Osmoprotection

Osmolyte accumulation is a critical strategy for maintaining cellular function under combined heat and drought stress. The principal osmolytes documented in heat-stressed wheat include proline, glycine betaine, soluble sugars (sucrose, fructose, glucose, trehalose), and mannitol (Nyaupane *et al.*, 2024; Qaseem *et al.*, 2019). Osmolytes function through multiple mechanisms: lowering water potential, stabilizing proteins, scavenging ROS, and serving as mobilizable reserves during recovery.

Proline is among the most extensively studied osmolytes in heat-stressed plants. Its accumulation in wheat under combined heat and drought stress is regulated at the transcriptional level through the differential expression of proline biosynthesis (P5CS) and degradation (proline dehydrogenase) genes, with the balance of cytosolic synthesis and mitochondrial breakdown determining net cellular proline concentration (Nyaupane *et al.*, 2024). Proline acts as a redox buffer maintaining cellular antioxidant capacity. Heat-tolerant genotypes show higher proline, making it a useful screening marker (Kumar *et al.*, 2023). Glycine betaine, produced from

choline through two enzymatic steps, protects biological membranes from ROS-mediated damage by improving tissue water status and stabilizing PSII under high-temperature conditions (Wang *et al.*, 2010).

Hormone Signaling in Heat Stress Response

Phytohormones play pivotal regulatory roles in coordinating wheat responses to heat stress, integrating stress-perception signals with downstream physiological and gene-expression responses. Abscisic acid (ABA), classically associated with drought responses through its role in stomatal closure, also plays an important role in heat stress signaling by activating sucrose transporter and sucrose metabolism genes that are critical for maintaining assimilate transport to grains under heat stress (Li *et al.*, 2022). Cytokinins (CTKs) play a particularly important role in delaying leaf senescence under heat stress and maintaining the stay-green phenotype, with CTK signaling protecting the photosynthetic apparatus from heat-induced degradation and promoting grain filling by maintaining the sink strength of developing endosperm (Li *et al.*, 2022). Brassinosteroids (BRs) enhance thermotolerance by upregulating the ascorbate-glutathione cycle and the expression of antioxidant defense genes (Li *et al.*, 2022).

Combined Heat and Drought Stress in Wheat

Why Combined Stress is Not the Sum of its Parts

Yashavanthakumar *et al.*, (2021) studied 25 genotypes in India. Some maintained 68% yield under combined stress, while susceptible genotypes lost >70%. Their study highlighted that phenological traits such as days to heading and physiological maturity, along with canopy temperature depression, were the most discriminating parameters for identifying combined stress-tolerant genotypes. Heat and drought stress rarely occur independently in fields. Heat increases evaporative demand; drought closes stomata, reducing cooling. This creates a feedback loop intensifying heat damage (Craufurd *et al.*, 2013). This feedback between stomatal closure and canopy temperature represents a fundamental physiological mechanism through which drought exacerbates heat stress and vice versa. Furthermore, the magnitude of combined stress effects varies substantially across genotypes due to genotype-by-environment interactions; analysis of wheat genotypes under combined heat and drought stress revealed that some

genotypes maintained up to 68% of yield while susceptible genotypes lost over 70%, highlighting the importance of multi-environment evaluation for identifying stable, stress-tolerant germplasm (Kumari *et al.*, 2025b)

Rampino *et al.*, (2012) showed that combined stress elicits a distinct response. Combined stress affected 224 genes, versus 129 for heat alone and 27 for drought alone. The much larger transcriptional perturbation under combined stress reflects a qualitatively different stress-response program, with the specific activation of a pool of genes not induced by either stress alone. This finding aligns with earlier work on Arabidopsis and tobacco demonstrating that combined stress responses engage distinct regulatory networks from single stress responses (Rizhsky *et al.*, 2002, 2004).

Effects on Reproductive Development and Grain Yield

Zahra *et al.*, (2021) documented the impacts of H+D stress on grain development. During gametogenesis, it causes arrested cell division, multinucleated pollen, and reduced viability. Fábíán *et al.*, (2019), as reviewed by Zahra *et al.*, (2021), reported that H+D stress decreased pollen cells in apical anthers by up to 81% and in basal anthers by up to 63%, and reduced the length of stylodia in the drought-sensitive variety Cappelle Desprez but not in the tolerant variety Plainsman V.

The consequences for grain yield are dramatic and well-documented across multiple experimental systems and environments. As shown in Table 2, grain yield reductions under H+D stress have ranged from approximately 28.4% to 93.3% across diverse wheat types, experimental conditions, and stress timings (Zahra *et al.*, 2021). Winter wheat varieties consistently show greater susceptibility than spring wheat types under controlled H+D stress conditions imposed at anthesis. Post-anthesis H+D stress is more detrimental than stress at anthesis, but does not affect grain number. Its primary effect is on individual grain weight (Pradhan *et al.*, 2012).

Contrasting Effects of Heat versus Drought on Grain Quality

A particularly important and practically relevant finding from studies on wheat quality under abiotic stress is that heat and drought have contrasting, and in some cases

opposing, effects on dough rheological properties and bread-making quality (Li *et al.*, 2013a). Li *et al.*, (2013a) studied 15 cultivars under control, drought, and heat conditions. Both stresses increased protein but had opposite effects on dough rheology.

Drought stress (E2) increased alveograph tenacity (P), decreased extensibility (L), and increased the P/L ratio, indicating stronger but less extensible dough, along with increased gluten strength parameters (W, LARC, SIG) and decreased loaf volume (Li *et al.*, 2013a). In contrast, heat stress (E3) decreased tenacity (P), increased extensibility (L), decreased the P/L ratio, and increased loaf volume, indicating a slight weakening of gluten strength but an improvement in dough extensibility (Li *et al.*, 2013a). Drought increases large glutenin polymers (strengthening gluten), while heat decreases them (weakening gluten) by altering the glutenin-to-gliadin ratio (Blumenthal *et al.*, 1995; Flagella *et al.*, 2010; Li *et al.*, 2013a).

Li *et al.*, (2013b) found similar contrasting patterns in durum wheat: LARC and mixograph peak time (MPT) increased significantly under drought stress but decreased significantly under heat stress, consistent with drought enhancing and heat stress weakening gluten strength. These findings have important practical implications for wheat quality breeding: cultivars selected under optimal or drought-stress conditions may not maintain their quality advantage under heat stress conditions, and vice versa. Li *et al.*, (2013a) specifically recommended that screening for wheat quality stability should be conducted under both favorable and abiotic stress conditions to identify genotypes with reliable quality performance across environments.

Starch Biosynthesis Pathway Under Combined Stress

The pathway of starch biosynthesis in the wheat endosperm is particularly sensitive to combined H+D stress, with multiple points of vulnerability within the sucrose-to-starch conversion cascade (Zahra *et al.*, 2021). Under H+D stress, sucrose arriving at the grain sink from phloem loading must be converted through a series of enzymatic reactions involving sucrose synthase, ADP-glucose pyrophosphorylase (AGPase), and various starch synthases to produce amylose and amylopectin that fill the starch granules of the endosperm. Lu *et al.*, (2019) demonstrated that H+D stress significantly reduced the activities of all key starch biosynthesis enzymes and

downregulated the expression of 11 of 23 genes encoding these enzymes, with the only gene showing upregulation under H+D being ISA2 (isoamylase 2). The peak starch accumulation rate under H+D stress occurred at 14 days after anthesis, compared to 18 days in unstressed controls, reflecting the accelerated but truncated grain-filling trajectory characteristic of heat-stressed wheat.

Breeding Strategies for Heat Stress Tolerance

Heterosis (hybrid vigor) is one approach to achieving rapid gains in heat- and drought-stress tolerance and yield potential. F₁ hybrids in wheat often display significantly improved performance compared to parental lines, with multiple crosses demonstrating economic heterosis values of 13-19% for grain yield under diverse environmental conditions (Kumari *et al.*, 2025d). These performance gains, combined with desirable component traits such as higher harvest index, biological yield, and stable grain quality, make heterotic crosses valuable for both commercial cultivation and as sources of favorable alleles in breeding programs

Physiological Traits as Breeding Targets

The development of heat-tolerant wheat cultivars requires the identification of reliable, heritable, and measurable physiological traits that are causally associated with yield maintenance under heat stress. Combining ability analysis in wheat breeding provides insights into the genetic architecture of these traits by partitioning phenotypic variation into general combining ability (GCA, reflecting additive gene action) and specific combining ability (SCA, reflecting non-additive gene action), enabling identification of superior parental lines and promising hybrid combinations (Kumari *et al.*, 2025c). Several such traits have been identified through decades of research and represent priority targets for phenotypic selection in breeding programs (Yadav *et al.*, 2022). Canopy temperature depression (CTD), the difference between canopy temperature and ambient air temperature, is among the most widely used and validated indirect selection criteria for heat tolerance in wheat, reflecting the ability of the crop to maintain high transpiration rates that keep canopy temperatures below ambient through evaporative cooling (Pinto & Reynolds, 2015).

The stay-green trait, the ability to maintain green leaf area and photosynthetic activity during the grain-filling period, is positively associated with grain yield under

both drought and H+D stress in both durum and bread wheat (Foulkes *et al.*, 2007; Gupta *et al.*, 2012). The stay-green phenotype maintains carbon assimilation and the supply of assimilates to developing grains during periods of elevated temperature and can be selected using normalized difference vegetation index (NDVI) measurements in the field. Chlorophyll fluorescence parameters, membrane stability index (MSI), pollen viability assays, and grain-filling duration measurements represent additional physiological screening tools that can be efficiently deployed in large breeding populations.

Li *et al.*, (2013a, 2013b) demonstrated that rapid small-scale quality tests, specifically the swelling index of glutenin (SIG) and lactic acid retention capacity (LARC), are reliable screening parameters for predicting gluten strength under both favorable and stress conditions. In their field study, SIG showed the highest correlation with alveograph W ($r = 0.90$) and LARC ($r = 0.88$) under non-stress conditions, and both parameters showed differential responses under drought versus heat stress that tracked well with the more comprehensive quality measurements, making them valuable tools for quality screening in early-generation breeding materials.

The recommendation by Li *et al.*, (2013a) to evaluate wheat quality under both optimal and abiotic stress conditions is particularly important given the contrasting effects of drought and heat on dough rheological properties.

Quantitative Trait Loci and Marker-Assisted Selection

Quantitative trait loci (QTL) analysis identifies genomic regions associated with heat and drought tolerance. This enables marker-assisted selection (MAS) in breeding programs. Molecular markers such as SSR (Simple Sequence Repeats) provide a complementary approach to QTL mapping by directly assessing genetic diversity in wheat germplasm, enabling the identification of genetically diverse parental lines for strategic breeding programs (Kumari *et al.*, 2025a) Zahra *et al.*, (2021) compiled a comprehensive catalog of QTL identified for heat and drought tolerance in wheat, including loci on chromosomes 1B, 2B, 3B, 4A, 5B, 6A, 6B, 6D, 7A, 7B, and several others associated with traits including grain yield, thousand-grain weight, canopy temperature, chlorophyll content (SPAD), days to maturity, and spikelet compactness (Table 4).

A key QTL on chromosome 2B controls cool canopies and efficient water extraction. This maintains transpirational cooling under limited soil water (Pinto & Reynolds, 2015). Acuña-Galindo *et al.*, (2015) found 43 meta-QTL co-localizing under both stresses. Also, 137 SNP markers from candidate genes provide a rich MAS resource. Tahmasebi *et al.*, (2016) found a large-effect QTL on chromosome 4A explaining 19.6% of H+D yield variation. This region controls multiple traits and is high-priority for MAS.

Genomic Selection

Genomic selection (GS) uses genome-wide markers to predict breeding value without explicit QTL identification. It complements traditional MAS for heat tolerance. The first application of GS in wheat was reported by CIMMYT in 2009, and the technology has since been validated for yield-related traits, disease resistance, and abiotic stress tolerance across multiple genetic backgrounds and environments (Yadav *et al.*, 2022). GS suits heat tolerance because many small-effect loci control the trait. Prediction accuracy increases with larger training populations and higher marker density. Combined with combining ability assessments, genomic selection can efficiently identify crosses with high specific combining ability effects for heat tolerance and related traits, thereby accelerating the development of high-performing hybrids (Kumari *et al.*, 2025c).

Wild Relatives and Landraces as Genetic Resources

Wild relatives of cultivated wheat represent invaluable reservoirs of genetic diversity for heat and drought stress tolerance traits that have been lost or reduced through the genetic bottlenecks associated with domestication and intensive breeding for high yield under favorable conditions. Zaharieva *et al.*, (2001) identified tolerance potential for H+D stress among 157 accessions of *Aegilops geniculata* and recommended its use in wide hybridization programs and trait-specific introgression into cultivated wheat (Zahra *et al.*, 2021).

Wild emmer wheat (*Triticum turgidum* var. *dicoccoides*) has been identified as a valuable source of genes to enhance wheat resilience to heat stress, with inherent diversity in agronomic, physiological, and yield-related characteristics associated with thermotolerance (Peng *et al.*, 2013).

CIMMYT has developed a suite of H+D stress-tolerant wheat genotypes (LM02, LM13, LM23, LM41, LM44, LM71, LM73, and LM75) with high grain protein content and yield potential under combined stress conditions, which serve as valuable donor parents and reference materials for international heat stress tolerance breeding programs (Thungo *et al.*, 2020). These stress-tolerant genotypes and landraces can be strategically combined through controlled hybridization to generate F₁ hybrids that combine favorable traits from both parents, and promising hybrid combinations should be evaluated under both favorable and combined heat-drought stress conditions to assess economic heterosis, genetic stability across environments, and grain quality parameters (Kumari *et al.*, 2025d). Aberkane *et al.*, (2020) developed 77 lines through backcrossing of Haurani durum varieties and Cham5 with *Ae* accessions. *speltoides*, *T. uratu*, *T. dicoccoides*, and *T. aegilopoides* to evaluate H+D stress tolerance, concluding that gene introgression from wild relatives significantly enhances the resilience of wheat to simultaneous stresses.

Transgenic Approaches

Genetic transformation of wheat with stress-tolerance genes has been explored as a strategy to improve thermotolerance beyond what is achievable through conventional breeding. Wang *et al.*, (2010) studied transgenic wheat over-accumulating glycine betaine. GB modulated osmotic adjustment and antioxidant systems, showing shared protective mechanisms. The transgenic expression of the Td4TF1 chaperone gene, isolated from adult durum wheat plants responding to H+D stress, has been proposed as a strategy to improve wheat H+D tolerance (Rakszegi *et al.*, 2014). Overexpression of TaHsfC2a-B has also been proposed as a valuable transgenic approach, given its role in upregulating HSP genes during grain filling under water stress conditions.

CRISPR-Based Genome Editing

CRISPR/Cas9 enables precise modification of heat-responsive genes. Editing heat shock factors like HsfA1b shows promise for enhancing thermotolerance. Functional studies have demonstrated the important role of HSF1b in regulating heat stress responses, while recent reviews highlight the growing potential of CRISPR/Cas systems for improving abiotic stress tolerance in wheat (Tian *et al.*, 2019; Elsharawy and Refat, 2023). CRISPR enables editing of heat shock

factors, transcription factors, antioxidant genes, osmolyte genes, and starch biosynthesis genes. This provides a toolkit for improved thermotolerance (Saeed, 2025; Qu *et al.*, 2026). CRISPR editing of endogenous genes may face fewer regulatory barriers than transgenes. This could accelerate deployment of edited varieties. Critical CRISPR targets for improving heat tolerance in wheat include HSFA1 family members, DREB2A and its targets, AGPase isoforms that regulate thermostability of starch biosynthesis, and genes encoding key antioxidant enzymes.

Agronomic Management Strategies for Heat Stress Mitigation

Sowing Date and Crop Scheduling

Optimizing sowing date is a simple, widely applicable strategy. Early sowing ensures anthesis and grain filling occur during cooler periods (Nyaupane *et al.*, 2024; Zahra *et al.*, 2021). In South Asia, early sowing completes grain filling before extreme heat. In other regions, delayed sowing may be appropriate. Chen *et al.*, (2020), found that the optimal flowering period in Western Australia had an opening date approximately 6 days earlier under wet conditions compared to dry conditions, highlighting the interaction between sowing date, soil moisture, and thermal stress avoidance.

Irrigation Management

Adequate soil water during critical stages reduces drought stress and supports transpirational cooling. This buffers against heat damage (Zahra *et al.*, 2021). Subsurface drip irrigation, which delivers water directly to the root zone and minimizes surface evaporation losses, has been identified as a particularly efficient irrigation approach for minimizing combined H+D stress damage under water-scarce conditions (AL-Busaidi *et al.*, 2011). Optimal irrigation maintains stomatal conductance for CO₂ assimilation and cooling without inducing water deficit.

Mulching and Soil Temperature Management

Mulching reduces soil temperature, conserves moisture, and suppresses weeds. All of these benefit water availability (Kader *et al.*, 2017). Li *et al.*, (2013a&b) found that plastic sheet mulch was more effective than wheat straw mulch in reducing evaporative loss from the

soil surface. Plastic film mulching in combination with ridge-furrow sowing patterns, which maximize rainfall capture and soil temperature regulation in rainfed areas, has been shown to improve soil water content, reduce temperature fluctuations in the crop root zone, and increase grain yield under H+D stress conditions in semi-arid environments (Li *et al.*, 2013a&b).

Nutrient Management

Targeted application of macro- and micronutrients can meaningfully enhance wheat tolerance to heat stress by supporting key metabolic and physiological processes impaired by high temperatures. Potassium (K) and calcium (Ca) supplementation modulates stomatal opening and closing, contributing to improved canopy temperature control under heat stress (Waraich *et al.*, 2012). Nitrogen (N) and zinc (Zn) application together increased leaf area, crop growth rate, biomass, and grain yield of wheat under combined heat and drought stress in late-planted conditions (Kibe *et al.*, 2006). Magnesium (Mg) application supports chlorophyll synthesis and photosynthetic function, helping to maintain photosynthetic capacity under heat-stressed conditions. Selenium (Se) and manganese (Mn) applications have also been associated with improved antioxidant enzyme activity and reduced oxidative damage under heat stress conditions (Waraich *et al.*, 2012).

Seed Priming and Biostimulant Applications

Seed priming, the controlled hydration of seeds to initiate pre-germinative metabolic processes before re-drying and sowing has been shown to enhance heat stress tolerance by improving seedling establishment, accelerating early crop development, and improving the antioxidant preparedness of germinating seedlings (Nyaupane *et al.*, 2024). Foliar application of plant growth-promoting biostimulants derived from allelopathic plant extracts has demonstrated promising results for alleviating H+D stress impacts in wheat. Farooq *et al.*, (2017), reported that foliar sprays of sorghum, brassica, sunflower, or moringa water extracts enhanced gas exchange parameters, total soluble phenolics, chlorophyll content, 1,000-grain weight, and grain yield under combined terminal heat and drought stress. Endophytic fungal inoculation represents another innovative management approach: Hubbard *et al.*, (2014) found that the endophytic fungal strain SMCD 2206 improved H+D stress tolerance in wheat compared to

other endophytic strains, with some beneficial effects potentially persisting into the subsequent plant generation, although further validation is required.

Biochar Application

Biochar is a stable carbonaceous material produced by pyrolysis of organic matter has gained significant research attention as a soil amendment for improving water retention, soil structure, and thermal buffering capacity in heat and drought-prone environments. Zhang *et al.*, (2020), demonstrated that biochar addition improved root traits under drought stress, while Ding *et al.*, (2019) found that optimal biochar concentration improved water and heat resistance and increased the effectiveness of border irrigation. The porous structure of biochar enhances soil water-holding capacity, improving plant access to water during drought periods and supporting the transpiration-based canopy cooling that protects wheat from heat damage.

Genotype × Environment Interactions and Quality Stability

Genetic (G), environmental (E), and interaction effects all significantly influence heat tolerance and grain quality in wheat (Li *et al.*, 2013a, 2013b; Zahra *et al.*, 2021). Li *et al.*, (2013a) analyzed 15 cultivars across six environments. G, E, and G×E all significantly affected every quality parameter ($p < 0.0001$). The G versus E contribution varied by trait. Environment dominated grain yield (78%) and test weight (56%), reflecting sensitivity to growing conditions. In contrast, most gluten quality-related traits, including mixograph peak time (MPT at 89.1% G), alveograph extensibility (L at 86.2% G), and water retention capacity parameters (AWRC at 90.4% G, WRC at 93.1% G) were primarily controlled by genotype, indicating strong genetic determination of these processing quality traits (Li *et al.*, 2013a). This pattern was replicated in durum wheat, where Li *et al.*, (2013b) found that flour yellowness (87% G), swelling index of glutenin (53% G), and mixograph peak time (54% G) were primarily genotype-determined, while yield (90% E), thousand-kernel weight (73% E), and grain protein content (60% E) were predominantly environmentally determined.

These results show quality traits are heritable and improvable through breeding. However, G×E interactions require multi-environment testing, including

stress conditions, to assess genotype stability. Li *et al.*, (2013a) explicitly recommended selecting for wheat quality under both favorable and abiotic stress conditions to identify genotypes with quality stability across environments, a recommendation that is particularly important in the context of increasing climate variability.

Conclusions and Future Research Directions

Heat stress represents one of the most pressing and complex challenges to sustainable global wheat production, and its severity and frequency will only increase as anthropogenic climate change continues to reshape the thermal regimes experienced by wheat crops in major production regions. This review has synthesized current understanding of heat stress impacts across physiological, molecular, grain quality, and agronomic dimensions, revealing a multifaceted challenge that requires equally multifaceted and integrated solutions.

Several key conclusions emerge from this synthesis. First, the reproductive stage, particularly meiosis, anthesis, and early grain filling is the most heat-sensitive phase of wheat development, with temperatures exceeding 30-32°C capable of causing severe and irreversible damage to pollen viability, fertilization efficiency, and endosperm development. Protecting wheat fertility and grain set under heat stress must therefore be a central priority for both breeding and management interventions.

Second, combined heat and drought stress, the condition most frequently encountered in agricultural environments, elicits a distinct and often more severe physiological and molecular response than either stress applied individually. Consequently, breeding programs should specifically target combined stress tolerance, while management strategies must simultaneously address both thermal and water-deficit stresses.

Analysis of genotypic stability across multiple environments reveals differential responses of wheat genotypes to environmental variation, with parent lines such as HD 3086 demonstrating superior adaptation to unfavorable (heat-drought) conditions while others like MP 1203 perform optimally under favorable conditions (Kumari *et al.*, 2025b). This pattern underscores the importance of environment-specific cultivar selection or the development of broadly adapted varieties stable across diverse stresses

Table.1 Summary of Heat Stress Effects on Physiological Parameters in Wheat.

Physiological Parameter	Effect of Heat Stress	% Change	Key Reference
Photosynthesis rate	Decreased due to PSII disruption and Rubisco inactivation.	-15 to -40%	Yadav <i>et al.</i> , (2022)
Chlorophyll content	Reduced by chlorophyllase activation and ROS damage.	-13 to -35%	Nyaupane <i>et al.</i> , (2024)
Pollen viability (sensitive cv.)	Severely reduced; microspore development arrested.	-65 to -84%	Fábíán <i>et al.</i> , (2019)
Spikelet fertility	Reduced by pollen sterility and ovule abortion.	-71 to -91%	Mahrookashani <i>et al.</i> , (2017)
Total starch content	Reduced by heat inactivation of starch synthases.	-21 to -26%	Lu <i>et al.</i> , (2019)
Thousand-kernel weight	Reduced by shortened grain-filling duration.	-10 to -16%	Blumenthal <i>et al.</i> , (1995) - Stone & Nicolas (1995)
Grain protein content	Concentration effect: increases despite lower yield.	+9 to +65%	Balla <i>et al.</i> , (2011)
Glutenin-to-gliadin ratio	Decreased: weakens dough rheological properties.	Decreased	Li <i>et al.</i> , (2013a)
Membrane stability index	Reduced; tolerated genotypes show less loss.	Decreased	Yadav <i>et al.</i> , (2022)
Antioxidant enzymes (SOD, APX)	Increased in tolerant genotypes to scavenge ROS.	Increased	Kumar <i>et al.</i> , (2023)
Grain yield	Severely reduced under combined heat + drought.	-33 to -94%	Balla <i>et al.</i> , (2011), Mahrookashani <i>et al.</i> , (2017), Zahra <i>et al.</i> , (2021)

Table.2 Key Genes and Molecular Mechanisms Involved in Heat Stress Tolerance in Wheat.

Gene/Protein	Family	Function in Heat Tolerance	Expression Pattern	Reference
TdHSP101	HSP100/ClpB	Disaggregates heat-denatured protein aggregates; acquired thermotolerance.	Strongly induced at 34-42°C; basal expression at control temp.	Rampino <i>et al.</i> , (2012)
TdHSP17.6	Small HSP	Molecular chaperone; protects proteins from aggregation under heat.	Induced at 34°C; high expression at 40-42°C.	Rampino <i>et al.</i> , (2012)
TaHSFA2-10	HSF class A	Master transcriptional activator; upregulates downstream HSPs in wheat.	Heat-inducible; overexpression improves thermotolerance.	Zahra <i>et al.</i> , (2021)
TaHsfC2a-B	HSF class C	Upregulates HSP genes in leaves and during grain filling under water stress.	Induced by heat and water deficit.	Zahra <i>et al.</i> , (2021)
DREB2A	AP2/ERF	Bridges heat and drought response; regulates HSFA3 transcription.	Induced by heat and drought; regulates HSE-containing promoters.	Guo <i>et al.</i> , (2016)

TdDHN15.3/15.1/9.6	Dehydrin (LEA)	Membrane protection; protein stabilization under dehydration.	Strongly induced by drought and combined stress.	Rampino <i>et al.</i> , (2012)
Td4TF1	Chaperone (CCT)	Homolog of t-complex protein 1 theta chain; protein folding under stress.	Upregulated by heat and combined heat-drought stress.	Rampino <i>et al.</i> , (2012); Zahra <i>et al.</i> , (2021)
Td3ITG3/Td2ITG3	Transcription factor	Novel wheat genes; key regulators of combined stress response.	Specifically upregulated by combined heat and drought stress.	Rampino <i>et al.</i> , (2012)
TdDRG1	Drought-related gene	Drought response; high basal expression; involved in stress signaling	Constitutively expressed; slightly induced by drought and combined stress.	Rampino <i>et al.</i> , (2012)
SOD, APX, CAT, POX	Antioxidant enzymes	ROS scavenging; preventing oxidative damage under heat stress	Higher activity in heat-tolerant vs. susceptible genotypes.	Kumar <i>et al.</i> , (2023)

Table.3 Impact of Combined Heat and Drought Stress on Wheat Grain Yield Across Multiple Studies.

Wheat Type	Variety	Stress Conditions	Stage	Yield Change ^a (%)	Reference
Winter wheat	Plainsman V	35/20°C day/night; 45% soil moisture.	12 days after heading	-75.9	Balla <i>et al.</i> , (2011)
Winter wheat	Batis	Glasshouse heat; 20-40% soil moisture.	Anthesis to maturity	-93.3	Mahrookashani <i>et al.</i> , (2017)
Spring wheat	Scirocco	Glasshouse heat; 20-40% soil moisture.	Anthesis to maturity	-83.3	Mahrookashani <i>et al.</i> , (2017)
Spring wheat	Inqlab-91	Late sowing; 40% ETo irrigation.	Throughout study	-71.5	Ali <i>et al.</i> , (2013)
Spring wheat	Vinjett	32/24°C; water withholding.	Heading to harvest	-59.6	Zhang <i>et al.</i> , (2013)
Spring wheat	Galaxy L7096	Late sown; 50% FC.	Throughout study	-32.57	Ihsan <i>et al.</i> , (2016)
Spring wheat	Mairaj-2008	4°C above normal; 35% WHC.	Booting to maturity	-28.4 to -45.7	Farooq <i>et al.</i> , (2017)
Spring wheat	Genotype 1	36/30°C; 30% FC.	After heading	-56.5	Qaseem <i>et al.</i> , (2019)
Spring wheat	Faisalabad-2008	50% FC in plastic tunnel.	Heading stage	-32.9	Sattar <i>et al.</i> , (2020)
Common wheat (15 cv.)	Multiple	Late planting (heat); limited irrigation (drought).	Grain filling	-25 to -45%	Li <i>et al.</i> , (2013a)
Durum wheat (9 cv.)	Multiple	Late planting (heat); limited irrigation (drought).	Grain filling	-24 to -54%	Li <i>et al.</i> , (2013b)

^adepending on stress intensity and developmental stage

Table.4 Selected QTL Identified for Heat and Drought Stress Tolerance in Wheat.

QTL Name	Trait	Chromosome	Wheat Population	Reference
QYLD.wPt-2052-1B-a	Grain yield (g m ⁻²)	1B	SeriM82 × Babax RIL	Tahmasebi <i>et al.</i> , (2016)
QGM2.aca/caa-3-1B	Grain per m ²	1B	SeriM82 × Babax RIL	Tahmasebi <i>et al.</i> , (2016)
QCTv.wPt-3465-1B-a	Canopy temperature (vegetative)	1B	Seri/Babax RIL	Pinto <i>et al.</i> , (2010)
QCTg.agc/cta-1B-a	Canopy temperature (grain filling)	1B	Seri/Babax RIL	Pinto <i>et al.</i> , (2010)
QGM.wPt-0021-3B-b	Grain number	3B	Seri/Babax RIL	Pinto <i>et al.</i> , (2010)
QGWTagg/cat-3-3Ba	Thousand-grain weight	3B	Seri/Babax RIL	Pinto <i>et al.</i> , (2010)
Q.Yld.aww-3D	Tiller number/yield	3D	RAC875/Kukri DH	Bennett <i>et al.</i> , (2012)
QTGW.acg/cta-3-4A	Thousand-grain weight	4A	SeriM82 × Babax RIL	Tahmasebi <i>et al.</i> , (2016)
QHT.gwm006a-4B-b	Plant height	4B	Seri/Babax RIL	Pinto <i>et al.</i> , (2010)
Qyld.csdh.7AL	Grain yield	7AL	Hexaploid wheat genome	Acuña-Galindo <i>et al.</i> , (2015)
QCTllg-6D.1 / QCTvg-6D.1	Canopy temperature	6D	Weebill 1	Liu <i>et al.</i> , (2019)
QSPAD.agc/cta-9-1B	Chlorophyll content	1B	SeriM82 × Babax RIL	Tahmasebi <i>et al.</i> , (2016)
QGWt.ara-3B.3	Grain weight/tiller	3B	Asian/African landraces	Schmidt <i>et al.</i> , (2020)
QGWt.ara-7B.6	Grain weight/tiller	7B	Asian/African landraces	Schmidt <i>et al.</i> , (2020)

Table.5 Summary of Agronomic Management Strategies for Heat Stress Mitigation in Wheat.

Strategy	Mechanism	Practical Benefit	Limitations	Reference
Optimized sowing date	Avoids anthesis coinciding with peak heat	Phenological escape from heat stress	Location and year-specific; requires local calibration	Nyaupane <i>et al.</i> , (2024)
Supplemental irrigation at anthesis	Supports evaporative cooling; prevents drought-heat synergy	Reduces canopy temperature; maintains grain number	Requires water availability; costly in water-scarce regions	Zahra <i>et al.</i> , (2021)
Plastic film mulching	Reduces soil evaporation; buffers soil temperature	Conserves moisture; improves yield under H+D stress	Environmental concerns over plastic waste	Kader <i>et al.</i> , (2017)
Nitrogen + zinc co-application	Supports leaf area and photosynthetic capacity	Improved biomass and yield under late-sown heat stress	Risk of N leaching under excess rainfall	Kibe <i>et al.</i> , (2006)
Potassium and	Modulates stomatal	Improved canopy	Requires soil-	Waraich <i>et al.</i> ,

calcium application	behavior; supports membrane stability	temperature regulation	specific calibration	(2012)
Seed priming (hydro/osmo-priming)	Pre-activates germination metabolism and antioxidant systems	Faster establishment; improved seedling stress tolerance	Complex management; storage issues after priming	Nyaupane <i>et al.</i> , (2024)
Foliar allelopathic extracts (moringa, sorghum)	Enhances antioxidant capacity and gas exchange	Improved chlorophyll, grain weight, and yield under H+D	Variable field-level efficacy; application timing critical	Farooq <i>et al.</i> , (2017, 2018)
Endophytic fungal inoculation	Enhances antioxidant systems; reduces ROS damage	Improved tolerance transmissible to next generation	Strain-specific results; needs scale-up research	Hubbard <i>et al.</i> , (2014)
Biochar soil amendment	Improves water-holding capacity; buffers soil temperature	Enhanced root growth; better water access under drought-heat	High initial cost; long-term effects require study	Zhang <i>et al.</i> , (2020)
Growing tolerant varieties	Genetic resistance to heat damage at molecular level	Among the most sustainable long-term approaches	Development takes years; adoption barriers in some regions	Zahra <i>et al.</i> , (2021)

Table.6 Variance Partitioning (% of Model Sum of Squares) for Grain Yield and Quality Traits in Common Wheat Across Six Treatment-Year Environments.

Trait	% Genotype (G)	% Environment (E)	% G × E	Primary Control
Grain yield	15.1	78.1	6.9	Environment
Test weight	32.0	55.6	12.4	Environment
Grain protein content	49.3	40.6	10.1	Genotype
Flour protein content	66.2	23.2	10.6	Genotype
SDS sedimentation volume	71.2	13.3	15.5	Genotype
Mixograph peak time	89.1	4.2	6.7	Genotype
Alveograph extensibility (L)	86.2	3.7	10.1	Genotype
Alveograph energy (W)	83.4	8.1	8.4	Genotype
Loaf volume (LV)	61.1	21.1	17.8	Genotype
Lactic acid retention capacity	74.4	11.6	14.1	Genotype
Swelling index of glutenin (SIG)	74.8	15.3	9.9	Genotype
Water retention capacity (WRC)	93.1	4.1	2.8	Genotype

Source: Li *et al.*, (2013a). Values represent percentage of total model sum of squares attributable to each variance source. All effects significant at $p < 0.0001$.

Third, heat and drought stress have contrasting and sometimes opposing effects on wheat grain quality parameters, particularly dough rheological properties. Drought stress tends to strengthen gluten by increasing the proportion of large glutenin polymers, while heat stress weakens gluten by reducing very large polymers and altering the glutenin-to-gliadin ratio. These differential effects mean that variety evaluations for quality must be conducted under both drought and heat stress conditions to ensure quality stability across the range of environments where the variety will be deployed.

Fourth, molecular mechanisms of heat tolerance including the HSP chaperone network, HSF transcription factors, antioxidant enzyme systems, and compatible solute accumulation are well-characterized enough to be exploited in biotechnology-based crop improvement, including transgenic overexpression of key tolerance genes and CRISPR-based editing of target loci. However, the translation of laboratory-identified tolerance mechanisms to field-level performance improvements remains a critical challenge that requires substantially more investment in field-based validation studies.

Looking forward, several research priorities stand out as particularly important. The development of high-throughput phenotyping platforms capable of characterizing reproductive-stage heat tolerance in large breeding populations including, pollen viability, stigma receptivity, and early seed set would dramatically accelerate the identification and selection of heat-tolerant wheat genotypes. Multi-omics integration approaches combining transcriptomics, proteomics, and metabolomics under combined H+D stress conditions will help identify novel regulatory hubs and biomarkers for stress tolerance that have not yet been identified through single-omics analyses. The development and deployment of genome-wide association studies (GWAS) and genomic selection models specifically trained on H+D stress tolerance phenotypes will improve the accuracy and efficiency of molecular breeding for this complex trait. Finally, participatory variety selection and adaptation trials conducted in farmers' fields across the full range of heat-stressed wheat production environments will be essential to ensure that laboratory and experiment station advances are translated into real-world productivity gains for the smallholder and commercial wheat farmers who depend on this crop for their livelihoods and food security.

Author Contributions

Manisha Kumari: Investigation, formal analysis, writing—original draft. Amit Godara: Validation, methodology, writing—reviewing.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical Approval Not applicable.

Consent to Participate Not applicable.

Consent to Publish Not applicable.

Conflict of Interest The authors declare no competing interests.

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