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Molecular and physiological mechanisms of heat and drought stress tolerance in maize (*Zea mays* L.)

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ABSTRACT

Maize (*Zea mays* L.) is one of the most important cereal crops worldwide, yet its growth and productivity are increasingly threatened by abiotic stresses, particularly drought and heat. These stresses, often occurring simultaneously under field conditions, severely impair photosynthesis, disrupt cellular homeostasis, and reduce yield potential. This review summarizes recent advances in understanding the physiological, biochemical, and molecular mechanisms underlying maize responses and tolerance to drought and heat stress. Key signaling pathways involving abscisic acid (ABA), calcium, reactive oxygen species (ROS), and mitogen-activated protein kinases (MAPKs) play central roles in stress perception and signal transduction. Transcription factors such as DREB, NAC, bZIP, HSF, and WRKY families coordinate downstream gene expression, regulating protective responses including osmotic adjustment, antioxidant defense, and protein stabilization. Moreover, the involvement of epigenetic modifications and transcriptional reprogramming highlights the complexity of maize adaptation and stress memory. Crosstalk between drought- and heat-responsive networks, exemplified by shared regulators such as ZmDREB2A, provides new insight into combined stress tolerance. Integration of multi-omics technologies, genome editing tools, and precision breeding holds great promise for developing climate-resilient maize varieties. Overall, a comprehensive understanding of these mechanisms is crucial for sustaining maize productivity and global food security under the escalating impacts of climate change.

Keywords: ABA signaling | Climate resilience | Drought stress | Heat stress | Maize (*Zea mays* L.) | Stress tolerance

1 | INTRODUCTION

Abiotic stresses exert extensive and often detrimental effects on global crop productivity. As the Earth's average surface temperature continues to rise, agricultural systems are increasingly exposed to severe and unpredictable environmental challenges, including drought, heat, and other forms of climatic stress [1]. Current projections estimate that by 2040, global mean temperatures will have increased by approximately 1.5°C to 2.0°C compared with pre-industrial levels. Such climatic shifts are expected to destabilize global food systems, compromise food security, and could result in a 30%–40% decline in worldwide crop yields if adaptive strategies are not implemented [2,3]. Consequently, developing climate-resilient crop varieties capable of maintaining productivity under fluctuating and extreme environmental conditions has become an urgent priority for global agriculture and food security.

Maize (*Zea mays L.*) is one of the world's most widely cultivated cereals, serving as a fundamental source of food, feed, bioenergy, and industrial materials [4]. Owing to its high photosynthetic efficiency and diverse applications, maize plays a pivotal role in sustaining both human and animal populations. However, it is particularly sensitive to environmental fluctuations. Predictions from the Intergovernmental Panel on Climate Change (IPCC) indicate that for each 1°C increase in global temperature, maize yields could decrease by approximately 7.4% [5]. This decline poses a major challenge for ensuring stable production in maize dependent regions, particularly in sub-tropical and tropical zones where climatic extremes are intensifying (Figure 1). To address this challenge, it is essential to elucidate the genetic, molecular, and physiological determinants of abiotic stress resilience. Recent advances in quantitative genetics, multi-omics integration, genome-wide association studies (GWAS), and high-throughput phenotyping have provided powerful tools to identify key genes, quantitative trait loci (QTLs), and signaling networks that contribute to maize stress adaptation [6,7]. These findings provide the molecular foundation for precision breeding and biotechnological interventions to enhance stress tolerance.

Plants experience multiple abiotic stressors such as drought, salinity, and heat throughout their life cycles, each of which triggers extensive reprogramming of cellular metabolism, growth, and development. When these stressors occur simultaneously, as often happens in natural environments, their combined effects can be synergistically detrimental [8]. Plant survival under such conditions depends on a complex network of molecular and physiological responses, including perception of external stimuli, signal transduction through intracellular cascades, and activation of stress-responsive transcriptional programs [9]. Understanding these interconnected processes is critical for unraveling how plants integrate multiple stress signals to maintain cellular homeostasis and sustain growth under adverse conditions.

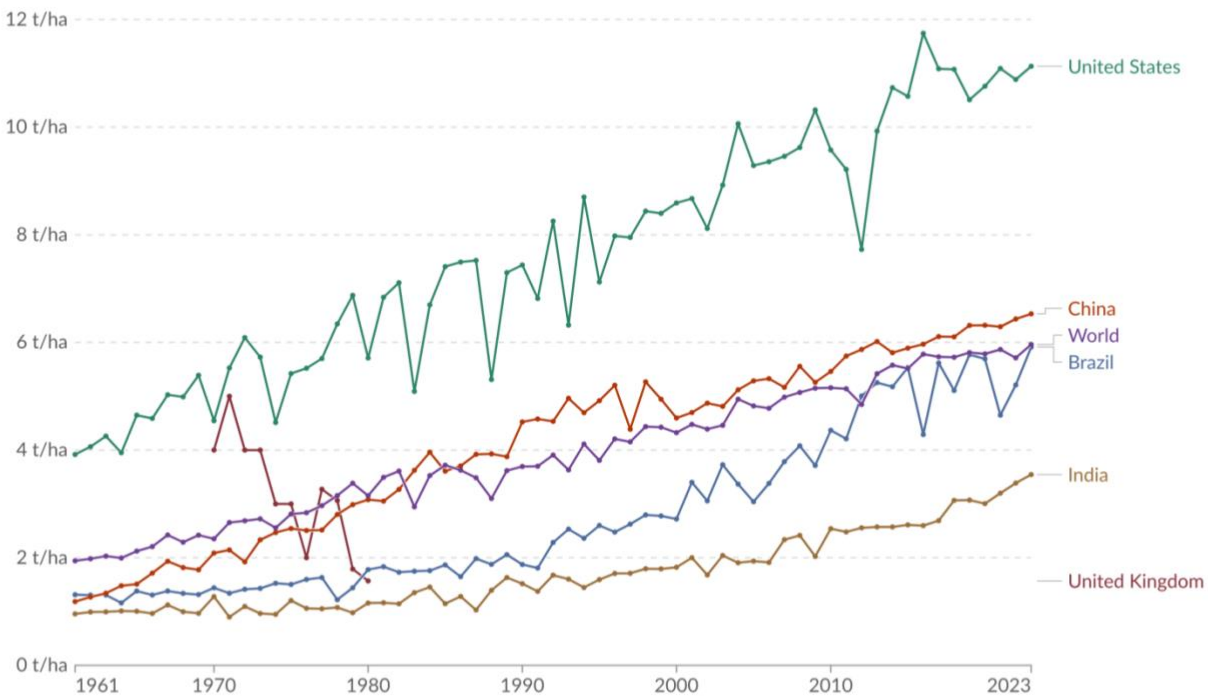

Figure 1 | Environmental stresses pose significant risks to maize production. Maize yields from 1961 to 2023 in selected countries and globally. Yield is presented as tonnes per hectare (t/ha) for the United States, China, Brazil, India, the United Kingdom, and the global average. Data highlight substantial regional differences and overall temporal trends in maize productivity over six decades. Source: Food and Agriculture Organization of the United Nations (2025), Our World in Data (https://ourworldindata.org/).

Stress perception in plants is primarily mediated by membrane-localized receptors and mechanosensitive or ion channels that detect changes in osmotic potential, temperature, or redox state. Upon perception, signals are transmitted through diverse molecular mediators, including receptor-like kinases (RLKs), mitogen-activated protein kinase (MAPK) cascades, calcium-dependent protein kinases (CDPKs), and transcription factors (TFs) that modulate downstream gene expression [10]. Secondary messengers such as cytosolic calcium ions (Ca^{2+}), reactive oxygen species (ROS), and nitric oxide (NO) act as dynamic signaling molecules, integrating external cues with intracellular responses to orchestrate appropriate defense mechanisms [11]. These signaling pathways often converge to regulate phytohormonal balance, cellular redox homeostasis, and metabolic adjustments that collectively determine the plant's stress tolerance level.

Abiotic stresses frequently lead to common downstream effects, including osmotic and ionic imbalances as well as oxidative stress [12]. These conditions trigger the accumulation of phytohormones such as abscisic acid (ABA), which serves as a central regulator of drought and heat responses. Concurrently, plants synthesize compatible osmolytes, small organic molecules such as soluble sugars, polyols, proline, and glycine betaine that stabilize proteins, membranes, and macromolecular structures. Additionally, antioxidant enzymes, including superoxide dismutase, catalase, and peroxidases, play crucial roles in detoxifying ROS and maintaining cellular redox equilibrium [10]. These biochemical and physiological adaptations are essential to ensure cellular integrity and survival under prolonged stress conditions.

In this review, we present a comprehensive overview of current insights into the mechanisms by which maize perceives and responds to abiotic stresses, with particular emphasis on drought and heat stress. We discuss recent advances in understanding stress-signal perception, intracellular signaling cascades, and the regulation of osmotic and ionic homeostasis. Furthermore, we explore the roles of phytohormones, ROS scavenging systems, and metabolic reprogramming in modulating maize stress responses. Finally, we highlight opportunities for leveraging genomic and biotechnological approaches to accelerate the breeding of maize cultivars with enhanced resilience to climate-induced environmental stresses.

2 | HIGH TEMPERATURE AND DROUGHT STRESS CONDITION

Extreme temperature and water availability are two of the most critical abiotic factors limiting maize growth and productivity worldwide (Figure 2). Exposure to excessively high or low temperatures disrupts various physiological, biochemical, and molecular processes, leading to impaired development, reduced photosynthetic efficiency, and ultimately, yield losses [13,14]. Likewise, fluctuations in soil moisture significantly affect crop growth and grain yield, as maize has a high transpiration rate and substantial water demand, making it particularly vulnerable to drought, the major cause of yield reduction globally [15-17].

Plants perceive and respond to temperature fluctuations through complex signaling networks that regulate gene expression and metabolic adjustments [14]. The initial perception of temperature changes occurs mainly at the plasma membrane, where variations in membrane fluidity are detected by membrane-associated thermosensors or ion channels [18,19]. These early sensing events activate secondary messengers such as cytosolic Ca^{2+}, which serve as key mediators of thermal signaling. Changes in Ca^{2+} concentration activate calcium-dependent protein kinases and other signaling enzymes that regulate transcription factors (TFs) controlling stress-responsive gene expression [20-22]. The activation of these pathways leads to diverse physiological responses that enhance thermotolerance.

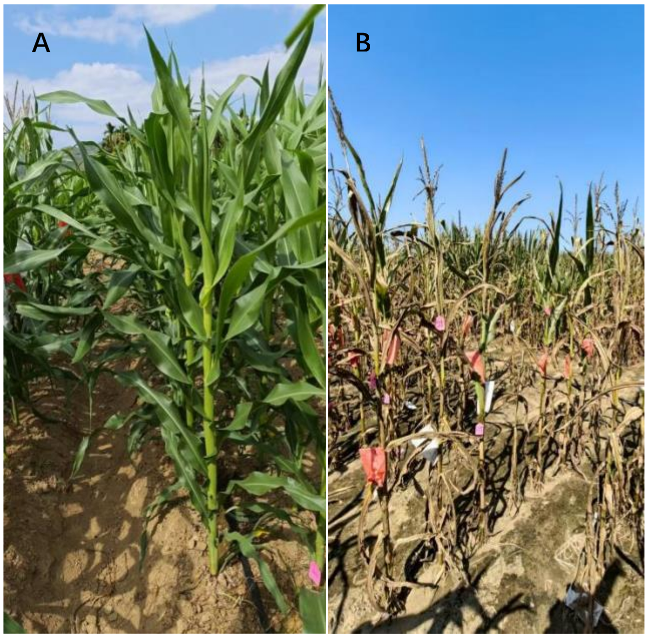

Figure 2 | Contrasting phenotypes of maize under well-watered (A) and heat+drought stress (B) field conditions. Well-watered plants display healthy growth and leaf expansion, while heat+drought stressed plants exhibit severe wilting, leaf senescence, and reduced vigor. These images highlight the impact of water deficit on maize morphology and productivity.

Similarly, under water stress, maize activates a range of physiological and molecular mechanisms to maintain growth and productivity. Drought stress not only limits biomass accumulation but also affects grain filling and quality, posing a serious challenge to sustainable production [23]. Understanding the molecular basis of maize responses to water deficit is therefore crucial for improving drought and waterlogging tolerance. Research efforts have focused on identifying drought-responsive genes, transcription factors, and regulatory networks involved in stomatal regulation, osmotic adjustment, and antioxidant defense. Insights gained from these studies are contributing to the development of stress-resilient maize cultivars through molecular breeding and genetic engineering approaches.

2.1 | Mechanisms underlying maize heat stress adaptation

Maize, a thermophilic C_4 crop of tropical and subtropical origin, thrives optimally under moderate temperature conditions ranging between 25 °C and 28 °C. However, with the ongoing global climate change and the predicted rise in mean surface temperature, episodes of heat stress are becoming more frequent, intense, and prolonged, posing a major constraint to agricultural productivity and food security. Among the world's four major crops, maize, rice, wheat, and soybean, maize has been identified as the most heat-sensitive species, with its grain yield showing the steepest decline under elevated temperature conditions [24]. When exposed to temperatures above 35 °C for extended periods, maize experiences irreversible physiological impairments that disrupt cellular homeostasis, reproductive development, and grain filling (Figure 2). Particularly during anthesis and grain formation, heat stress can reduce kernel set, pollen viability, and silk receptivity, leading to yield reductions of up to 90% [25].

Heat tolerance is an intricate and polygenic trait governed by multiple physiological, biochemical, and molecular mechanisms (Figure 3). Understanding the genetic architecture and signaling pathways involved in thermotolerance is crucial for developing resilient maize varieties through molecular breeding and biotechnological interventions. At the physiological level, heat stress perturbs membrane integrity, alters thylakoid fluidity, inhibits photosystem II (PSII) activity, and suppresses carbon assimilation. These effects impair energy metabolism and elevate the production of reactive oxygen species (ROS), resulting in oxidative damage and protein denaturation [26]. The early perception of heat stress is thought to occur at the plasma membrane and within organelle membranes, where changes in lipid fluidity and protein conformation act as thermosensory cues. These cues trigger Ca^{2+} influxes and ROS accumulation in the cytosol, which together initiate downstream signal transduction cascades that activate heat-responsive gene expression [26].

In rice, the plasma membrane-localized E3 ubiquitin ligase TT3.1 functions as a thermosensor, working in concert with the chloroplast precursor protein TT3.2 to protect chloroplast structure and maintain photosynthetic efficiency [27]. Similarly, the G protein TT2 facilitates Ca^{2+} influx under thermal stress, thereby amplifying heat-induced signaling [28]. Although such mechanisms are well documented in other cereals, the molecular perception of heat in maize remains less clearly defined. Recent findings indicate that ZmRBOHB, a maize NADPH oxidase responsible for ROS production, is activated through phosphorylation by ZmCPK7, a calcium-dependent protein kinase. This modification enhances ROS-mediated signaling and contributes to acquired thermotolerance [29]. These findings collectively suggest that Ca^{2+}-dependent phosphorylation and ROS accumulation form a core component of maize's heat-sensing and defense system.

At the transcriptional level, plants deploy complex gene regulatory networks to reprogram metabolism and enhance thermoprotection. Central to these networks are heat shock transcription factors (HSFs), which act as master regulators of the heat shock response [30,31]. HSFs are evolutionarily conserved among eukaryotes and are classified into three classes, A, B, and C, based on their structural domains and transcriptional activity [32]. Members of the HSFA1 subgroup serve as primary regulators that initiate downstream transcriptional cascades by activating key stress-responsive genes such as *DREB2A*, *HSFA2*, *HSFA7a*, and *HSFB* [33]. Functional disruption of HSFA1 in tomato (*Solanum lycopersicum*) and *Arabidopsis thaliana* severely compromises heat tolerance, confirming its critical regulatory role [33].

In maize, RNA-seq analyses have revealed that high-temperature treatment markedly induces expression of HSF-A2, HSF-A6, and HSF-B2 subgroup genes [34]. Furthermore, overexpression of maize HSF-A subgroup members such as *ZmHSF01*, *ZmHSF05*, and *ZmHSF06* in transgenic *Arabidopsis* enhances heat resilience, indicating functional conservation across species [35-37]. HSFs recognize specific DNA motifs known as heat shock elements (HSEs) within the promoter regions of heat shock protein (HSP) genes, driving their rapid transcriptional activation under heat stress [38]. HSPs, which act as molecular chaperones, are crucial for maintaining protein homeostasis by preventing aggregation, facilitating refolding, and promoting degradation of denatured proteins.

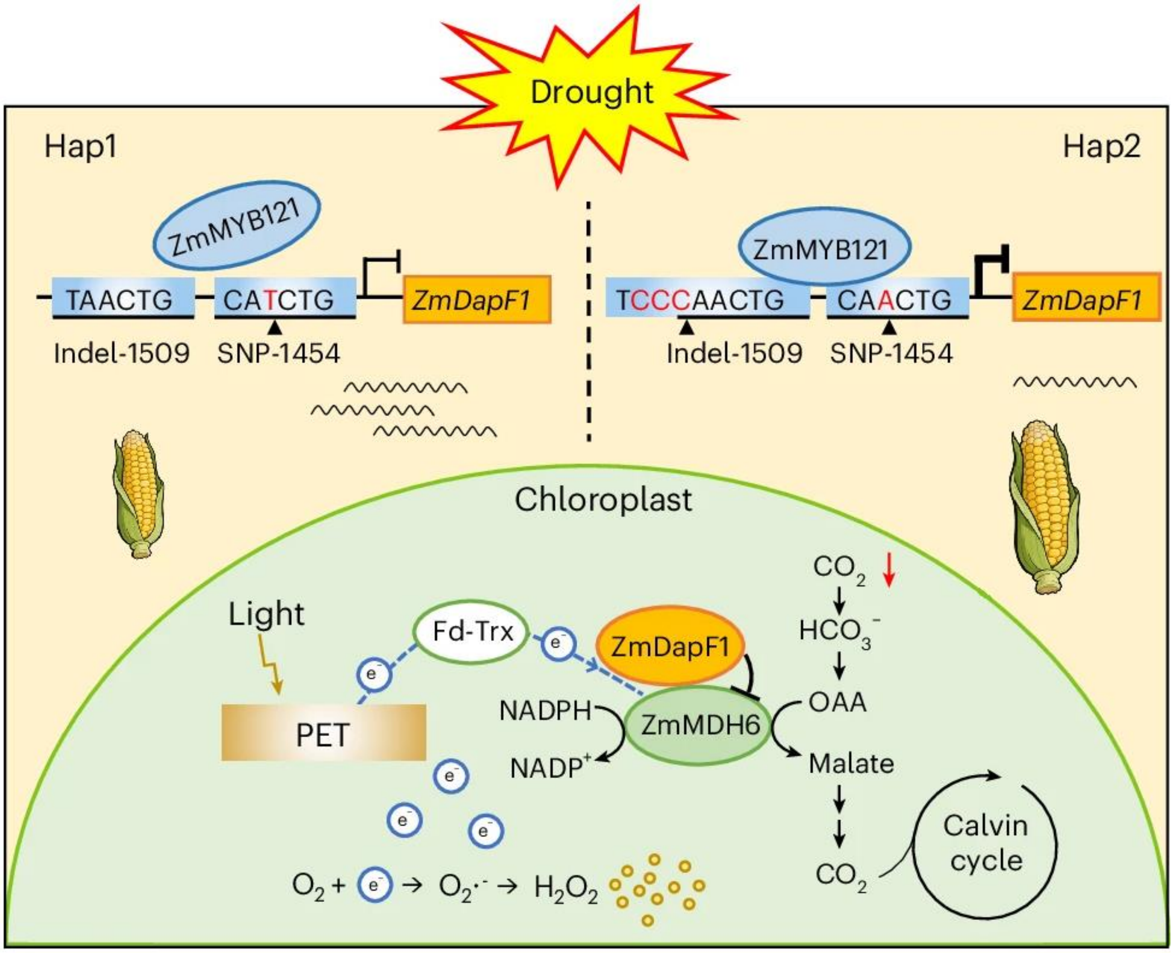

Figure 3 | Schematic representation illustrating the proposed mechanism by which ZmDapF1 regulates maize drought tolerance. Natural promoter variations in ZmDapF1 enhance MYB121 binding to the ZmDapF1-Hap2 allele, leading to suppression of ZmDapF1 expression. This alleviates ZmDapF1-mediated inhibition of ZmMDH6. During drought, stomatal closure limits CO_2 uptake, but increased ZmMDH6 activity in ZmDapF1-Hap2 germplasm redirects excess electrons into oxaloacetate (OAA), generating malate and regenerating $NADP^+$, supporting chloroplast redox homeostasis. Additionally, malate decarboxylation releases CO_2 for Calvin cycle carbon fixation. The figure is reprinted from published article of Lian et al [39].

Although the general functions of HSPs are well characterized in plants, their maize-specific roles remain incompletely defined. Quantitative trait locus (QTL) analyses have identified HSP101, a member of the HSP100 family, as a determinant of thermotolerance during male meiosis, ensuring normal pollen development under high temperatures [40,41]. In addition to the cytosolic chaperone network, the unfolded protein response (UPR) in the endoplasmic reticulum (ER) plays a pivotal role in restoring proteostasis under heat stress. In *Arabidopsis*, the transcription factor bZIP60 mediates UPR activation by inducing stress-responsive genes [42]. In maize, its ortholog ZmbZIP60 directly regulates *Hsftf13*, thereby linking ER stress signaling with the cytosolic heat shock response [43]. Heat exposure triggers unconventional splicing of *ZmbZIP60* mRNA, likely catalyzed by ZmIRE1, implying conservation of the IRE1–bZIP60 signaling module in monocots [43]. Genetic and transcriptomic analyses indicate that *ZmbZIP60* expression varies between tropical and temperate maize lines, suggesting that this locus underwent adaptive selection during domestication [44]. Moreover, ZmbZIP60 interacts with the ER-localized chaperone ZmHUG1, which prevents heat-induced protein aggregation, thereby reinforcing ER proteostasis and thermotolerance [45]. These insights highlight the central importance of the bZIP60-mediated UPR pathway in maize adaptation to elevated temperatures. Future studies should explore whether other conserved UPR regulators, such as bZIP28 and autophagy-related protein ATG8, also contribute to ER quality control and heat stress resilience [46].

Heat stress rarely occurs in isolation; rather, it often coincides with drought, compounding the severity of abiotic stress effects. Crosstalk between heat and drought signaling pathways ensures coordinated activation of protective responses. In *Arabidopsis*, DREB2A acts as a dual-function transcription factor regulating genes involved in both heat and drought stress [47]. Likewise, in maize, ZmDREB2A enhances tolerance to these stresses by activating downstream genes encoding late embryogenesis abundant (LEA) proteins and various HSPs [48]. This evidence suggests that the DREB2A–HSP module forms an evolutionarily conserved regulatory circuit that integrates multiple abiotic stress responses, enabling plants to maintain homeostasis under fluctuating environmental conditions.

2.2 | Integrative signaling and adaptive strategies for maize drought resilience

Drought is among the most pervasive abiotic stresses limiting plant productivity and global food security. The ability of plants to perceive, respond to, and adapt to water-deficit conditions has therefore been extensively explored at morphological, physiological, biochemical, and molecular levels [49]. Plants exhibit remarkable plasticity, having evolved multiple adaptive mechanisms to withstand drought stress, which can be broadly categorized into drought escape, drought avoidance, and drought tolerance [17]. Drought escape enables plants to complete their life cycle rapidly before the onset of severe water limitation, primarily through accelerated flowering and seed set (Figure 2). Drought avoidance minimizes water loss and enhances water uptake via structural and physiological optimization, such as reduced stomatal density and aperture, smaller and more reflective leaf canopies, and extensive or deeper root systems capable of accessing subsurface moisture [49,50]. In contrast, drought tolerance involves cellular and metabolic reprogramming that permits physiological activity under low water potential (Figure 4). This includes the synthesis of hydrophilic proteins, detoxification enzymes, and osmoprotectants (e.g., proline, glycine betaine, and soluble sugars), which collectively stabilize macromolecules, maintain osmotic balance, and protect cellular structures from dehydration-induced damage. Together, these diverse adaptive responses constitute drought resistance, a term encompassing the integrated strategies plants employ to survive and reproduce under water-limited environments.

Among the internal regulators of drought adaptation, abscisic acid (ABA) serves as a central signaling molecule mediating systemic and cellular responses to water deficit. ABA accumulation under drought conditions triggers a signaling cascade involving the interaction between ABA receptors PYRABACTIN RESISTANCE 1 (PYR)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCARs) and members of the clade A protein phosphatase type 2C (PP2C-A) family, resulting in PP2C inhibition [51,52]. The suppression of PP2Cs releases SNF1-RELATED PROTEIN KINASE 2s (SnRK2s) from inhibition, allowing them to phosphorylate downstream effectors such as SLOW ANION CHANNEL-ASSOCIATED 1 (SLAC1), RESPIRATORY BURST OXIDASE HOMOLOG F (RBOHF), and the ABA-responsive transcription factors ABRE-BINDING PROTEIN (AREB) and ABRE-BINDING FACTOR (ABFs). These interactions orchestrate stomatal closure, ROS generation, and transcriptional regulation of drought-responsive genes, thereby contributing to water conservation and enhanced drought resilience [53,54].

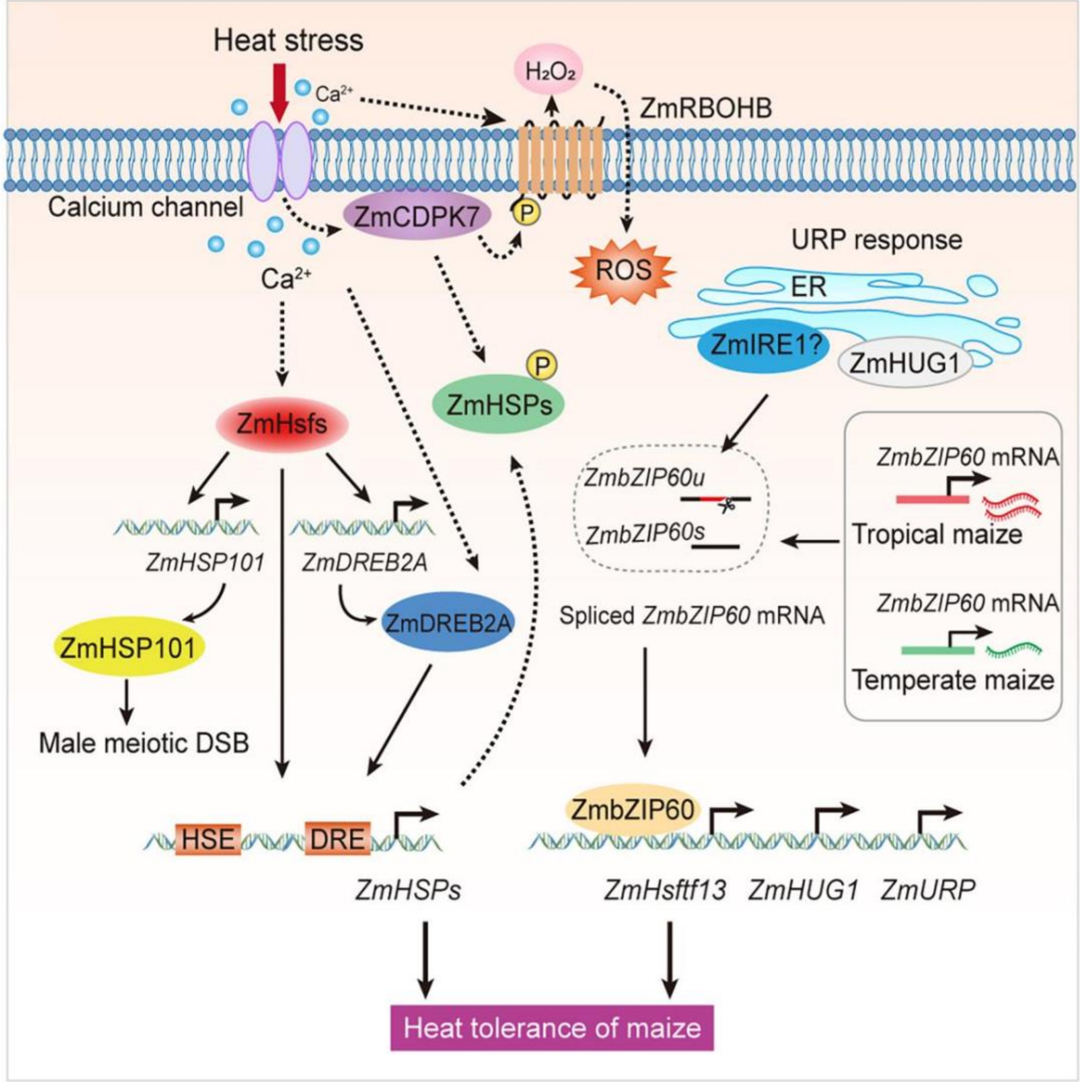

Figure 4 | Maize heat stress response model. Upon exposure to elevated temperatures, ZmCPK7 activates ROS production by phosphorylating RBOHB. Heat also triggers transcriptional activation of heat-responsive genes through key transcription factors, including ZmHsfs and ZmDREB2s. The unfolded protein response (UPR) is coordinated by bZIP60, when spliced enters the nucleus to induce UPR gene expression. Notably, tropical maize lines show stronger bZIP60 induction under heat stress compared to temperate lines, reflecting domestication-driven selection for heat resilience. The figure is reprinted from published article of Yang et al [6].

In maize, the core ABA signaling components and their interactions have been characterized through molecular and genetic approaches, including yeast two-hybrid screening [55]. For instance, *ZmOST1*, a homolog of *Arabidopsis* OPEN STOMATA 1 (OST1)/SnRK2.6, is transcriptionally upregulated in response to drought and ABA treatments [56]. Functional studies have revealed that ZmOST1 deficiency impairs ABA-mediated stomatal closure, leading to reduced drought tolerance. Similarly, ZmPP2CA10 contributes to ABA signaling by interacting with SnRK2s and ZmPYL receptors under drought stress [57]. The maize anion channel ZmSLAC1, homologous to *AtSLAC1*, is also crucial for ABA-induced stomatal closure [58]. In addition, plasma membrane-localized Ca^{2+}-dependent protein kinases (ZmCPK35 and ZmCPK37) activate ZmSLAC1 to facilitate stomatal closure in response to ABA and Ca^{2+} signals, while ZmRBOHC, an *AtRBOHF* homolog, promotes reactive oxygen species (ROS) accumulation in guard cells to reinforce stomatal closure [59].

Mitogen-activated protein kinase (MAPK) cascades also contribute significantly to drought signaling and ABA crosstalk [60-62]. PP2Cs from clades B and F serve as regulators of MAPK signaling in maize. For example, ZmPP2C26 (clade B) dephosphorylates ZmMAPK3 and ZmMAPK7, thereby acting as a negative regulator of drought tolerance [63,64]. Likewise, ZmPP84 (clade F) interacts with and dephosphorylates ZmMEK1, suppressing its activity. Upon ABA accumulation, inhibition of ZmPP84 is alleviated, allowing ZmMEK1 to activate SALT-INDUCED MITOGEN-ACTIVATED PROTEIN KINASE 1 (ZmSIMK1), which in turn phosphorylates ZmSLAC1, facilitating stomatal closure [65]. While ABA is the primary drought-related hormone, ethylene also plays a significant role in modulating maize drought responses and yield stability [66-68]. Downregulation of 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID SYNTHASE 6 (ACS6), a key enzyme in ethylene biosynthesis, enhances grain yield during drought conditions [69]. Overexpression of ZmARGOS1 (ZAR1) and ZmARGOS8 an auxin-regulated genes that modulate ethylene sensitivity, confers improved drought tolerance and higher grain yields under both well-watered and water-limited environments [66-68].

Transcriptional regulation forms another major layer of drought adaptation. Numerous transcription factor (TF) families are involved in maize drought signaling, including DREB/CBF, bZIP, NAC, WRKY, MYB, bHLH, and AP2/ERF [70,71]. Notably, ZmbZIP4 enhances ABA biosynthesis and promotes root system development [72], while ZmPTF1, a bHLH TF, positively regulates root elongation and ABA-mediated drought responses [73]. ZmDREB2.7 functions in an ABA-independent pathway, improving drought tolerance [74], whereas NAC family TFs such as ZmNAC48, ZmNAC49, ZmNAC111, and ZmNAC075 act as transcriptional activators that enhance drought resistance [75-77]. Members of the AP2/ERF superfamily further contribute to drought resilience by regulating ethylene- and ABA-responsive gene networks [78,79]. ZmFDL1/ZmMYB94 regulates genes associated with cuticular wax deposition to minimize water loss [80], while ZmLBD5 modulates gibberellin and ABA biosynthesis during drought adaptation [81]. Additionally, NF-Y transcription factors have been implicated in ABA-dependent drought regulatory pathways [78,82,83].

At the reproductive level, drought-induced asynchrony between anthesis and silking (ASI) remains a key yield-limiting factor in maize [84]. Drought delays silk emergence more than pollen shedding, leading to poor fertilization and reduced kernel set. The downregulation of cell-expansion-related genes such as ZmEXPA4 contributes to this delay. Field trials have shown that upregulation of ZmEXPA4 via drought-inducible promoters shortens ASI and alleviates drought-associated yield loss [85], underscoring the value of maintaining cell wall loosening and expansion processes during stress. Emerging evidence also points to epigenetic regulation as a crucial dimension of drought adaptation [86,87]. DNA methylation, histone modifications, and chromatin remodeling alter transcriptional activity without changing the DNA sequence, thereby establishing a heritable stress memory that primes plants for future stress encounters. ATP-dependent chromatin remodeling complexes SWI/SNF, ISWI, CHD, and INO80—modulate histone-DNA interactions to control gene accessibility [88]. The SWI/SNF complex, in particular, directly communicates with transcriptional activators or repressors to regulate gene expression via RNA polymerase II. In maize, *ZmCHB101*, a homolog of *Arabidopsis* SWI3D, functions as a core component of this complex and plays an essential role in osmotic stress response by ensuring RNA polymerase II occupancy at promoter regions of stress-responsive genes [89].

Although early functional characterizations of drought-responsive genes in maize relied heavily on homologous studies from *Arabidopsis thaliana*, advances in genome editing and transgenic technologies have now enabled species-specific functional validation. These tools, including CRISPR/Cas-mediated gene editing, RNA interference, and overexpression systems, have provided robust platforms to elucidate gene function directly in maize. Consequently, laboratory findings can now be more effectively translated into field applications, paving the way for the genetic improvement of maize drought resilience and sustainable crop production under climate change.

3 | CONCLUSION AND FUTURE PERSPECTIVES

Drought and heat stresses are among the most critical abiotic constraints limiting maize productivity worldwide. Both stresses severely disrupt cellular homeostasis, photosynthetic efficiency, and reproductive success, ultimately leading to substantial yield losses. Despite the differences in their primary physiological triggers, water deficit in drought and elevated temperature in heat stress, these stresses often co-occur and induce overlapping molecular and biochemical responses. Plants have evolved intricate adaptive strategies that encompass morphological plasticity, physiological regulation, biochemical adjustment, and transcriptional and epigenetic reprogramming to maintain growth and survival under adverse environmental conditions. Abscisic acid (ABA) signaling serves as a central integrator of drought responses, orchestrating stomatal regulation, osmotic adjustment, and antioxidant defense through PP2C–SnRK2–ABF signaling cascades. Similarly, ethylene, gibberellin, and calcium-dependent pathways modulate drought-induced developmental and metabolic changes. In maize, numerous genes and transcription factors such as *ZmDREB2.7*, *ZmNAC111*, *ZmHSF01*, and *ZmOST1* have been identified as key regulators of drought tolerance through both ABA-dependent and -independent mechanisms. Moreover, recent advances in understanding MAPK signaling and epigenetic regulation, including chromatin remodeling and histone modification, have revealed additional layers of drought-responsive control that contribute to stress memory and long-term adaptation. Heat stress, on the other hand, primarily compromises protein stability, membrane integrity, and redox balance. The perception of high temperature in maize involves calcium and ROS signaling networks, exemplified by *ZmCPK7*-mediated activation of *ZmRBOHB*. The downstream transcriptional response is largely governed by heat shock transcription factors (HSFs) and heat shock proteins (HSPs), which together maintain proteome stability and cellular homeostasis. The *bZIP60*-mediated unfolded protein response (UPR) further links ER stress signaling to heat tolerance, highlighting the interconnected nature of cytosolic and organellar stress mitigation pathways. Importantly, functional studies of *ZmHSF*, *ZmHSP101*, and *ZmbZIP60* have deepened our understanding of maize thermotolerance and its evolutionary diversification between tropical and temperate germplasm. Crosstalk between drought and heat signaling networks is increasingly recognized as a critical determinant of stress resilience. Shared regulatory hubs such as *ZmDREB2A*, which activate both LEA and HSP genes, exemplify how plants integrate multiple stress responses at the transcriptional level. These convergent pathways allow maize to mount coordinated defenses against complex environmental challenges.

Looking ahead, integrating multi-omics approaches, including genomics, transcriptomics, proteomics, metabolomics, and epigenomics, will be vital for elucidating the complex gene networks that underpin drought and heat tolerance. Genome editing technologies such as CRISPR/Cas systems, together with precision phenotyping and machine-learning-based modeling, offer unprecedented opportunities to accelerate the development of climate-resilient maize varieties. Ultimately, translating molecular insights into field-level applications will be key to sustaining maize productivity and global food security under the escalating impacts of climate change.

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AUTHOR CONTRIBUTIONS

Conceptualization: Y.H. and T.Y. | Visualization: D.S. and R.Z. | Writing – original draft: Y.H. and T.Y. | Writing – review and editing: D.S. and R.Z. The authors confirm their contributions to the paper as follows.

DATA AVAILABILITY STATEMENT

The authors have nothing to report.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the preparation of this work the author(s) used ChatGPT 3.5 in order to improve readability and language. After using this tool, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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