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The Impact of High Temperature Stress on Maize Reproductive Development and the Regulation Mechanism of Heat Tolerance

Zhonggang Li [1], Minli Xu [2]
1 Tropical Specialty Crops Research Center, Hainan Institute of Tropical Agricultural Resouces, Sanya, 572025, Hainan, China
2 Hainan Provincial Key Laboratory of Crop Molecular Breeding, Sanya, 572025, Hainan, China
Corresponding author: minli.xu@hitar.org

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Abstract Maize (*Zea mays* L.) is particularly vulnerable to heat stress during its reproductive stage, making its yield closely tied to weather conditions—an issue that's becoming more pressing as global temperatures continue to rise. This study looks at how heat stress negatively impacts both male and female reproductive parts of maize. For instance, pollen loses its viability, anthers may fail to open properly, filaments emerge late, and ovule development can be interrupted, all of which disrupt the pollination and fertilization processes. These reproductive issues are not just surface-level—they reflect deeper physiological and molecular changes. Heat stress can upset hormone balance, increase oxidative stress, and alter how certain genes behave. One clear outcome is a drop in the number of kernels formed and overall grain yield. Timing also plays a key role; when and how long the plant is exposed to high temperatures can make a big difference. This study brings together recent findings on heat-responsive genes, key QTLs, and regulatory networks. It highlights the involvement of heat shock proteins (HSPs), systems that manage reactive oxygen species (ROS), transcription factors, and non-coding RNAs in helping maize cope with high temperatures. Real-world examples also show that it's possible to breed maize varieties that are more heat-tolerant. Finally, this study suggests that combining these insights with omics tools could lead to better strategies for future crop improvement. It underlines the need to accelerate breeding programs that are prepared for climate challenges and offers a solid foundation for future work on heat tolerance in maize.

Keywords High temperature stress; Maize reproductive development; Heat tolerance mechanisms; Seed setting rate; Molecular breeding

1 Introduction

Maize (*Zea mays* L.) is an important food crop in the world and one of the main sources of food, feed and industrial raw materials. About one-third of the world's population relies on maize as their main food. Its reproductive development process plays a decisive role in the formation of crop yield because it is directly related to the formation and development of grains. The key processes in the reproductive stage, including flowering, silking and filling, are highly sensitive to environmental stress, among which high temperature stress has a particularly significant impact on maize production (Lizaso et al., 2018; Tiwari and Yadav, 2019). Temperature has a certain effect on the differentiation and development of male and female ears. Excessive temperature will inhibit the differentiation of ears. In this process, successful fertilization and grain formation are affected by physiological characteristics such as pollen vitality, stigma receptivity and fruiting rate. High temperature stress can lead to pollen sterility, decreased fruiting rate and grain abortion, resulting in a significant reduction in maize yield (Raviteja et al., 2024). Among them, the anthesis-silking interval (ASI) and the duration of pollen shedding are the key phenotypic characteristics that affect reproductive success under high temperature stress. High temperature stress promotes the shedding of stamens and pollen, prolongs the silk interval, and reduces the number and vitality of pollen shedding, but has no significant effect on the silking time, which affects the fertilization and fruiting of corn (Alam et al., 2017).

High temperature stress is one of the main limiting factors in corn production, and the intensification of climate change and global warming has further exacerbated this problem. High temperature stress significantly affects the key growth stages of corn. The yield loss caused by high temperature stress in each growth stage is as follows:

flowering stage > filling stage > ear stage > seedling stage. High temperature stress during the flowering stage of corn will lead to a decrease in pollen viability, and the higher the temperature, the greater the decrease in pollen viability, which also leads to a decrease in the number of grains, which is one of the main reasons for the reduction in corn yield (Jagtap et al., 2023). The physiological and molecular response mechanisms of corn to high temperature stress involve the regulation of carbon metabolic pathways, the maintenance of reactive oxygen species (ROS) homeostasis, and changes in plant hormone signaling networks. Mechanisms such as signal transduction pathways, regulation of transcription factors, and expression of genes related to high temperature stress resistance provide key molecular markers and candidate gene resources for accelerating the breeding of new corn varieties (Chen et al., 2023; Lv et al., 2024).

This study focuses on understanding how high temperatures affect maize during its reproductive stage and explores the underlying mechanisms that help the plant cope with heat. By reviewing recent findings on the physiological, biochemical, and molecular responses of maize under heat stress, this study seeks to identify important traits and genetic pathways linked to heat tolerance. The goal is to offer a solid scientific foundation for breeding and management approaches that enhance maize's resilience to rising temperatures, ultimately supporting stable production in a warming climate.

2 Effects of High Temperature on Male Reproductive Development

2.1 Impairment of anther and pollen development

High temperature stress has a significant negative impact on the development of maize anthers and pollen, making the anther wall thicker and difficult to crack, resulting in less pollen shedding and low pollen vitality, resulting in male sterility and reduced yield (Figure 1). At critical stages of pollen development, such as the tetrad stage, high temperature stress can cause abnormal meiosis and premature spore abortion, produce pollen with germination defects, and thus lead to serious yield losses in maize (Begcy et al., 2019). The high sensitivity of anthers and pollen grains to high temperature stress at certain developmental stages is one of the main factors for maize fruiting failure. The tapetum cells on the surface of pollen grains will degenerate due to high temperature damage (Giorno et al., 2013). High temperature stress can also damage the differentiation of the anther tapetum and microspore formation, inhibit anther cracking, reduce pollen dispersal, further aggravate the degree of fertility damage, and affect food production and safety.

2.2 Altered hormonal balance and gene expression

High temperature stress affects hormone homeostasis and related gene expression patterns in maize male reproductive organs. Wang et al. (2024) showed that high temperature stress changes the levels of key hormones such as abscisic acid (ABA), jasmonic acid (JA) and its derivatives, indoleacetic acid (IAA) and gibberellin (GA3), which affect pollen development. The ratio of IAA to ABA and ABA to GA3 increases, ultimately impairing pollen fertility. Transcriptome analysis further revealed the dysregulated expression of genes related to starch, lipid and energy biosynthesis. The starch stored in pollen can provide energy and carbon skeleton for pollen development, germination and pollen tube elongation. Although the expression of some genes involved in the development process remains stable, the changes in transcriptional regulatory networks and metabolic pathways caused by high temperature stress show significant and lasting effects, characterized by the inhibition of normal cellular protein synthesis mediated at the transcriptional and translational levels and the induction of heat shock protein (HSP) synthesis (Howarth and Ougham, 1993).

2.3 Physiological and cellular damage in male organs

Under high temperature stress, physiological and cellular damage to maize male reproductive organs is mainly manifested as reduced starch content, decreased enzyme activity and blocked pollen germination. Although heat stress can induce an increase in the activity of antioxidant enzymes in pollen, it can also cause irregular and loosely arranged epidermal cells of the anther wall, damaged connective vascular tissue, wrinkled pollen surface, sunken or severely deformed pollen germination holes, and reduced volume and density of starch grains in pollen. These physiological changes ultimately lead to weakened pollen vitality and germination ability, and then cause maize fertility loss. Sensitivity to heat stress is not uniform during pollen development and function, and pollen grains are more sensitive in the early stages of development than in the later stages. Although the heat shock response of mature pollen is relatively limited, heat shock proteins (HSPs) induced by heat stress still play a role in physiological responses (Dupuis and Dumas, 1990).

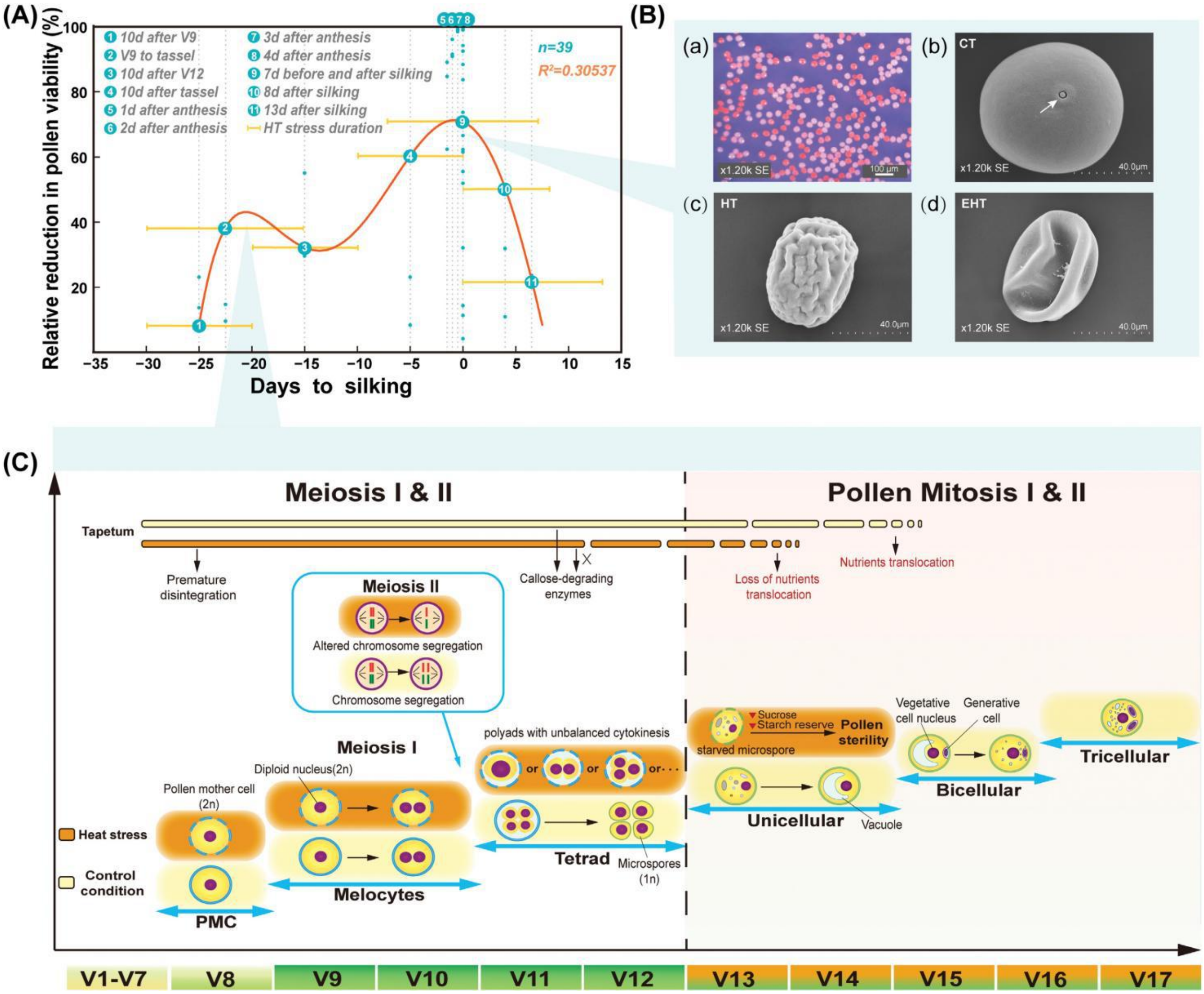


Figure 1 Effect of heat stress on pollen viability of maize at different periods (Adopted from Lv et al., 2024)

Image caption: (A) The blue circles indicate the period of heat stress application in maize from different trials; the yellow bars represent the period for which heat stress lasted; the dotted line is positioned at the midpoint of the heat stress period in each trial, and the numbers in the blue circles are the data number of each trial; the orange line is obtained by fitting all data points. (B) Picture of pollen viability by 2,3,5-triphenyltetrazolium chloride (TTC) staining (darker colors show increased viability) (a) SEM images of pollen grains under control temperature (CT; 32/22 °C), (b) high temperature (HT; 36/26 °C), (c) extremely high temperature (EHT; 40/30 °C; d) treatments. White arrows indicate the aperture of pollen. (C) Schematic overview of cytological alterations imposed by heat stress during male gametophyte development tracked by the leaf collar method of maize. PMC, pollen mother cell (Adopted from Lv et al., 2024)

3 Effects of High Temperature on Female Reproductive Development

3.1 Inhibition of ovule and silk development

High temperature stress has a significant impact on the development of maize female reproductive structures, especially the development of ovules and filaments. The rate of filaments spitting out bracts is significantly reduced, the number of hairs on filaments is reduced, and the vitality of filaments is reduced. High temperature stress can delay the development of stigma, make it difficult for female ears to spin silk, prolong the interval between tasseling and silking, shorten the pollination time, and thus prolong the anthesis-silking interval (ASI), which is the critical window period for successful fertilization (Alam et al., 2017). Delayed filament development will lead to dehydration and wilting under high temperature conditions, loss of mucus on the surface, and ultimately affect the grain setting rate and grain yield (Waqas et al., 2021). High temperature stress changes the sugar composition of silk, and the supply of hexose inhibits the growth of pollen tubes (Wang et al., 2023).

3.2 Heat-induced disturbances in pollination and fertilization

High temperature stress has a destructive effect on the pollination and fertilization process of corn. When the temperature is higher than 32 ℃-35 ℃, it is not conducive to pollination. The interaction stage between pollen and stigma and the early grain development stage are highly sensitive to high temperature stress, which directly leads to a decrease in crop yield (Mitchell and Petolino, 1988). In the post-pollination stage, high temperature stress inhibits the early growth of pollen tubes. The growth process of pollen tubes in the style/filament and ovary transport bundle tissue is more sensitive to high temperature, which in turn causes grain sterility (Lizaso et al., 2018). When the pollinated spikelets are exposed to a high temperature environment exceeding 36°C, continuous high temperature stress can cause abortion of plant fruiting organs during flowering and maturity, and the fertilization rate is significantly reduced. This phenomenon shows that high temperature stress has a serious negative impact on the fertilization process.

3.3 Hormonal and molecular dysregulation in female tissues

High temperature stress can cause changes in hormone and molecular levels in female reproductive tissues of maize. Superoxide dismutase (SOD) first decreases and then increases, and the activities of peroxidase (POD) and catalase (CAT) continue to increase, thus affecting their development and function. The accumulation of reactive oxygen species (ROS) and significant changes in the levels of plant hormones (such as abscisic acid and auxin) can affect the growth of pollen tubes. High temperature stress can also induce the synthesis of heat shock proteins (HSPs) in female tissues. Under normal conditions, the content of Hsps is less than 5% of the total protein, but under adverse external environmental conditions, especially when stimulated by heat stress, it will be synthesized in large quantities, accounting for about 15% of the total protein. This is one of the important defense mechanisms of plants to cope with heat stress (Dupuis and Dumas, 1990).

4 Impact of Heat Stress on Seed Setting Rate and Yield Formation

4.1 Reduction in kernel number and grain filling

High temperature stress significantly reduces the number of maize grains and affects the grain filling process. High temperature accelerates the dry weight accumulation in the early stage of grain filling, but reduces the dry weight of grains in the mature stage, thus having a negative impact on yield formation. In key reproductive stages such as pollen development and flowering, high temperature stress can cause pollen abortion and reduced stigma receptivity, resulting in reduced fertilization rate and fewer grains (Lizaso et al., 2018; Waqas et al., 2021). Among them, the period from meiosis of pollen mother cells to the early stage of microspore formation is sensitive to high temperature stress. High temperature affects the meiotic process of pollen mother cells, resulting in increased frequency of homologous chromosome crossing and recombination, abnormal chromosome separation, and the formation of incomplete tetrads and microspores with abnormal chromosome ploidy, leading to male sterility and reduced grain number. High temperature stress also impairs grain filling efficiency by interfering with the activities of bound starch synthase (GBSS), soluble starch synthase (SSS), sucrose synthase (SS) and sucrose synthase phosphatase (SPS), resulting in a significant decrease in corn yield (Bheemanahalli et al., 2022).

4.2 Timing and duration of stress exposure

In recent years, the frequency of high temperature weather has increased and the duration of stress has prolonged, and the impact on corn has become increasingly serious. During sensitive developmental stages, such as pollen development and the microspore tetrad stage of flowering (especially shortly after pollination), even a short temperature peak can cause severe grain loss (Lv et al., 2024). The reproductive stage, especially the critical period after pollination, is highly sensitive to high temperature stress, and a short temperature increase can cause significant grain abortion (Mitchell and Petolino, 1988). Therefore, it is necessary to clarify the specific exposure time of high temperature stress and develop strategies to alleviate its negative impact on yield, so as to increase crop yield (Hill and Li, 2022; Zenda et al., 2022).

4.3 Physiological and biochemical markers of reduced yield

Physiological and biochemical markers, such as pollen viability, stigma receptivity, and chlorophyll content, can effectively indicate the specific reasons for the decrease in maize yield under high temperature stress. Phenotypic traits such as leaf wilting, tassel sterility, and prolonged flowering-silking interval (ASI) caused by high temperature reduce grain yield, while pollen shedding time and fruiting rate are positively correlated with yield (Alam et al., 2017). High temperature stress interferes with metabolic pathways and dysregulates genes related to starch, lipid, and energy biosynthesis, resulting in reduced starch content, reduced enzyme activity, and reduced pollen germination, leading to sterility (Begcy et al., 2019). The above research results will accelerate the process of developing heat-tolerant maize genotypes (Figure 2) (Djalović et al., 2023).

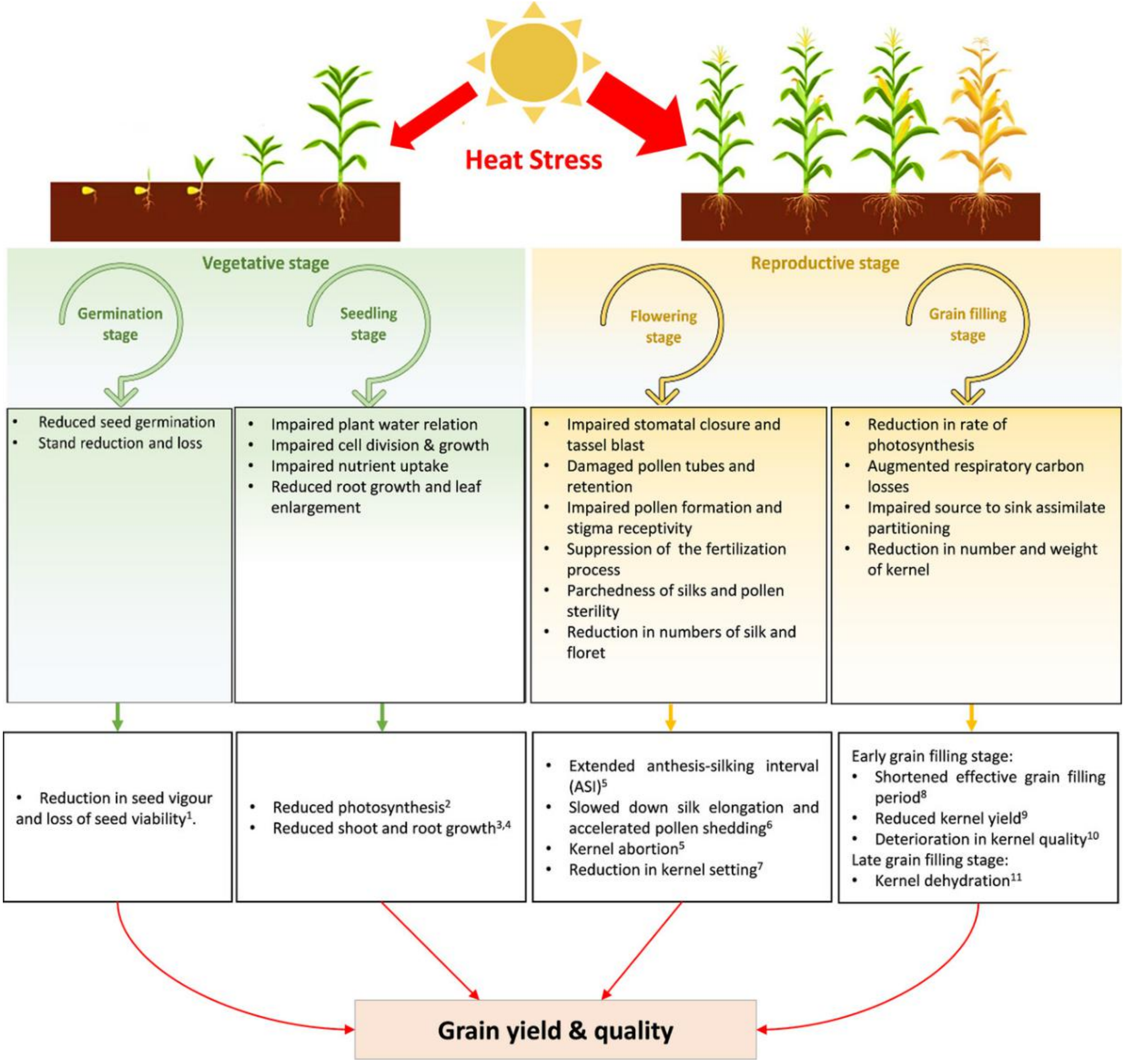


Figure 2 An overview of the impact of heat stress at different developmental stages of maize, impairing maize growth, production, and quality. The reproductive and grain filling period are the most susceptible stages in maize under heat stress. The red colored arrows depict the adverse effect of heat stress and the thickness of those arrows shows the degree of impact on these stages (Adopted from Djalović et al., 2023)

5 Heat Tolerance Genes and Regulatory Mechanisms in Maize

5.1 Identification of heat-responsive genes and QTLs

Identification of heat-responsive genes and quantitative trait loci (QTLs) can help analyze and improve heat tolerance in maize, and this method can be used to select heat tolerance at the seedling stage. Transcriptome analysis revealed a large number of differentially expressed genes (DEGs) under high temperature stress. For example, a study by Chen et al. (2023) identified 770 commonly up-regulated and down-regulated genes in maize kernels under high temperature stress, and predicted 41 putative TFs, indicating that pathways such as protein processing in the endoplasmic reticulum and ethylene signaling play a key role in heat tolerance. Many genes in maize kernels that respond to heat stress were identified, and 7 genes and 4 pathways that were highly correlated with maize kernel heat tolerance were found. Genome-wide association analysis (GWAS) provides an important means to identify potential heat-resistant QTLs and dominant genes, and to select superior maize varieties for enhanced stress resistance (Djalović et al., 2023). Inghelandt et al. (2019) identified six QTLs, each of which individually explained 7% to 9% of the phenotypic variance, all of which explained a significant portion of the phenotypic variation associated with heat tolerance, highlighting the genetic diversity that can be used in breeding programs.

5.2 Molecular regulation of heat tolerance pathways

The molecular regulatory mechanism of heat tolerance involves a complex signaling network, including the participation of heat shock proteins (HSPs) and transcription factors (TFs). The expression of heat shock factors (HSFs) and HSPs is a widely studied heat tolerance response in transgenic maize, which can significantly enhance the tolerance of plants to high temperature stress. HSPs are not only key regulators of plant heat stress response, but also play an important role in plant reproductive development and response to various adversities. For example, the ZmNAC074 transcription factor provides a key candidate regulatory gene for the regulation and genetic improvement of maize heat stress tolerance by regulating the accumulation of stress metabolites and upregulating the expression of reactive oxygen species (ROS) scavenging genes (Xi et al., 2022). Among the heat-tolerant maize lines, a total of 35 common regulatory genes overlapped in five maize inbred lines, and the expression of genes related to protein folding and temperature stimulus response was significantly upregulated, indicating that the genetic response of maize to high temperature stress is highly coordinated (Xue et al., 2024).

5.3 Transcriptional and post-transcriptional regulation

Transcriptional and post-transcriptional regulatory mechanisms play a key role in the heat stress response of maize. Researchers can conduct molecular regulatory network mechanism research on the response of maize to heat stress and explore key regulatory genes with great utilization value. Members of the transcription factor family such as AP2, MYB and WRKY are involved in regulating the expression of heat-responsive genes. The up-regulated genes identified in the heat-tolerant inbred CML 25 will become potential candidate genes for the development of heat-tolerant maize using marker-assisted backcross breeding (Jagtap et al., 2023). Transcriptional kinetic analysis of maize leaves, pollen and ovules under heat stress conditions showed that their gene expression profiles changed significantly, and some genes showed more significant expression characteristics in heat-tolerant inbred lines. Metabolic overview pathways and secondary metabolite biosynthesis pathways involved 264 and 146 genes, respectively, which were highly enriched in heat stress response. The study by Liang et al. (2022) also identified cis- and trans-expression quantitative trait loci (eQTLs), which regulate genotype-specific heat stress responses by affecting promoter activity and transcription factor binding ability, providing an opportunity to better characterize the transcriptome responses of important genotypes that may produce important genotypes through environmental interactions.

6 Case Study: Regional Impact and Genetic Response of Heat Stress in Maize

6.1 Field observations in heat-prone areas

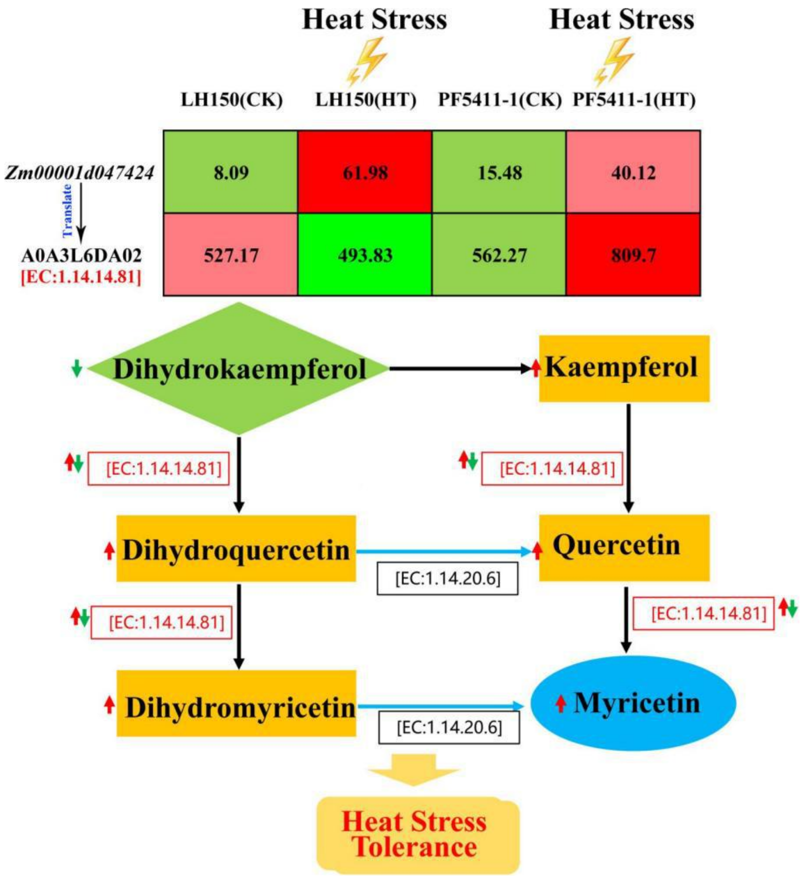
In heat-prone areas such as the North China Plain and sub-Saharan Africa, maize is frequently subjected to heat stress, which has a significant impact on its reproductive development and yield formation. Field trials on maize cultivation have shown that the suitable daily average temperature for maize grain filling is 22 °C-24 °C, and high temperature stress during the reproductive and grain filling periods can lead to a significant decrease in yield. Under high temperature stress conditions, phenotypic traits such as leaf wilting, male tassel sterility, and anthesis-silking interval (ASI) are negatively correlated with grain yield, while pollen shedding time and fruiting rate are positively correlated with yield (Alam et al., 2017). These research results highlight the urgent need to develop heat-resistant maize varieties in heat-prone areas to maintain stable production in response to the increasing risk of heat stress in maize.

6.2 Application of heat-tolerant maize varieties

Global warming has led to frequent high-temperature weather, which has severely restricted the growth and yield of corn. The development and application of heat-resistant corn varieties are of great significance to alleviate the negative effects of high temperature stress. The core of genetic improvement programs is to identify and utilize genetic variation to enhance heat tolerance. This includes germplasm screening, marker-assisted selection, genomic locus mapping and candidate gene identification. Genes related to heat tolerance and their regulatory networks are identified through genome assembly technology and integrated into breeding programs to cultivate more stress-resistant genotypes (Hill and Li, 2022). The application of transgenic technology, such as overexpression of specific transcription factors (such as ZmNAC074) encoding a positive regulator, activates the expression of ROS scavenging genes and HSR and UPR-related genes, and enhances the heat tolerance of plants under heat stress conditions (Xi et al., 2022).

6.3 Gene expression and phenotypic responses in case studies

Studies on the transcriptional dynamics of maize under heat stress have shown that gene expression profiles change significantly, especially between heat-tolerant and sensitive inbred lines. For example, the more heat-tolerant inbred line CML 25 showed more significant differences in the expression regulation of heat stress-responsive genes compared with the sensitive inbred line LM 11. The expression changes of the most common HS-responsive genes were generally more significant in CML 25, which may be an important reason for the higher heat tolerance of CML 25 (Jagtap et al., 2023). The identification of differentially regulated genes and related pathways, such as those involved in endoplasmic reticulum protein processing, myricetin biosynthesis, and raffinose metabolism, further revealed the complex genetic response mechanism of maize to heat stress (Figure 3). In order to adapt to heat stress, the expression levels of thousands of genes are changed to rescue damage (Chen et al., 2023).



	LH150(CK)	LH150(HT)	PF5411-1(CK)	PF5411-1(HT)
Zm00001d047424	8.09	61.98	15.48	40.12
A0A3L6DA02 [EC:1.14.14.81]	527.17	493.83	562.27	809.7

Figure 3 Sketch map of the synthesis of myricetin. Red arrows indicate up-regulated protein and metabolites after heat stress, and green ones indicate the down-regulated protein. Values in the table represent the expression levels of *Zm00001d047424* gene and its protein (Adopted from Chen et al., 2023)

7 Future Perspectives and Breeding Strategies

7.1 Breeding for heat tolerance through molecular tools

With global temperatures climbing steadily, breeding maize that can withstand heat has become a pressing goal. Tools like quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS) have helped researchers pinpoint regions in the genome that are linked to heat resilience. For instance, Seetharam et al. (2021) discovered 269 SNPs that showed strong associations with heat stress. Their haplotype trend regression (HTR) analysis further identified 26 haplotype blocks and 96 single SNP variants tied to grain yield in high-temperature environments—valuable clues for breeding more heat-resilient varieties. Studies combining transcriptomics and metabolomics have uncovered important genes and metabolic pathways, including those involved in protein folding and flavonoid production, that play a role in how maize copes with heat (Chen et al., 2023). Meanwhile, Guo et al. (2024) found that applying salicylic acid helped boost grain weight and yield by extending grain-filling time, increasing endosperm cell numbers, improving polyploidy, and adjusting hormone levels and metabolic activities. These insights form a solid foundation for breeding maize varieties that can perform better in hot climates.

7.2 Integrating omics approaches in heat tolerance research

Omics tools—like genomics, transcriptomics, proteomics, and metabolomics—offer a broad view of how maize responds to heat stress. By using these methods, researchers have been able to spot which genes and metabolites are activated or suppressed during heat exposure. In one recent study, Zhao et al. (2024) identified 1 062 metabolites involved in maize's response to high temperatures. These findings deepen our understanding of the plant's physiological and molecular coping mechanisms. Joint analyses have highlighted how compounds such as lipids and flavonoids are central to heat stress tolerance. With this toolbox, scientists can move more quickly in identifying new candidate genes and pathways, ultimately speeding up the development of heat-tolerant maize.

7.3 Policy, extension, and climate-smart agriculture

To truly tackle heat stress in the field, breeding work must go hand in hand with supportive policies and effective outreach. Climate-smart farming strategies—like adjusting planting times or improving soil and nutrient management—can work together with genetic improvements to enhance maize's performance under heat (El-Sappah et al., 2022). Policies that invest in heat-tolerance research and promote the use of resilient varieties at the farm level are essential. Collaboration across government bodies, private companies, and research institutions can help push these ideas forward, ensuring maize production remains sustainable in a warming world (Driedonks et al., 2016).

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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