



REVIEW ARTICLE

# Heat stress tolerance in maize - An overview

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## Abstract

Maize (*Zea mays* L.), one of the world's most important staple crops, is increasingly vulnerable to rising temperatures and erratic climatic conditions. Among various abiotic stressors, heat stress stands out as a critical factor that disrupts the crop's growth by impairing morphological, physiological, biochemical and molecular processes ultimately leading to substantial yield losses. The severity of this issue is expected to escalate with the intensification of global warming and water scarcity. To ensure sustainable maize production, there is an urgent need to develop heat-resilient, high-yielding hybrids. This review explores recent advances in identifying thermotolerant donor lines and employing them in hybrid development. Emphasis is placed on integrated strategies, including advanced agronomic interventions, molecular breeding, CRISPR/Cas-based genome editing and the application of multi-omics platforms transcriptomics, proteomics, metabolomics and phenomics to decipher heat-responsive mechanisms. Furthermore, the integration of high-throughput phenotyping, machine learning and climate-smart agricultural practices offers promising pathways to accelerate breeding efficiency and improve field-level adaptation. By synthesizing these cutting-edge approaches, this review provides a comprehensive framework to mitigate the adverse impacts of heat stress and support climate-resilient maize cultivation in the face of future challenges.

**Keywords:** advanced genomic tools; heatomics; heat shock protein; maize; thermo-resilience

## Introduction

Climate change poses a serious threat to humanity, with rising temperatures, floods and disease outbreaks impacting global food security. Among these, global warming significantly affects agriculture, endangering livelihoods as millions depend on farming for survival. In general, plants are exposed to a variety of environmental conditions, consisting of heat, drought and saline stress. Amongst which, heat stress exerts a profound negative impact. The progressive increase in global climate change, caused by extreme heat waves and intermittent drought is a major concern for crop production (1). Heat stress refers to a rise in temperature beyond the optimal range, causing irreversible damage to crop growth and development. The heat stress severely affects the crop during seedling and reproductive stage (2). Globally, heat stress compromises the productivity and resilience of major crops viz., rice, wheat, maize and soyabean. In case of Wheat (*Triticum aestivum* L.), global production is decreased by more than 6 % (3). In the USA, there is a significant reduction in yield loss of Maize (> 9 %), followed by China (> 7 %) and India (> 4 %) (4).

Heat stress has emerged as a major limiting factor in agriculture, adversely affecting crop growth and productivity by disrupting morphological, physiological, biochemical and molecular processes (5). It leads to reduced seed germination,

stunted growth, leaf damage, impaired reproductive development and ultimately a decline in yield. To cope with these challenges, there is an urgent need to develop climate-resilient crop varieties. This includes adopting stress avoidance strategies such as altering plant architecture, leaf orientation and growth duration, along with deploying advanced genetic tools like mutagenesis, marker-assisted selection, genome editing and quantitative trait loci (QTL) mapping to improve stress tolerance (6). In addition to genetic improvements, agronomic practices like optimal soil and nutrient management, crop rotation, precise sowing time and irrigation scheduling can help mitigate heat-related damage. Furthermore, the external application of protective agents such as osmo-protectants, antioxidants, phytohormones, polyamines and heat shock proteins (HSPs) has shown potential in alleviating heat stress effects in crops (7).

## Impact of climate change on maize

Maize (*Zea mays* L.) is a tall, determinate, annual C4 crop widely cultivated across the globe for its diverse uses in food, animal feed and industrial applications. Owing to its adaptability and productivity, maize contributes approximately 40 % of the total global cereal production (FAO, 2023) (8). However, the increasingly erratic climatic patterns, including rising temperatures and prolonged dry spells, have made it difficult to sustain crop productivity. According to projections by the Intergovernmental

Panel on Climate Change (IPCC), the global mean temperature is expected to rise by 0.3 °C between 2025 and 2100 (9), posing serious challenges to crop growth. In maize, the detrimental effects of heat stress are evident across all developmental stages from germination to maturity manifesting as reduced leaf area, lower net photosynthetic efficiency, decreased biomass accumulation, pollen sterility, poor grain set and ultimately reduced grain yield and quality (4). These impacts are particularly severe during sensitive phases like tasselling and grain filling.

Given the growing urgency of climate adaptation in maize, this review aims to provide a comprehensive synthesis of heat-induced changes at morphological, physiological, biochemical and molecular levels. It focuses on identifying key traits linked to thermotolerance and compiles current strategies including stress-responsive breeding, omics technologies, gene expression regulation, genome editing and adaptive agronomic practices. The objective is to present an integrative framework that can support the development of heat-resilient maize cultivars suitable for changing climatic conditions. A systematic literature review was conducted using scientific databases like Scopus, Google Scholar and Web of Science with relevant keywords to ensure up-to-date and evidence-based insights.

Heat stress response framework in plants is depicted in Fig. 1

## Response of plant to heat stress

### Morphological adaptations

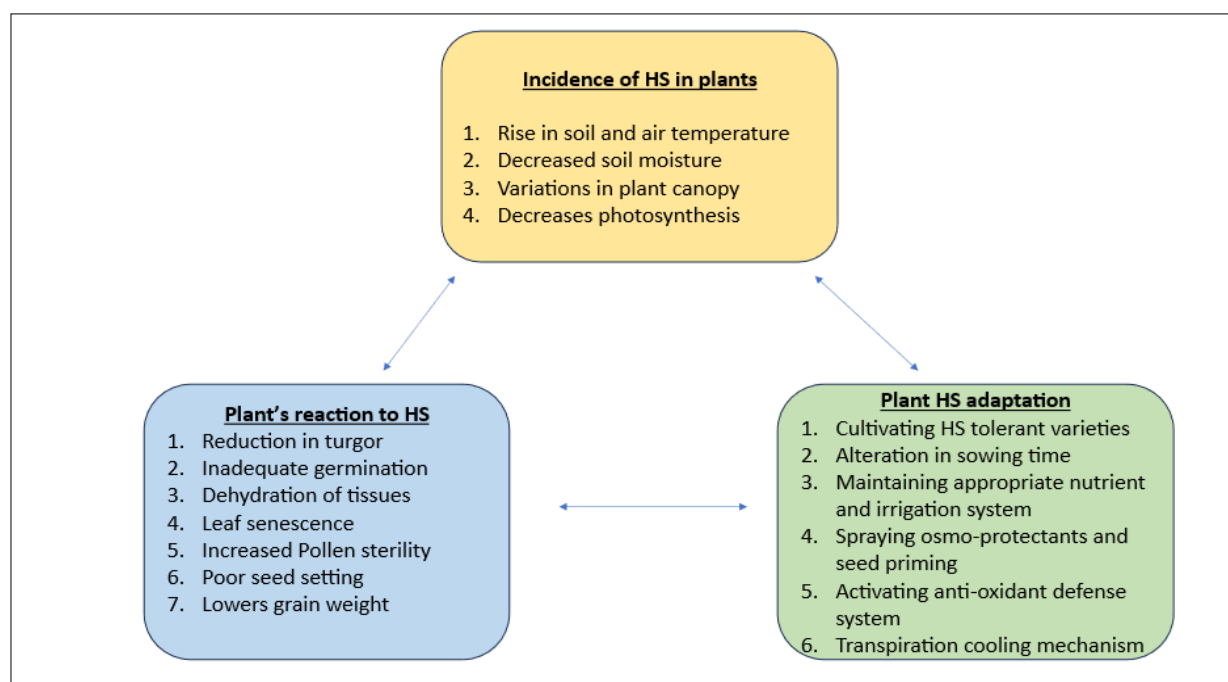
The plant's life cycle is broadly categorized into two phases: the vegetative stage, comprising seed emergence, root, stem and leaf development; and the reproductive stage, including flowering and grain filling (Fig. 2). Both stages are highly sensitive to heat stress, although the reproductive phase is often more critically affected due to its direct influence on fertilization and yield (8). High temperatures, especially in tropical zones, result in notable yield losses by impairing reproductive structures and processes. For instance, maize genotypes with high leaf wax content, lower cob and leaf angle and compact tassels have shown better adaptation under elevated temperatures, as these traits reduce direct solar radiation exposure and evaporation.

Heat stress leads to structural injuries such as leaf sunburn, shoot inhibition, abscission and fruit discoloration, ultimately lowering marketable yield (Fig. 1). It can extend the grain-filling period, resulting in smaller kernels and decreased grain weight and density (9). The nutritional quality of maize kernels including carbohydrate, protein and oil content also declines under heat stress. Additionally, anatomical changes such as smaller cell size, reduced internode length, stomatal closure, increased stomatal and trichome density and wider xylem vessels in both roots and shoots help conserve water and sustain growth under high temperatures. At the sub-cellular level, elevated temperatures disrupt organelle functions, leading to impaired cell division and expansion (10). Heat stress during flowering may cause irreversible damage, including floral abortion and reduced pollen viability, thus hindering fertilization and seed development (11).

### Physiological changes

The morphological responses to heat stress are closely tied to a cascade of physiological adjustments that help plants survive under elevated temperatures. Key physiological parameters such as membrane fluidity, photosynthetic rate, respiration, osmolyte accumulation and hormone balance are significantly disrupted (12). Heat stress also alters stomatal conductance, disturbing the normal gas exchange processes and leading to reduced tissue water potential, which ultimately affects plant water status and photosynthetic efficiency (13). Critical traits including seed germination, root elongation, leaf expansion and the anthesis-silking interval (ASI) are compromised, particularly during flowering and grain filling, thereby reducing both grain quality and yield potential (14).

Maintaining a high photosynthetic rate under stress is considered a major physiological mechanism for heat tolerance, as it directly influences biomass and economic yield (15). Selection of heat-responsive traits such as leaf area, elongation rate, photosynthetic capacity and reproductive characteristics like kernel number per row, tassel sterility, pollen viability and stigma receptivity have proven useful in maize breeding



**Fig. 1.** Main impacts of high temperature on plants.

programs (16). Trait-based phenotyping, especially under environment-specific stress conditions, is one of the most effective strategies to screen and select tolerant genotypes (17, 18). The integration of advanced tools such as robotics and artificial intelligence has further enhanced the precision and efficiency of phenotyping under field conditions (19).

Other relevant physiological indicator heats include chlorophyll fluorescence parameters (e.g., Fv/Fm ratio) reflecting photoinhibition and canopy temperature depression (CTD), which correlates with transpiration efficiency and yield stability. Heat stress also impairs mitochondrial respiration and ATP synthesis, causing cellular energy imbalance. Plants accumulate compatible solutes such as proline, glycine betaine and soluble sugars to stabilize membranes and maintain osmotic balance. Hormonal signalling, especially involving abscisic acid (ABA), salicylic acid and ethylene, is crucial for stress perception and response.

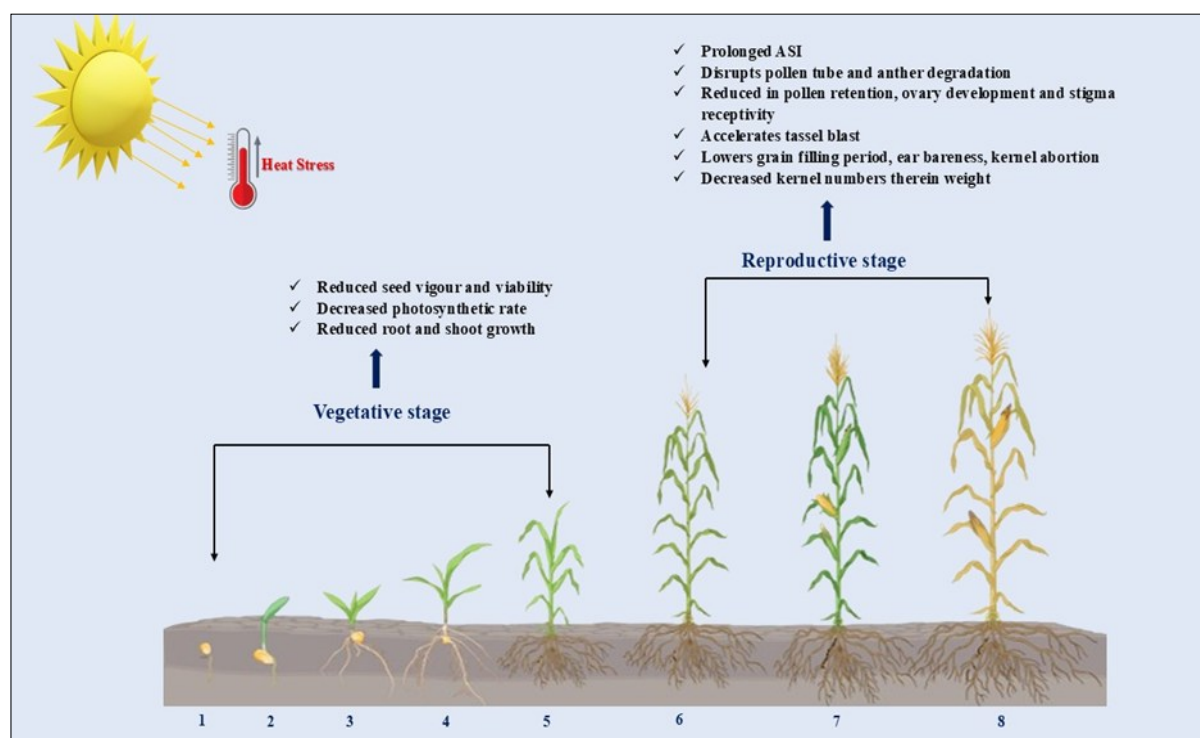
A robust antioxidant system is essential for heat tolerance. Enzymes like superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) play critical roles in scavenging reactive oxygen species (ROS). SOD converts superoxide radicals ( $O_2^-$ ) into hydrogen peroxide ( $H_2O_2$ ), which is further detoxified by CAT and APX, thereby protecting cellular structures from oxidative damage. Elevated activity of these enzymes is commonly associated with enhanced thermotolerance in maize genotypes. Additional mechanisms such as increased cuticular wax deposition reduce transpirational water loss and prevent overheating. The stay-green trait, which prolongs photosynthetic activity under heat stress, also contributes to yield stability. Nevertheless, thermotolerance remains a complex and multigenic trait influenced by physiological plasticity and genotype × environment interactions (13).

Schematic representation of heat stress effects on maize during vegetative and reproductive growth stages is given below in Fig. 2.

### Biochemical mechanisms

Heat stress triggers a cascade of physiological disruptions at the cellular level, primarily through the generation of highly reactive and toxic oxygen species (ROS) (20). These oxygen radicals disturb the delicate cellular equilibrium by attacking vital macromolecules and compromising both cellular and sub-cellular membrane integrity (21). In response, plants have evolved sophisticated defence systems against oxidative stress, including an arsenal of enzymes, proteins, vitamins and secondary metabolites collectively known as antioxidants (20). Numerous studies have confirmed that higher levels of antioxidants are linked with improved thermal tolerance. By modulating the activity of key antioxidative enzymes, plants can effectively mitigate oxidative damage under heat stress (22). These antioxidative enzymes (e.g., superoxide dismutase, catalase and peroxidases) safeguard plants by neutralizing toxic ROS, while non-enzymatic antioxidants (e.g., ascorbate, glutathione, tocopherols) play critical roles in redox homeostasis and signal transduction (23). Ascorbate, for instance, not only functions as a cofactor for various enzymes but also regulates physiological processes and the synthesis of other protective molecules like tocopherols (24). While  $H_2O_2$  is typically harmful at high concentrations, it also acts as a signalling molecule that activates stress-responsive pathways in plants (25).

In addition to antioxidant defences, plants accumulate a suite of low-molecular-weight compounds, collectively called osmolytes, which significantly contribute to stress tolerance under extreme temperatures (26). These osmolytes including sugars, proline, ammonium compounds, sulphonium derivatives, glycine-betaine and trehalose stabilize proteins and membranes, preserve enzyme function and maintain cell turgor during stress. One of the most studied osmolytes, glycine-betaine (GB), accumulates in response to abiotic stress and plays a vital role in membrane protection and enzyme stabilization (26). Interestingly, its biosynthesis varies across species; for example, maize produces



**Fig. 2.** Schematic representation of heat stress effects on maize during vegetative and reproductive growth stages.



higher GB levels compared to sugarcane (27).

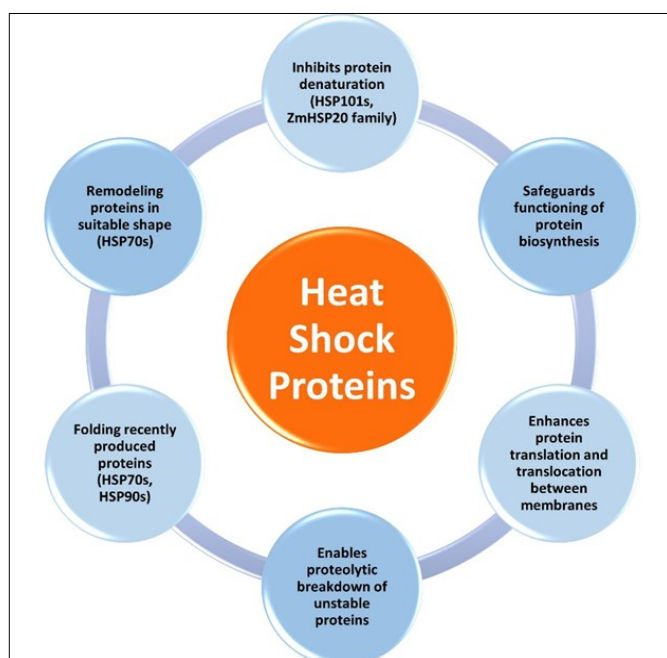
Moreover, osmolytes not only protect cells but also serve as metabolic signals, triggering gene expression linked to stress adaptation. Their accumulation is tightly regulated by complex metabolic pathways, many of which have been identified as quantitative trait loci (QTLs) useful in stress-tolerant breeding. Through marker-assisted selection (MAS) and genetic engineering, breeders can enhance osmolyte biosynthesis in elite cultivars (3). Several studies have demonstrated that overexpression of key biosynthetic genes leads to higher osmolyte content and improved thermotolerance in transgenic plants.

Additionally, osmolytes aid in maintaining photosynthetic efficiency under heat stress by protecting chloroplast structure and reducing photoinhibition. They also contribute to stomatal regulation, ensuring better water-use efficiency. Some osmolytes, such as proline and trehalose, have been shown to act as chemical chaperones, stabilizing unfolded proteins during thermal stress. Recent research even suggests that osmolyte accumulation enhances plant immune responses, indirectly contributing to overall stress resilience.

### Molecular mechanisms

In molecular approach, the heat shock protein, advanced genomics and omics technology plays a major role. Plant cell organelles have an effective heat sensing mechanism that generates a signalling cascade for quick adaptive changes (28). The plasma membrane contains  $\text{Ca}^{2+}$  conducting channels known as cyclic nucleotide-gated ion channels (CNGCs) (29). In maize, 11 plasma membrane localized CNGC genes play a significant role in heat tolerance (30). Heat stress causes an increase in the production of specific proteins known as Heat Shock Proteins (HSPs), which maintain protein stability and help retain their original structure under stressful conditions. These proteins act as molecular chaperones and are vital for protecting plant cells from heat-induced damage by preventing misfolding and aggregation of proteins (3). Role of different HSPs in maize is described in Fig. 3

Firstly, Vierling in 1991 proposed the significance of HSPs



**Fig. 3.** Role of different HSPs in maize.

in plants. Based on the molecular weight, they are categorized into five conserved classes, viz., Small Heat Shock Proteins (sHSPs), HSP60, HSP70, HSP90, HSP100 (31). Mainly, HSP101 and sHSPs are found in maize. HSP101s and members of the ZmHSP20 family function primarily to inhibit irreversible protein denaturation, preserving protein integrity and assisting in the reactivation of aggregated protein. HSP70s play a dual role by re-modelling misfolded proteins into their correct conformations and refolding newly synthesized polypeptides, especially during heat stress. Alongside HSP70s, HSP90s also aid in the proper folding and stabilization of nascent proteins, ensuring cellular functionality under stress. Moreover, HSPs are involved in the proteolytic breakdown of unstable or misfolded proteins, preventing cytotoxic accumulation and maintaining proteome homeostasis. They also enhance protein translation and translocation across cellular membranes, ensuring efficient intracellular protein trafficking. Importantly, HSPs safeguard the functioning of protein biosynthesis by stabilizing ribosomes and the translation machinery, thereby supporting continued growth and development under elevated temperatures (32). In maize, *Nicotiana PK1* gene improves moisture stress resistance (33). Additionally, bacterial RNA chaperons were used in transgenic method to increase moisture stress tolerance in maize (34). Transgenic maize with higher *ZmVPP1* expression restores drought (35). Previous researchers reported that over-expression of *OsMYB55* activates stress-responsive genes and increases heat and drought tolerance (36). Transcription factors (TFs) play a pivotal role in regulating gene expression during heat stress, enabling plants to activate defence mechanisms at the molecular level. Among them, heat shock transcription factors (HSFs) are key regulators that activate the expression of heat shock proteins (HSPs), which maintain protein stability under stress. In maize, 31 HSFs have been identified and grouped into three classes: A, B and C. Class A HSFs, including ZmHsf1, ZmHsf4, ZmHsf5, ZmHsf6 and ZmHsf17, are primarily involved in transcriptional activation under heat stress. These TFs enhance thermotolerance by inducing protective genes like HSP70 and HSP101. Class B members such as ZmHsf3, ZmHsf11 and ZmHsf25 often function as co-regulators, fine-tuning the heat stress response by modulating expression levels of target genes. Other TF families like DREB, bZIP, WRKY and MYB are also reported to modulate abiotic stress responses in maize. For instance, ZmDREB2A is crucial for heat and drought tolerance, while ZmbZIP60 activates HSF genes and downstream chaperones. Collectively, these TFs coordinate signalling networks that reprogram cellular metabolism, promoting survival and adaptation under elevated temperatures. (37, 38)

Heat stress tolerance traits such as pollen viability and anthesis-silking interval (ASI) are governed by multiple genes or loci. Identifying heat-tolerance-associated QTLs is critical for developing high-yielding maize cultivars. Several QTLs influencing key reproductive traits like pollen production, grain filling and leaf senescence have been mapped. For instance, two grain yield-related QTLs have been recognized among the 11 reported for heat tolerance. Molecular markers linked to these QTLs have been successfully used in breeding programs. For example, former researchers identified QTLs associated with grain yield under stress and used them in hybrid development in tropical maize (39). Previous researchers employed genomic prediction and marker-assisted selection (MAS) to develop stress

-resilient hybrids in sub-Saharan Africa (40). Similarly, the release of heat-tolerant hybrids like CHH 101 and CHH 105 in South Asia using QTL-based breeding strategies was reported earlier (41). Further demonstrated successful introgression of heat-tolerant QTLs into elite maize lines, improving pollen viability and grain yield under high temperatures (42). These studies highlight the utility of integrating molecular markers into breeding pipelines for the successful development of heat-resilient maize hybrids (Table 1).

QTLs/genes involved in regulation of heat stress in maize is mentioned in Table 1.

### Omics technology

In the era of climate uncertainty, decoding the complex survival strategies of plants has become more important than ever. Modern science is now unlocking these secrets through Omics technologies, a powerful suite of tools that dives deep into the molecular orchestration of heat stress responses. These approaches provide an opportunity to explore translational, transcriptional and post-translational mechanisms, along with key signalling pathways that govern plant adaptation under extreme conditions (54). Omics helps identify the intricate links between alterations in plant genomes, micromes and proteomes during heat stress (55). In micromics studies, plants employ microRNAs to fine-tune gene expression post-transcriptionally, critical regulators in plant development and stress adaptation (56). Their role in ensuring transcriptome balance, cellular resilience and phenotypic plasticity offers immense potential for engineering heat-resilient cultivars (55). On the biochemical side, proteomes drive essential

functions and lead to the generation of numerous metabolomes within the broader metabolomics landscape (54).

By integrating phenotyping and crop modelling, researchers can now zero in on complex traits linked to stress adaptation (57). High-throughput phenotyping (phenomics), an emerging breeding strategy allows precise and large-scale trait screening. Although its high cost currently limits use to advanced breeding programs, recent advancements have significantly improved varietal development (6, 58).

Microarrays, which are tools used to assess the expression levels of thousands of genes simultaneously, have been instrumental in studying heat-related gene activity (55). Similarly, transcriptomes (the complete set of RNA transcripts) and phenomics (quantitative assessment of plant traits using imaging or sensors) provide detailed insight into plant responses at multiple stages. Therefore, omics-based methods offer promising avenues for identifying, selecting and developing maize genotypes better equipped to withstand rising temperatures (59).

### Enhancing heat stress tolerance using genetic approaches

To deal with the detrimental effects of severe temperature fluctuations, adopting diverse agronomic and breeding options as well as modern genomic technologies is a crucial step. Here, we can offer various ways to control the temperature extremes in maize cropping system.

### Agronomic practices

Climate-smart agronomic practices are key strategies to combat the adverse effects of rising temperatures on maize yield. These

**Table 1.** QTLs/genes involved in the regulation of heat stress in maize

QTLs name	Related function in the previous study	References
<i>ZmHSF01</i>	<i>ZmHsf01</i> enhances thermotolerance via H3K9 promoter hyperacetylation in tropical and sub-tropical maize	(4)
<i>ZmHSF03</i>	Heat stress response	(37)
<i>ZmHSF04</i>	Overexpression boosts heat and salt stress tolerance	(38)
<i>ZmHSF05</i>	Improves heat and drought tolerance	(38)
<i>ZmHSF06</i>	Promotes thermo- and drought tolerance	(1)
<i>ZmHSF08</i>	Suppresses ABA and stress-responsive genes under salt and drought stress	(3)
<i>ZmHSF11</i>	Lowers heat stress tolerance	(43)
<i>ZmHSF17</i>	Heat stress response particularly in Chinese maize varieties	(44) (45)
<i>ZmHSF23</i>	Contributes to heat stress response in sub-tropical maize lines	(1)
<i>ZmHSF25</i>	Associated with heat stress response in thermotolerant tropical maize genotypes	(45)
<i>ZmHSF28</i>	Enhances drought tolerance in both maize (a monocot) and Arabidopsis (a dicot)	(39)
<i>ZmDREB2A</i>	Crucial to withstand heat and drought during vegetative and reproductive stages.	(40)
<i>ZmMYB-R</i>	In tropical maize lines, <i>ZmMYB-R</i> is induced under abiotic stresses like heat, drought and cold.	(41)
<i>ZmbZIP60</i>	Activates <i>ZmHSF01</i> and regulates many HSP genes in heat-tolerant sub-tropical maize genotypes	(42)
<i>Zm00001d043634</i>	Causes leaf burning and plant death at vegetative stage	(46)
<i>Zm00001d025343</i>	Causes leaf burning and plant death	(47)
<i>ZmDHN13</i>	Enhances oxidative stress tolerance and positively regulates copper tolerance in transgenic yeast and tobacco	(48)
<i>ZmWRKY106</i>	Heat and drought tolerant in transgenic plants	(49)
<i>ZmERD3</i>	Heat and cold tolerance	(50)
<i>ZmbZIP4</i>	Regulates ABA accumulation and root development	(51)
<i>GRMZM2G377194</i>	Thermotolerance	(52)
<i>GRMZM2G060349</i>	Thermotolerance and increased seed set	
<i>GRMZM2G122199</i>	Thermotolerance	(42)
<i>GRMZM2G026892</i>	Thermotolerance and increased seed set	
<i>GRMZM2G148998</i>	Heat tolerance and enhances grain yield at flowering time	(42)
<i>GRMZM2G115658</i>	Heat tolerance at grain filling stage	
<i>GRMZM2G537291</i>	Heat tolerance, high grain yield	
<i>GRMZM2G324886</i>	Heat tolerance, high grain yield	
<i>GRMZM2G436710</i>	Heat tolerance	(53)
<i>GRMZM2G094990</i>	Heat tolerance	
<i>GRMZM2G178486</i>	Cold tolerance	
<i>GRMZM5G806387</i>	Cold tolerance and better germination	
<i>GRMZM2G148793</i>	Cold tolerance, faster germination	

practices reduce productivity loss through strategic cropping patterns tailored to withstand climate variability (60). Adjusting planting times allows crops to avoid critical growth stages during periods of extreme heat (61). For instance, in North China, changing sowing dates minimized yield losses during silking and grain filling phases under fluctuating heat and cold stress (62). Adoption of long-season cultivars led to a 13 % to 38 % increase in grain yield, mitigating heat damage (63). In semi-arid regions, the dry soil planting (DSP) technique where seeds are sown before the onset of the rainy season to enable immediate germination has proven effective in achieving stable yields (64, 65). Cultivars with higher thermal time requirements can extend the reproductive period and maturity, contributing to yield advantages under heat-prone conditions (66). Thus, practices such as early sowing, DSP and selecting early-emerging cultivars with high thermal time adaptability are essential for addressing local climate and soil conditions.

### Role of Plant Growth Regulators (PGRs)

PGRs serve as powerful allies in the battle against heat stress in maize. These substances, effective even in low concentrations, modulate plant responses to environmental stresses. Application of PGRs like thiourea, proline, salicylic acid and ascorbic acid strengthens stress resilience by scavenging reactive oxygen species (ROS), regulating osmotic pressure, stabilizing membranes and enzymes and inducing antioxidant gene expression (67). Methods like seed priming and coating enhance plant tolerance during critical temperature fluctuations (68). Melatonin, a potent antioxidant PGR, boosts maize resilience to both heat and cold stress (69). Seed coating (SC) technologies, which combine PGRs with fertilizers, insecticides and fungicides, protect germinating seeds and are gaining global popularity (70, 71). For instance, SC with thermo-responsive hydrogels containing salicylic acid improved germination, shoot and root growth and enzymatic defences (72). Similarly, chitosan and H<sub>2</sub>O<sub>2</sub> coatings enhanced protein content and seedling emergence (73). Natural and synthetic PGRs applied via foliar sprays significantly improve crop physiology and antioxidant capacity under heat stress (74, 75). Despite their benefits, PGR application must be guided by scientific recommendations, as effectiveness depends on crop type, variety, dose and timing.

### Molecular tools

Tapping into the genetic toolbox of maize is now more exciting and promising than ever. Developing heat-resilient cultivars using molecular tools has emerged as a sustainable and cost-effective strategy to combat climate change (76). Tools like conventional breeding, quantitative trait loci (QTL) mapping, which helps locate specific regions of DNA associated with key traits, genomics and marker-assisted selection (MAS) are crucial in improving stress tolerance. MAS is a precise technique that uses DNA markers to select plants with desirable characteristics early in the breeding cycle. For example, in African regions, such climate-resilient maize cultivars have led to yield increases of 5-25 % (77). The integration of smart sensor technologies is also fast-tracking plant breeding efforts (78). Moreover, traditional landraces and wild maize relatives serve as treasure troves of untapped genetic variation for heat resilience (79, 80). By creating core collections from these sources, researchers can

conduct mapping and association studies to identify valuable QTLs that boost heat stress tolerance (81).

### CRISPR and Genome editing

Genome-wide association studies (GWAS), a method that scans the entire genome to find genetic differences linked to important traits have teamed up with next-generation sequencing to improve our understanding of how plants handle stress. These tools have helped identify key heat-responsive genes in maize, particularly active during flowering, by focusing on single nucleotide polymorphisms (SNPs), small but powerful DNA changes that vary between plants and influence traits (82, 83).

Meanwhile, marker-assisted selection (MAS) emerges as a speed-boosted compass for breeders, enabling the efficient stacking of beneficial genes and rapid identification of complex traits like heat tolerance (84). MAS leverages molecular markers, short DNA sequences that tag genetic traits to fast-track plant selection. Among these, SNPs stand out for their frequency, ease of detection and ability to distinguish both gene copies (co-dominance). Other key markers include simple sequence repeats (SSRs), random amplified polymorphic DNA (RAPDs) and amplified fragment length polymorphisms (AFLPs), all playing vital roles in maize genetic enhancement (85, 76).

Map-based cloning is another powerful method for studying specific genes. It involves using recombinant inbred lines to pinpoint and isolate functional genes (86). Genes such as ZmCCT and ZmCCA1 have been mapped and cloned for their roles in heat stress response (87). Transgene-free genome editing techniques, such as biolistic (gene gun) delivery in maize embryos, offer a promising path forward (88). The CRISPR/Cas9 system, Clustered Regularly Interspaced Short Palindromic Repeats, is a revolutionary gene-editing tool that enables precise modification of DNA. It offers faster and more accurate trait selection, especially in stress-resilient cultivars (89, 90). In maize, CRISPR has been effectively used to enhance drought tolerance by editing the ARGOS8 gene under the GOS2 promoter (91). Since its debut in 2013 with *Arabidopsis* and *Nicotiana* species, CRISPR has revolutionized crop improvement (92).

### Conventional vs marker-assisted breeding

While conventional breeding has long been the backbone of crop improvement, it faces significant challenges due to its slow pace and heavy reliance on favourable environmental conditions (93). For example, pyramiding multiple genes through conventional means can be inefficient and labour-intensive. In contrast, innovative strategies like shuttle breeding, as pioneered by CIMMYT, where breeding cycles are accelerated through multi-location field trials within a year offer a smart solution to fast-track variety development (6). Moreover, collaborative efforts among CIMMYT, ITA and National Agricultural Research Systems (NARS) in West Africa have resulted in drought-tolerant maize cultivars adapted to harsh climates. On the flip side, Marker-Assisted Selection (MAS) stands out as a game-changer. Unlike conventional breeding, MAS uses molecular markers, genetic signposts like SNPs and SSRs to precisely identify and select stress-resilient plants. This method not only speeds up the breeding process but also boosts the accuracy of selecting multiple stress-related traits simultaneously, ultimately saving time, labour and resources (84, 85).



## Conclusion

Heat stress is one of the most devastating abiotic stresses affecting plants at all stages, particularly during the reproductive phase, where it significantly reduces maize productivity. Although maize, a C<sub>4</sub> crop, exhibits some heat tolerance, temperatures above 35 °C hinder its growth and development. Studies reveal that maize responds to heat stress through morpho-physiological, biochemical and molecular changes. The core objective remains to identify suitable donor parents and develop thermotolerant cultivars. Modern strategies such as QTL mapping, genetic engineering, genomics, epigenetic regulation and conventional breeding, when integrated with smart agronomic practices like optimized sowing time and seed treatments, offer a holistic solution to managing heat stress. Especially under the current climate crisis, combining genetics, agronomy and biotechnology provides a sustainable pathway to develop resilient maize cultivars that withstand rising temperatures, reduce yield losses and ensure food security. As heat and drought often co-occur, future breeding programs must tackle both stresses in tandem to maximize crop stability and productivity.

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## Authors' contributions

KVN helped in conceptualization, supervision and editing. HS writing original draft. SS helped in conceptualization and supervision. SS, KP and VK helped in supervision. All authors were involved in the manuscript preparation and editing. All authors read and approved of the final manuscript.

## Compliance with ethical standards

**Conflicts of interest:** The authors declare that there is no conflict of interest.

**Ethical issues:** None

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