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Review Article

Heat Stress Effects on Maize: A Comprehensive Review of Stage-Specific Effects and Climate-Resilient Strategies

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ABSTRACT

Heat stress, intensified by global climate change, has a serious adverse impact on maize (*Zea mays L.*) productivity through all developmental stages. This review synthesizes current knowledge on the physiological, biochemical, molecular, and genetic maize responses to elevated temperatures, focused on stage-specific vulnerabilities. Heat stress during flowering particularly anthesis and silking is identified as the most critical, leading to impaired pollen viability, disrupted floral synchrony, and reduced kernel set. During grain filling, elevated temperatures hasten senescence, hinder carbohydrate translocation, and diminish kernel weight and quality. On the molecular level, heat stress induces reactive oxygen species (ROS) accumulation, disrupts hormonal balance. This mechanism triggers heat shock protein (HSP) expression through transcription factors such as HSFs and DREB2A. Genetic studies reveals key heat-resilient genes, including ZmHSF01, ZmHSP17.9, and others involved in antioxidant defense, osmolyte biosynthesis, and reproductive stability. Climate models project up to 30% yield losses by 2050 if mitigation strategies are not adopted. Moreover, adaptation involve gene editing, molecular breeding, stress-resilient cultivars, and climate-smart agronomic practices. These are crucial for sustaining maize production in a warming world. This review focuses on the need for integrated genetic, physiological and management approaches to enhance maize thermotolerance and secure future food supplies.

Keywords: Maize Heat Stress, Stage-Specific Effects, Physiological Response, Biochemical Response, Molecular Mechanisms, Reproductive Development, Climate-Resilient Strategies.

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INTRODUCTION

Maize (*Zea mays L.*) ranks among the most vital cereal crops worldwide, with broad usage across the food, feed, and industrial sectors. However, due to climate challenges, the sustainability and productivity of maize are under unprecedented threat, particularly due to heat stress. Moreover, due to global warming and other climatic conditions, heat stress emerged as a major threat to the production of maize (Yu et al., 2024). The world is currently facing a decline in maize production due to the ever-growing impact of climate change. This is due to the increase of global temperature by 1 °C since industrialization. It has been reported that by the end of 21st century, a 2 °C increase in global temperature is expected (Zhao et al., 2017). Maize is a temperature-sensitive crop, especially during reproductive growth periods such as anthesis, silking, and kernel development. The stage of anthesis is so critical that even few days of heat stress during that period can reduce the yield by 50%.

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Moreover, with 1 °C rise in global temperature, maize production is expected to decline by 7.4%, which makes it to decrease by 14.8% with 2 °C expected rise in temperature till the end of this century (Ali, 2021). Maize is expected to show a greater decline in production, as compared to Wheat and Rice (Lobell, Schlenker, et al., 2011). This sensitivity is most extreme in tropical and subtropical areas, where temperatures tend to already be at or above the physiological limit. Heat stress, which refers to temperatures greater than the optimum value for the development of a plant, impacts maize development from germination to maturity. At germination and seedling stages, high temperatures slow down root and shoot development, which effect enzymatic processes, and reduces the rate of germination by disrupting the equilibrium of major phytohormones such as gibberellins and abscisic acid (Iloh et al., 2014; Rosmaina et al., 2021). In the early vegetative stage, heat stress could slow leaf growth and decrease net photosynthesis and thereby constrain total biomass accumulation. (Gonzalez et al., 2019). Extreme temperature affects pollen viability, anther dehiscence, and flowering synchrony, which results in shallow fertilization and kernel set reduction (Lohani et al., 2020; Zhang et al., 2018). Moreover, heat extends the anthesis-silking interval (ASI), resulting in out-of-synchrony male and female flower component development, significantly affecting grain.

Heat stress and post-anthesis heat damage, linked with retarded senescence of leaves, adversely affect maturation of grains and grain filling. Senescence of leaves is enhanced by elevated temperatures, preventing carbohydrate partitioning and photosynthate transport to developing kernels, which causes reduced kernel weight and poor grain quality (Abeledo et al., 2020; Li et al., 2020). Biochemically, heat stress leads to increased production of reactive oxygen species (ROS), such as superoxide radicals and hydrogen peroxide, which damage cellular membranes, proteins, and nucleic acids (Foyer & Shigeoka, 2011).

To manage with such oxidative damage, maize activates various defense mechanisms. Antioxidant enzymes like catalase (CAT), peroxidases (POD) and superoxide dismutase (SOD) mitigate ROS damage, while osmolytes such as glycine and betaine help stabilize proteins and membranes. Concurrently, hormone signaling pathways involving abscisic acid, ethylene, and salicylic acid adjust physiological responses to minimize damage and maintain homeostasis (Yang et al., 2021). At the molecular level, heat stress activates the expression of heat shock proteins (HSPs), which function as molecular chaperones to refold denatured proteins and prevent aggregation. Heat Shock transcription factors (HSFs), such as ZmHSF01 and ZmHSF05, play a crucial role in maize thermotolerance. Additionally, regulatory genes like ZmDREB2A and ZmbZIP60 plays vital role in stress signal transduction and transcription (Zhang et al., 2021). Progress in functional genomics, transcriptomics, and gene editing, particularly CRISPR/Cas9, enable the identification and functional validation of stress-responsive genes (Qin et al., 2023). Given the estimated rise in global temperatures and increasing incidence of extreme heat events, maize production faces an imminent risk of large-scale yield reductions. Stress indicates up to 30% decline in maize yield by 2050 if heat stress adaptation strategies will not implemented (Kang et al., 2025). To mitigate this challenge, integrated approaches are essential. These include the development of heat-resilient cultivars through marker-assisted selection, deployment of climate-smart agronomic practices, and policy-driven support for adaptive agriculture. This review article discusses the impact of climate change on maize production, stage-specific impact of heat stress on maize and proposes possible ways of increasing its thermo-tolerance.

The Impact of Climate Change on Global Maize Production: Threats and Predictions

Global threats and current impacts

A number of research studies have demonstrated that climate change affects maize productivity directly in several ways. When temperature increases, especially during development phases such as flowering and grain filling, physiological processes are compromised, thus lowering the crop yield (Vogel et al., 2019) . For example, Lobell, Bänziger, et al. (2011) hypothesized that for each 1°C increase in temperature, globally there would be a decrease of about 7.4% in maize yield, exhibiting maize vulnerability to heat stress. In some areas like sub-Saharan Africa, the impacts are more devastating. Waha et al. (2013) found that warmer temperatures and shifts in rainfall pattern are harmful to the production of maize. Droughts and heatwaves have also become more frequent than before, resulting in less water availability leading to crop failure.

After recent assessment, drought stress is currently one of the most extreme limiting factors of maize production in Europe and the whole world, with different regional. The impact of drought is different in different regions and it is unpredictable because every region has different agronomic and environmental factors (El-Sappah et al., 2022). Heat stress, drought, and changed precipitation all over the world have interfered with photosynthesis, growth, reproductive development, and overall decrease in grain yield (Ahmad et al., 2024).

It is estimated that if current climatic effects are not mitigated on time, then maize crop will face significant reduction in yield. For example, Webber et al. (2018) predicted that drought and heat stress could result in yield reductions of up to 30% in certain European crops by 2050. But this is not only limited to Europe and can be observed in Asia and North America as well. In these regions, increased temperatures and uncertain rainfall patterns are impacting the quality and quantity of maize.

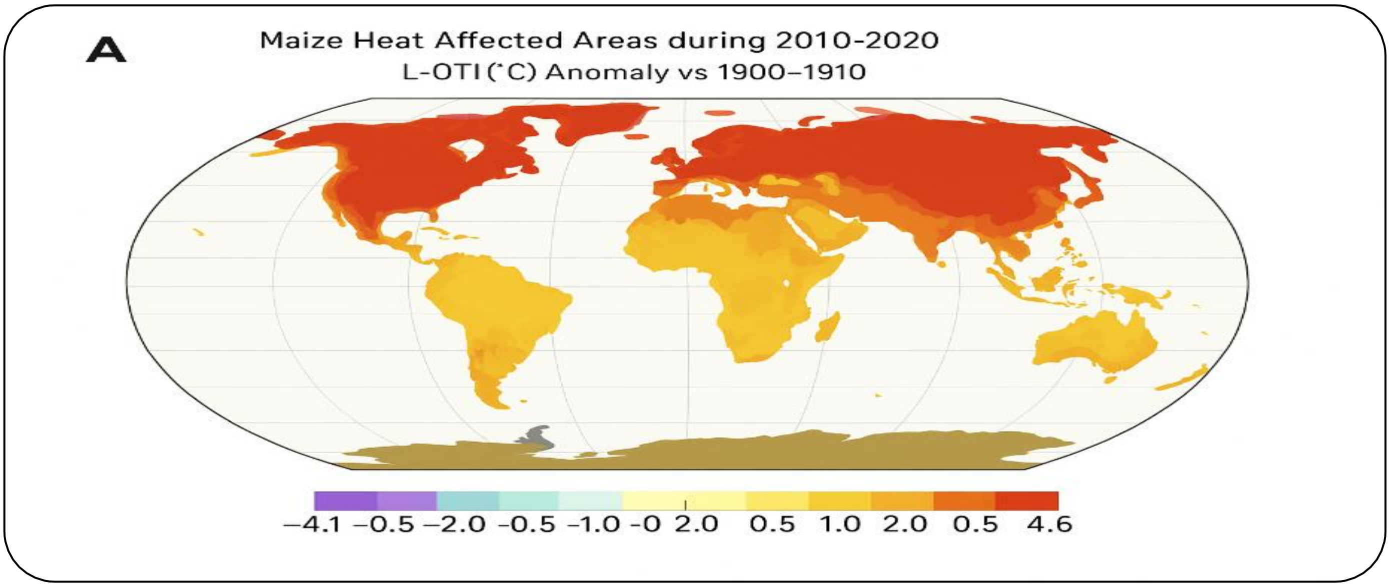

Figure 1. Global distribution of maize heat-affected areas from 2010 to 2020, showing land-surface temperature anomalies (°C) relative to the 1900–1910 baseline. Warmer colors (yellow to red) indicate regions with positive temperature anomalies, representing increased heat stress risk for maize cultivation, particularly in North America, South America, Europe, Asia, and parts of Africa. Cooler colors (blue to purple) represent areas with negative anomalies, indicating reduced temperatures compared to the baseline

Effect of heat stress on developmental stages of maize (*Zea mays L.*)

Heat stress during the germination phase and seedling stages can severely impair early plant establishment. Elevated temperatures, particularly around 40 °C or higher, reduce seed vigor and germination rates (Rosmaina et al., 2021). These effects are partly due to alterations in phytohormones such as gibberellins and abscisic acid, which influence starch metabolism and reserve mobilization (Iloh et al., 2014). Heat hampers enzymatic activities involved in starch breakdown, constraining nutrient supply to the embryo. Additionally, high temperatures inhibit shoot and root growth, limiting nutrient uptake and subsequent plant development (Rosmaina et al., 2021). Additionally, during early vegetative growth, high temperatures can influence processes such as net photosynthesis and biomass accumulation. While some studies indicate that photosynthesis remains relatively resilient up to around 38° C, irreversible damage can occur at higher temperatures, particularly in stages approaching flowering (Gonzalez et al., 2019). Heat stress at this phase can reduce leaf area, disrupt carbohydrate synthesis, and delay development, ultimately affecting the plant's productive capacity later (Lizaso et al., 2018).

The flowering stage is the temperature-most sensitive stage in maize. Pollen formation is very sensitive to temperature, with reduced pollen viability and anther dehiscence, resulting in worse pollination and kernel set (Zhang et al., 2018). Heat stress during this stage leads to increased anthesis-silking interval (ASI), kernel abortion, and reduction in kernel numbers, largely affecting yield. Developmental phases before anthesis, particularly ear shoot growth, also contribute significantly because heat can impair ear development and synchrony of silking and thereby reduce productivity (Lohani et al., 2020). Moreover, heat stress at the filling stage of grains would cause senescence in the leaves and interfere with sink-to-source translocation of carbohydrates, resulting in reduced kernel weight and grain quality (Li et al., 2020). Kernel dehydration might also be impacted, potentially on the overall yield. At this time, damage is cumulative and may cause colossal loss of grain size and weight (Yang et al., 2018).

Heat stress effects at the later grain filling phase (which would typically happen between 40 to 45 days after fertilization, and last for 10 to 15 days) have been sparingly studied. It’s effects includes cellular damage and hastened senescence mechanisms. Drying of the kernel and affecting quality traits are brought about by heat as the crop matures. Since such high percentages of dry matter have been lost early, its impact on final yield potentially could be less detrimental than at flowering but can affect harvest quality and post-harvest storage (Boehlein et al., 2019). The damage of cellular structure that can be done by the terminal-stage stress might reduce the viability of grain as well as the resistance of crop (Yang et al., 2017).

Figure 1. Poor grain filling in maize caused by high temperature. First cob (left): Scattered grain filling with large gaps; kernels formed mostly in patches along the middle portion, indicating partial pollination failure. Second cob: Severe grain filling reduction; only a few scattered kernels present, suggesting poor fertilization and early kernel abortion. Third cob: Extremely low kernel set with irregular distribution, mainly clustered in certain regions; typical of high temperature stress during silking. Fourth cob (right): Almost complete grain filling failure; only a few kernels formed at the tip, reflecting extreme heat stress impact. Source: Photo by author (Raviteja et al.).

Physiological effects of heat stress on maize

Cell elongation and division are inhibited under high-temperature conditions, resulting in stunted growth and decreased biomass yield. Membrane fluidity is negatively impacted, which jeopardizes cell integrity and performance (Jagadish et al., 2016). The optimum temperature for maize seed germination is 21 °C, with temperatures of below 13 °C having a serious inhibitory effect on germination, and below 10 °C halting germination altogether (Sánchez et al., 2014). Maize seedlings normally develop under temperatures of 30–35 ° C for development, best at about 20 °C (Khaeim et al., 2022). Additionally, heat stress halts photosynthesis through disrupting the chloroplast structure, which leads to low net photosynthetic rates. These physiological disruptions ultimately impair the plant's capacity for further reproductive development (Jagadish et al., 2016).

Moreover, reactive oxygen species (ROS) production increased due to heat stress, for example hydroxyl radical, singlet oxygen, hydrogen peroxide, etc. ROS are generally needed for cell signaling and immune responses, but excessive ROS can lead to oxidative stress, cellular damage, DNA damage and disease development by disrupting cell function (Mujahid et al., 2007). Generation of ROS species, under heat stress, damage the Photosystem II (PSII) reaction center by destabilization of core PSII protein (D1 protein) and reducing the photochemical efficiency of PSII. Thylakoid membrane, where PSII is embedded, undergoes structural damage due to increased fluidity and lipid peroxidation. As it is composed of lipid-protein matrix, integral proteins which are embedded in the thylakoid bilayer also face denaturation, which further collapse the photosynthetic function of cell membrane (Nijabat et al., 2020). However, plants do possess integrated antioxidant defense system to mitigate the effects of excessive ROS (ROS toxicity). These antioxidants includes detoxifying enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR), non- enzymatic antioxidants (such as ascorbic acid, glutathione, carotenoids, tocopherols, phenolic compounds and flavonoids), heat shock proteins. Whether plant can survive under heat stress depends upon the rate of ROS production and the mitigation ability of the plant's antioxidant defense system (Foyer & Shigeoka, 2011).

Under heat stress, plants initiates a coordinated physiological and biochemical response. Plants produce stress hormones and osmolytes to counter the effects of heat and stabilize cell structure and molecules. Heat stress either leads to increase or decrease in stress hormones such as abscisic acid (ABA), salicylic acid (SA), and cytokinins (Niu et al., 2021). Other plant hormones that are accountable for regulating plant functions include like auxins (IAA), ethylene (ET), brassinosteroids (BRs), strigolactone (SL), and jasmonic acid (JA) (Sharma et al., 2019). Every hormone has different way of regulation, such as Abscisic acid levels increase significantly under heat stress. These increased levels induce the closing of stomata in order to reduce water loss. Ethylene levels increase to regulate ROS signaling to cells and prevent cell death. While, auxins and cytokinins` production is reduced to inhibit root and shoot growth, to focus on localized regulation, which may help in cell recovery and survival.

Secondly, Osmolytes help plants to maintain osmotic balance, stabilize cell structure and molecules, and hunt down excessive ROS from cells. Examples of such osmolytes are proline (hunt osmotic adjustment, ROS, stabilization, signaling), glycine betaine (increases antioxidant enzyme activity, prevents denaturation from heat, stabilizes thylakoid membrances which is PSII center, soluble sugars (osmoprotectants, provide energy for stress repair mechanisms) and polyols (hunt ROS, osmotic regulation, stabilize structures). Such biochemical reactions are actually adaptive reactions which are necessary to protect against heat-reduced cell injury (Yang et al., 2021).

Effect of heat stress on the molecular mechanism of maize

Heat stress changes the chemistry of cells by impacting molecular mechanism and altering stable internal environment of cells (homeostasis). Now the question is that how cell perceive that it is under heat stress? Initially, it is perceived through direct biophysical changes such as increase in lipid bilayer fluidity and protein denaturation by partial folding or unfolding (Bahuguna & Jagadish, 2015). These changes trigger several molecular signaling pathways such as calcium influx into the cytoplasm (involving calmodulin, CaM-binding transcription activators). It also includes increase in reactive oxygen species in chloroplast and mitochondria, heat shock factors which are inactive under normal conditions (El-Sappah et al., 2022; Zhao et al., 2020). All these signaling helps cell to recognize that it is under stress, and take action accordingly.

The induction of heat shock proteins (HSPs), governed by heat shock factors (HSFs), is a key mechanism in plants' defense against heat stress. Heat shock factors are inactive under normal conditions. In maize, 31 HSFs have been identified, including HSFA1, a master regulator that dissociates from chaperones under heat to initiate transcription of HSPs like HSP70, HSP90, and HSP100 (Kazemi et al., 2023; Ohama et al., 2017). These factors stabilize denatured proteins (misfolded protein) and support cellular recovery by translocating to nucleus and activate heat shock genes (HSPs). The HSPs are not only important under stress, but also for maintaining balanced environment for the cell (Lin et al., 2011).

The other primary response by cells towards heat stress is given by the Endoplasmic reticulum (ER). It functions in protein folding, and heat stress causes misfolding of proteins in ER. Accumulation of misfolded proteins in ER triggers ER stress, and to counter that stress plant cell activates unfolded protein response (UPR). ER stress sensor IRE1 splices ZmbZIP60 mRNA, enabling its nuclear localization and activation of UPR genes. (Zhang et al., 2023). Additionally, ZmbZIP17 and ZmbZIP28 are cleaved in the Golgi apparatus and then moved to the nucleus under heat stress, contributing to HSP gene expression (Djalovic et al., 2024).

Reactive oxygen species (ROS) are main players. Plant produces ROS species under stress, which are generated by special enzymes on cell membrane, called RBOHs (a type of NADPH oxidase). The ROS then triggers a chain of signals inside the cell, which is called downstream signaling. These signals go through Mitogen-activated protein kinases (MAPK3/6) and Calcium-dependent protein kinases (CDPKs). These kinases do phosphorylation i.e. add phosphate group to HSF, which are that special proteins that turn on the HSPs. Additionally, mhenH_2O_2 acts as both a damaging agent and a secondary messenger that modulates stress-responsive genes (Hasanuzzaman et al., 2011). Moreover, ZmDREB2A is a transcription factor in maize, and this protein controls the activity of stress related response of cell, and it is activated under both heat and drought conditions. Under stress, plants upregulate ZmDREB2A, activating detoxification genes for ROS removal and LEA proteins for protection against dehydration and heat. (Qin et al., 2023). Thus, it helps the cell to regain the internal balance (homeostasis) and the plant becomes more resilient to high temperatures (thermo-tolerance).

Effect of heat stress on biochemical parameters of maize

One of the characteristic biochemical reactions to heat stress is enhanced lipid peroxidation, as analyzed by malondialdehyde (MDA) content. Enhanced MDA levels reflect membrane damage due to ROS attack, which reduces membrane fluidity and permeability. Enhanced levels of MDA during heat stress have been observed in maize, reflecting oxidative damage in cell membranes, which may disrupt nutrient uptake as well as cell homeostasis (Erman et al., 2021). As a strategy for fighting heat-mediated osmotic stress, maize plants store the osmolytes proline, glycine betaine, and soluble sugars. The molecules stabilize proteins and membranes, detoxify ROS, and

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preserve cellular turgor. Proline, in particular, has been widely studied; its accumulation correlates positively with heat tolerance, providing cellular protection against dehydration and oxidative damage (Chukwudi et al., 2021; Zhang et al., 2023). Heat stress influences the movement of various enzymatic antioxidants. For example, SOD activity tends to increase initially to detoxify superoxide radicals, while activities of enzymes involved in the ascorbate-glutathione cycle, such as glutathione reductase (GR) and ascorbate peroxidase (APX). However, excessive heat can overcome these protective mechanisms, leading to reduced enzyme activities and sustained oxidative damage (Erman et al., 2021).

Under heat stress, maize showed a prominent 67.4% decline in stomatal conductance and a rise in leaf temperature by 5.6 °C. Additionally, the genotypes transpired 19% more compared to those grown under normal conditions. Heat stress leads to a decline in chlorophyll content, impairing photosynthesis efficiency (Zahra et al., 2023). The destruction of 30 % chlorophyll molecules damages the ability of the plant to capture light energy, which further exacerbates oxidative stress by disrupting electron transport chains. The reduction in chlorophyll content correlates with decreased antioxidant enzyme activities, compounding cellular damage (Li et al., 2020). Heat stress in maize reduced the photosynthetic characteristics such as quantum yield of PSII and PSI, electron transport rate, and open reaction centre percentage (Mathur et al., 2021). Heat stress on maize affected PSII activity by damaging the oxygen-evolving complex on the donor side and inhibiting electron movement from QA to QB on the acceptor side. This resulted in PSII inhibition and D1 protein degradation, the binding site of QB, eventually halting electron transfer between QA and QB (Zahra et al., 2023). Heat treatment at 45 °C resulted in sudden inhibitions of photosynthesis in maize, and PEPC activity was inhibited by malate inhibition and complete inhibition of the Rubisco enzyme (Correia et al., 2021). Extremes of temperature also negatively impact the key metabolic enzymes such as nitrate reductase and carbonic anhydrase, limiting nitrogen assimilation and photosynthetic ability. Heat stress-induced inhibition of enzyme activity puts stress on biochemical resilience in maize adaptation (Tiwari & Yadav, 2019).

Effects of heat stress on maize sexual reproductive development

Maize reproductive growth has a number of key stages, such as tassel and ear development, anthesis, pollination and initial seed development. The most heat sensitive stages have proven to be the tetrad stage of microspore development and the immediate post pollination period. An elevated temperature (>36 to 38 °C) during these stages even for few hours will cause a significant reduction in seed set (Govind et al., 2022; Liu et al., 2023). The tassel, placed at the apex of the plant, is more vulnerable to direct solar radiation and elevated ambient temperatures than the ear. Heat stress disrupts the normal development of tassels by reducing tassel branch and floret numbers, impairing anther emergence, and shortening pollen shedding duration (Wang et al., 2021). The resulting asynchrony between pollen release and silk emergence, referred to as an extended anthesis-silking interval (ASI), negatively affects seed set (Liu et al., 2023). Ears are partially shielded by husks and leaves, but silks remain highly sensitive to heat stress. Heat stress delays silk emergence and reduces the number of emerged silks, especially at the apical ear position. Silk elongation is slowed due to impaired water uptake and cell expansion. Furthermore, reduced silk receptivity, along with delayed or uneven emergence, contributes to fertilization failure and kernel abortion (Fan et al., 2025).

Floral opening is essential for pollen release and is regulated by the expansion of the lodicules. Heat affects phytohormones such as brassinosteroids (BRs), and jasmonic acid (JA), which are important for lodicule swelling and glume opening. Decreased JA and BR levels under heat stress result in impaired floral opening and pollen entrapment (Yao et al., 2022). This severely limits pollen availability for successful fertilization. Moreover, Anther dehiscence involves the degeneration of septum and stoma tissues, proper tapetum development, and mechanical expansion of the anther wall. Heat stress interferes with each of these processes, resulting in reduced dehiscence pore size, poor pollen release, and male sterility (Yao et al., 2022). Tapetum degeneration is often premature under heat stress, compromising nutrient delivery to developing pollen. Pollen development, particularly during the tetrad and anthesis stages, is highly vulnerable to heat. Heat-induced chromosome abnormalities, disrupted sugar metabolism, and abnormal tapetum function all contribute to reduced pollen viability and increased sterility (Yu et al., 2024). Pollen under heat stress shows morphological shrinkage, poor starch accumulation, and a decline in germination rate.

Silk tissues supports pollen tube growth post-pollination. Heat disrupts silk physiology by accelerating senescence and increasing reactive oxygen species (ROS) levels. These changes hinder pollen tube progression in transmitting tracts and block fertilization (Gong et al., 2024). Reduced nutrient flow to silks under heat further exacerbates the problem. Short episodes of heat (e.g., 6 hours at 38 °C) post-pollination have been shown to severely reduce fertilization success and seed set (Wang, Lv, et al., 2023). These transient stresses induce invisible yet significant reproductive failure that ultimately impacts yield. Genotypic variation in heat tolerance exists in maize. Hybrids such as ZD958 display improved spikelet opening and higher pollen viability under heat stress compared to sensitive hybrids like XY335 (Wang, Sheng, et al., 2023). Identifying and incorporating genes involved in hormone signaling, tapetum development, and floral synchrony into breeding programs is key to developing heat-resilient cultivars (Lohani et al., 2025).

Genetic and transcriptional mechanisms of heat-stress tolerance in maize

Heat stress negatively affects maize yield, particularly during the reproductive phase. In response, maize has evolved genetic and transcriptional mechanisms to counteract heat stress. These responses are regulated by transcription factors, signaling molecules, and epigenetic modifications that work in coordination to establish thermotolerance. A major transcriptional reaction to heat stress is carried out by Heat Shock Factors (HSFs). These transcription factors are proteins that regulate the activation of specific genes, in response to heat stress. HSFs are activated through phosphorylation by kinases, as discussed earlier, and then move into the nucleus to bind with Heat shock elements (HSEs) which are specific DNA sequences. This binding activates Heat Shock Proteins (HSPs), which act as molecular chaperones to prevent misfolding of proteins or to refold denatured proteins. In maize, 31 HSFs have been identified so far, which are further classified as A, B, and C (Zhang et al., 2021). Class A HSFs, particularly ZmHSF01, ZmHSF04, ZmHSF05, and ZmHSF06, plays a significant role in activating stress-responsive genes and class HSFs act as co-regulators. ZmHSF01, for example, restores thermotolerance defects in Arabidopsis HSFs2 mutants (Zhang et al., 2021).

ZmHSF04 interacts with ZmHSBP2 to regulate galactinol synthase and raffinose biosynthesis, enhancing thermotolerance (Gu et al., 2017). ZmHSF05 and ZmHSF06 also improve tolerance by upregulating HSPs such as Hsp70 (Li et al., 2015). But some class B and C HSFs, such as ZmHSF08 and ZmHSF11 also act as possible repressors by negatively regulating the stress respons of plant. They repress oxidative stress-related genes (Qin et al., 2023).

ZmDREB2A plays a dual role in heat and drought tolerance and thus helps plant to survive both hot and dry conditions (Qin et al., 2023). It turns on Heat stress response (HSR) genes. Another gene ZmbZIP60 also plays the same role and activates ZmHSF01, which in turn switches on heat shock proteins. All these together form a chain reaction to handle heat stress (Z.-G. Li et al., 2021). Coordination among HSFs is also important. For example, ZmHSF17-I and ZmHSF17-II are two slightly different versions of the same gene. They interact with each other and control the activation of genes during heat stress (Liu et al., 2018). Some other HSFs like HSFA2 and HSFA3 also work as a team (called heteromeric complexes) to change how DNA is packed. They increase histone methylation (tag on DNA) which helps the plant to remember past stress memories, resulting in quicker responses next time (Friedrich et al., 2021).

Epigenetic controls also coordinate heat response. Histone modification and DNA methylation control chromatin accessibility to HSFs. Hypomethylation is responsible for thermotolerance (Shen et al., 2020), while histone marks like H3K4me3 promote expression of HS memory genes such as HSP18.2 (Liu et al., 2017). GCN5 adds acetyl group to histone, called histone acetylation, which helps activating HSF genes that are important for surviving heat stress (Hu et al., 2017). Heat-induced HDACs such as HDA9 regulate auxin biosynthesis genes, such as YUC8 by removing histone acetyl groups (Niu et al., 2023).

Other non-coding RNAs, such as miRNAs, tasiRNAs, lncRNAs, and circRNAs are also involved in giving heat response. miR398 and miR156 control antioxidant genes expression and various transcription factors (H.-T. Li et al., 2021). High-throughput sequencing in maize line CM1 identified 993 lncRNAs and 340 miRNAs heat responsive (Hu et al., 2022; Zhao et al., 2024).

In combination of maize heat stress adaptation, the transcriptional regulation mediated by HSFs, synergistic interaction with other transcription factors such as ZmbZIP60 and DREB2A, and epigenetic reprogramming and non-coding RNAs collectively shape a very complex yet strong network of heat stress adaptation in maize. The multi-omics, gene-editing (CRISPR/Cas9) and machine-learning advances will assist even more in elucidating this regulatory web and breed the heat-tolerant maize variants.

Heat stress-resistant genes in maize

Table 1: Summary of key heat stress–responsive genes in maize (*Zea mays*), including their gene IDs, functional descriptions, and roles in heat resistance in maize.

Genes	Genes Description	Function	References
GRMZM2G116452	Encodes Peroxidase superfamily protein	Engaged in the mechanism of stress response	Guo et al. (2019)

GRMZM2G060349	Encodes a DNA mismatch repair protein, MutS2	Increased by elevated temperature Participates in the stress response mechanism	Guo et al. (2019)
GRMZM2G032081	Encodes a cysteine-rich domain-containing protein	Engaged in the process of responding to stress	Guo et al. (2019)
GRMZM2G061515	Auxin-response GH3 family protein serves as an indole-3-acetic acid-amido synthetase	Participate in the stress response mechanism Function in signaling pathways Engage in sustaining auxin balance in vivo by facilitating the conjugation of excess IAA to amino acids.	Ludwig-Müller (2011)
GRMZM2G377194	Encodes a D-type cyclin, CYCD5;1	Increased by elevated temperature	Guo et al. (2019)
GRMZM2G062892	Encodes a cysteine-rich protein (CRP)	Lose its stability under HS, and which indicates it cannot safeguard the seed-set process.	Guo et al. (2019)
chloroplast sHSP26	Small heat shock protein, chloroplastic	Engaged in maize thermal resilience	Hu et al. (2015)
Zm00014a018076	Class I heat shock protein 1	Hs and exogenous çok H2O2 upregulate under 40 C treatments, in root, leaf, and stem tissues.	Sun et al. (2012)
Zm00001d028912	Zinc finger protein CONSTANS-LIKE 13	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d028992	Metalloproteinase 1-MMP	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d038505	Glutamate decarboxylase 1 (GAD 1)	Ca2+/calmodulin heat response gene has been found to be associated with binding with GAD in activating the latter	(Jagtap et al., 2020)
Zm00001d060036	Heat shock 70 kDa protein 9 mitochondrial	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d041701	Acyl carrier protein 2 chloroplastic	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d048592	rca2; RUBISCO activase2: encodes the beta form of RUBISCO activase	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d051056	S-adenosylmethionine decarboxylase proenzyme	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d077929	Serine/threonine-protein kinase MHK	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d039188	Putative leucine-rich repeat receptor-like protein kinase family protein	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d011760	DNAJ heat shock N-terminal domain-containing protein	DNAJ proteins are co-chaperones of the Hsp70 machine, a key helper in heating answer because they enhance the ATPase activity of the heating machine and hence hold it in contact with client proteins	(Pegoraro et al., 2011)
ZmNIP2-3	Aquaporin NOD26-like membrane integral protein	Heat response gene Differentially phosphorylated in response to heat Stress roles aquapories in silicon transport	(Jagtap et al., 2020)

Zm00001d045220	Late embryogenesis abundant protein group 2	Heat response gene The LEA proteins are group of hydrophilic proteins, which are assumed to have a protective effect that occurs when subjected to various abiotic stresses	(Jagtap et al., 2020)
Zm00001d046363	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	Gene related to heat response	(Jagtap et al., 2020)
Zm00001d005002	Carbohydrate transporter/sugar porter/transporter	The heat stress is associated with high grain yield QTL	(Frey et al., 2016)
Zm00001d013918	Thylakoid luminal 17.4 kDa protein chloroplastic	The heat stress is associated with high grain yield QTL	(Frey et al., 2016)
Zm00001d047096	Beta-expansin 1a	The heat stress is associated with high grain yield QTL	(Frey et al., 2016)
Zm00001d045675 (AS)	Asparagine synthetase homolog 1	High highest daily temperature produces such effect as alternative splicing and functions of SR (serine/arginine-rich) 45a	(Li & Howell, 2021)
Zm00001d047847 (SR45a)	Serine/arginine-rich splicing factor SR45a	High highest daily temperature produces such effect as alternative splicing and functions of SR (serine/arginine-rich) 45a	(Li & Howell, 2021)
GRMZM2G377194 CYCD5;1	Encode cyclin D5;1	Protective roles for reproductive stage under HS Increased seed set	Guo et al. (2019)
GRMZM2G062914 (MPK14)	Expresses a maize mitogen-activated protein kinase, MPK14	Its ortholog AtMPK1 of Arabidopsis can mediate and increase the signal of the ABA	Guo et al. (2019)
GRMZM2G059225 (ARF)	Discolored-paralog3 putative ARF GTPase-activating domain protein with ankyrin repeat-containing protein	GTPase activator activity	Guo et al. (2019)
Zm00001d028557 (ZmHSP17.9)	17.9 kDa class I heat shock protein	Heat stress response Induced by heat in diurnal temperature cycles	(Rashed et al., 2021)
Zm00001d047542 (ZmHSP17.6)	17.6 kDa class II heat shock protein	Heat stress response Induced by heat in diurnal temperature cycles	(Rashed et al., 2021)
Zm00001d038806 (HSP101)	Heat shock protein 101	Induced by heat in diurnal temperature cycles Plays essential roles in both induced and basal thermotolerance and primary root growth	(Nieto-Sotelo et al., 1990)
Zm00001d014090	Mitochondrial heat shock protein 60	Induced by heat in diurnal temperature cycles	(Prasad et al., 1990)

Future adaptations and mitigation strategies

Climate change impact on maize could be mitigated by some of the adaptation strategies. The genetic solutions comprise of the production of drought-tolerant maize species by use of molecular breeding and biotechnological techniques including marker-assisted selection and CRISPR/Cas9 genome editing. (Gillani et al., 2021). For example, genes like AOX, ZmAN13, and ZmSEC14p enhance resilience under thermal stress (Mir et al., 2025).

Water use efficiency can be improved and crops shielded during heatwaves through agronomic practices like optimum planting, intercropping, mulching and effective irrigation systems like drip irrigation. (Daryanto et al., 2016). Agroforestry and crop rotation further mitigate heat stress by improving soil structure and microclimate conditions. Integrated pest and disease management strategies also become critical in reducing heat-exacerbated infestations and infections (Fahad et al., 2017). At a higher level, there should be policy provisions to accommodate the climate-resilience agriculture. These are investment in climate-smart technologies, training of farmers and subsidies on sustainable practices. Establishing international alliances, such as CGIAR efforts, is crucial for disseminating adaptive methods to all parts of the world.

Predictions for 2050

Predictive models and climate scenarios forecast a grim outlook for maize production by mid-century if current trends continue unabated. According to the Intergovernmental Panel on Climate Change (IPCC, 2021), global mean temperatures are expected to rise by approximately 1.5°C to 2°C above pre-industrial levels by 2050, depending on emission pathways (Legg, 2021). Research shows that with every 1°C increase, maize production could drop by 7.4% (Lobell, Schlenker, et al., 2011). Elevated temperatures will not only increase the frequency and severity of heatwaves but will also lead to more irregular precipitation, impacting water availability crucial for maize cultivation (Legg, 2021).

Ahmad et al. (2024) studied that without significant adaptive measures, maize yields could decline by around 15-20% globally by 2050. The decreased grain yield in such regions as South Asia may be even more significant, where the combined effects of the heat stress and drought may trigger the loss of more than 30 percent of yield (Cohen et al., 2021). During flowering stage, heat stress is particularly devastating; it renders sterility and reduces grain set resulting into significant reduction in yields. They are expected to record a loss of up to 24 percent by the year 2050 particularly in those areas that are located in the tropics and the subtropics like Sub-Saharan Africa and certain sections of South America and Asia (Kang et al., 2025; Schauberger et al., 2017) .

CONCLUSION

Maize, a vital global staple, is increasingly threatened by heat stress, with reproductive stages, particularly anthesis and silking, being the most vulnerable, often leading to irreversible yield losses. Elevated temperatures affect every growth phase, from delayed germination and reduced seedling vigor to impaired photosynthesis and biomass accumulation during vegetative growth. Heat during flowering causes pollen sterility, delayed silk emergence, poor kernel set, and disruptions in fertilization due to oxidative damage. Protective mechanisms such as antioxidant enzymes (SOD, CAT, POD), osmolytes like proline and glycine betaine, and hormonal adjustments play significant roles in mitigating these effects.

Genetic and molecular advances have revealed key regulatory elements, including ZmHSFs, ZmbZIP60, DREB2A, and heat shock proteins, supported by epigenetic and RNA-mediated stress memory. Modern tools like omics analyses and CRISPR/Cas9 hold promise for breeding heat-tolerant varieties. However, sustainable solutions require an integrated strategy that includes combining genetic improvement, adaptive agronomic practices, and climate-resilient policies, which are underpinned by collaboration between governments, private sectors, and farmers to safeguard maize productivity under rising global temperatures.

AUTHOR CONTRIBUTIONS

Tayyaba Mahboob conducted the literature search and compilation. Mahmood ul Hassan and Zubair Ahmed synthesized and critically analyzed the reviewed studies. Tayyaba Mahboob, Safeena Abbas, Hassan Bin Munir wrote up the manuscript, Muhammad Wajid khan reviewed literature and done proofreading, Aswad Bashir Edited and formatted paper the manuscript. All authors interpreted the data, critically revised the manuscript for important intellectual content, and approved the final version.

COMPETING OF INTEREST

The authors declare no competing interests.

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