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# Adaptation Strategies to Heat Stress for Sustaining Wheat Crop Yield

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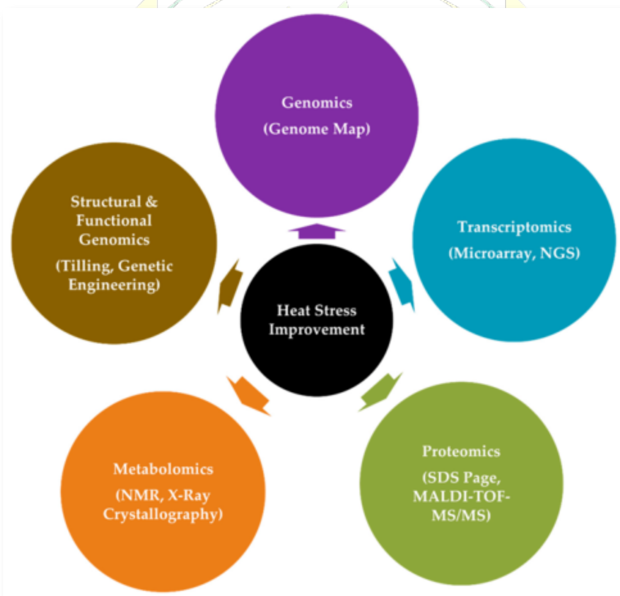
Rising temperatures under climate change increasingly expose wheat (*Triticum aestivum* L.) to heat stress (HS), causing severe yield and quality losses, particularly when stress coincides with reproductive and grain-filling stages. Wheat responds through a complex network of morphological, physiological, molecular, biochemical, epigenetic, and priming-mediated adaptations that collectively determine thermotolerance and yield stability. This review synthesizes current understanding of these mechanisms and highlights key traits and management options that can be exploited in breeding and agronomy to safeguard wheat productivity in heat-prone environments.




Wheat is the most widely grown rabi cereal and a major source of calories and protein for the global population, contributing nearly 20% of dietary protein [2,3]. Projections indicate that global wheat demand will rise by approximately 198 million tonnes by 2050, yet a large proportion of wheat-growing regions, particularly in low latitudes, already experience frequent heat stress during critical growth stages [2]. Crop modelling across multiple environments has shown yield reductions ranging from 1–28% for each 2 °C rise in temperature and 6–55% for a 4 °C increase [2,3]. Globally, wheat production is estimated to decline by around 6% per 1 °C rise in temperature [2,3]. In India, a 1 °C increase in mean temperature during March–April can reduce wheat yield by about 400 kg $ha^{-1}$, largely due to terminal heat stress during grain filling when temperatures exceed 31 °C [4,5].

Heat stress affects wheat growth, development, photosynthesis, hormonal balance, metabolism, water relations and reproductive success, mainly through excessive generation of reactive oxygen species (ROS) and stress hormones such as ethylene [1,4]. To survive and produce grain under high temperature, wheat relies on a hierarchy of adaptive mechanisms operating from the whole-plant to molecular and epigenetic levels. Understanding these adaptations is essential for designing climate-smart wheat production systems [1].

## Effects of Heat Stress on Wheat Growth, Yield and Quality:

### a. Vegetative stage

Heat stress at the vegetative stage primarily affects seed germination and early seedling establishment. Temperatures around 45 °C severely damage mitochondria in imbibing embryos, reduce ATP synthesis and oxygen uptake, and alter protein expression, resulting in poor seed vigor and weak plant stands [1,5]. Elevated temperatures (around 30/25 °C day/night) suppress biomass accumulation by restricting leaf development and productive tiller formation [1]. Although higher temperature increases leaf appearance and elongation rate, it shortens the elongation period, leading to reduced final leaf size, plant height and biomass [1,5].

Photosynthesis is one of the earliest and most heat-sensitive processes. High temperature disrupts Rubisco and Rubisco activase activity, damages thylakoid membranes and impairs photosystem II, reducing $CO_2$ fixation [1,4]. Increased photorespiration under high temperature further lowers net photosynthesis, while accelerated leaf senescence above 34 °C is associated with chlorophyll degradation and cellular dehydration [1,4].

### b. Reproductive Stage And Yield Formation

Heat stress during flowering and grain filling is far more damaging than during vegetative growth. A rise of just 1 °C during this period can cause severe yield losses [2,4]. Flowering and grain filling are optimal between 12 and 22 °C; heat stress during meiosis or anthesis disrupts pollen development, pollen tube growth and fertilization, causing floral abortion and reduced grain number [1,4]. Grain filling depends on both the rate and duration of dry matter accumulation, and even a 1–2 °C rise shortens grain-filling duration, reducing grain weight [1,4]. Short episodes of heat stress can reduce grain yield by up to about 23%, while reduced grain number also lowers harvest index [4,5].

### c. Grain Quality

Heat stress alters both starch and protein composition of wheat grains. Activities of ADP-glucose pyrophosphorylase and starch synthase decline under heat stress, causing up to one-third reduction in endosperm starch [1,4]. Heat stress increases amylose content and the amylose: amylopectin ratio, altering starch functionality [1]. Protein concentration and soluble sugars often increase due to smaller kernel size and altered nitrogen remobilization, but protein quality and bread-making properties may deteriorate, particularly when heat stress occurs early during grain filling [4,5].

## Morphological and Physiological Adaptation Strategies

### Morphological adaptations

Wheat exhibits several architectural modifications under heat stress that help sustain productivity. Rapid early seedling emergence and ground cover reduce soil evaporation and improve water availability for transpiration cooling [1,5]. Leaf rolling, thickening, and increased wax and hairs on leaves and stems reduce radiation load and heat absorption [1]. Flag leaf area and awn length are positively correlated with grain yield under heat stress because of their role in assimilate supply to grains [1,4]. Early-maturing genotypes escape terminal heat stress, while traits such as days to heading, maturity duration, plant height, effective tillers and biomass become important yield determinants under late-sown conditions [4,5].

### Physiological adaptations

Physiological tolerance is strongly associated with membrane stability, water relations and canopy cooling. Heat-tolerant genotypes maintain cell membrane integrity, reflected in lower electrolyte leakage and more stable osmotic potential [1,4]. Deep root systems and high transpiration capacity allow plants to access deeper soil moisture and maintain cooler canopies. Canopy temperature is negatively correlated with transpiration and grain yield, making it a valuable selection trait [1,5].

High-throughput tools such as infrared thermometers (canopy temperature), Green Seeker (NDVI), SPAD meters (chlorophyll) and porometers (stomatal conductance) facilitate screening for heat tolerance [1]. The stay-green trait is particularly important: tolerant genotypes retain chlorophyll longer, delay senescence and maintain photosynthesis, improving grain filling under heat stress [1,4]. Osmolytes such as proline, soluble sugars, glycine betaine and GABA stabilize proteins and membranes and improve redox balance [1,5].

## Molecular, Biochemical and Epigenetic Adaptations:

### Heat shock signalling

Heat stress disrupts membrane fluidity and ionic balance, triggering $Ca^{2+}$ influx, phosphatidic acid and $PIP_2$ signalling, and activation of MAPKs and calcium-dependent protein kinases [1]. These cascades activate heat shock transcription factors (HSFs), which induce heat shock proteins (HSPs) and other protective genes. Transcriptomic studies have identified numerous HS-responsive genes in wheat, including HSFs, HSPs and stress-related transcription factors. The transcription factor TaHsfA6f regulates multiple HSPs and enhances thermotolerance [1].

### Biochemical and Hormonal Regulation

Rubisco activase (Rca) is highly temperature sensitive; wheat expresses multiple isoforms, including a thermostable form (Rca1β) that is rapidly induced during heat stress [1]. Phytohormones such as abscisic acid (ABA), salicylic acid (SA) and cytokinins regulate stress responses. ABA controls stomatal closure and grain filling, SA modulates photosynthesis and HSP expression, and cytokinins promote stay-green and delay senescence [1,4].

Heat stress increases ROS production, necessitating efficient antioxidant systems. Enzymes such as superoxide dismutase, catalase, ascorbate peroxidase and glutathione reductase, together with non-enzymatic antioxidants, protect cellular structures from oxidative damage [1,5].

### Epigenetic Regulation And Stress Memory

DNA methylation, histone modifications and chromatin remodelling contribute to heat stress adaptation and stress memory. In wheat, several DNA methyltransferase genes and histone acetyltransferases (e.g., TaGCN5) regulate the expression of heatresponsive genes. These epigenetic changes enable plants and their progeny to remember previous heat exposure and respond more efficiently to subsequent stress [1].

## Heat Stress Priming and Yield Stability

Heat stress priming—exposure to mild heat stress—induces protective memory that enhances tolerance to later severe stress. Priming during early reproductive stages improves grain yield and photosynthesis under subsequent heat stress. Primed plants and their progeny show higher expression of HSPs and antioxidant genes due to epigenetic memory [1,5].

## Breeding and Management Perspectives

Breeding for heat tolerance should focus on early vigor, cooler canopy temperature, high NDVI and chlorophyll, deep roots, strong stay-green and osmolyte accumulation [1,4]. These traits can be integrated with molecular markers and genomic selection. Agronomic strategies such as adjusting sowing dates, selecting suitable maturity groups, providing irrigation for canopy cooling and optimizing nutrition to support antioxidant systems are critical for sustaining yields under heat stress [4,5].

## Conclusion

Heat stress is a major threat to wheat production under climate change. However, wheat possesses a wide range of adaptive mechanisms from morphology to epigenetics. Integrating physiological traits, molecular tools and agronomic practices offers a realistic pathway to sustaining wheat yield in heat-stressed environments.

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