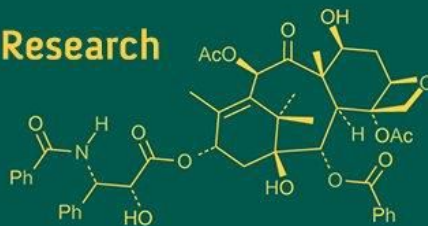


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A review: Heat tolerance aspect in maize (*Zea mays* L.)

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Abstract

Maize is one of the most widely cultivated cereal crops globally and serves as a staple food, feed and industrial raw material. Rising global temperatures and increased frequency of heat waves due to climate change pose a serious threat to maize productivity, particularly in tropical and subtropical regions. Heat stress adversely affects maize growth, phenology, reproductive development, physiological processes and grain yield. The sensitivity of maize to high temperature is especially pronounced during flowering and grain filling stages. Heat tolerance in maize is a complex trait governed by physiological, biochemical, molecular and genetic mechanisms. This review synthesizes current knowledge on the impact of heat stress on maize, mechanisms of heat tolerance, screening approaches, genetic and molecular strategies and agronomic interventions to enhance heat resilience. Understanding these aspects is essential for developing climate-resilient maize cultivars and ensuring food security under changing climatic scenarios.

Keywords: Maize, heat stress, heat tolerance, climate change, physiological traits, breeding

1. Introduction

Maize (*Zea mays* L.) is one of the most important cereal crops globally, serving as a staple food, livestock feed and raw material for several agro-industrial products. Owing to its high yield potential, wide adaptability and diverse uses, maize plays a critical role in global food and nutritional security, particularly in developing countries of tropical and subtropical regions (Cairns & Prasanna, 2018) [2]. However, maize productivity is highly vulnerable to climatic variability, especially temperature extremes, making it one of the crops most at risk under ongoing climate change scenarios (Lobell *et al.*, 2011) [7].

Global climate change has resulted in a steady rise in mean air temperature along with an increased frequency and intensity of heat waves. The Intergovernmental Panel on Climate Change has projected an increase of 1.5-2.0 °C in global surface temperature by the mid-21st century, with land areas experiencing more pronounced warming than oceans (IPCC, 2021) [6]. Elevated temperatures beyond the crop's optimum range negatively affect plant growth, development and yield by disrupting physiological, biochemical and molecular processes (Hatfield & Prueger, 2015) [5]. Consequently, heat stress has emerged as one of the most serious abiotic constraints limiting maize production worldwide (Farooq *et al.*, 2015) [4].

Maize is considered moderately sensitive to heat stress, with optimal growth occurring at temperatures between 25 and 30 °C. Exposure to temperatures above 35 °C, particularly for prolonged periods, can result in irreversible damage to growth and reproductive development (Wahid *et al.*, 2007) [9]. Among different growth stages, the reproductive phase—especially tasseling and silking is the most sensitive to high temperature stress. Heat stress during this stage leads to reduced pollen viability, impaired pollen shedding, silk desiccation and an increased anthesis-silking interval, resulting in poor kernel set and significant yield reduction (Barnabás *et al.*, 2008; Edreira & Otegui, 2012) [1, 3].

Apart from reproductive failure, heat stress adversely affects several physiological processes in maize. High temperature disrupts chloroplast ultrastructure, reduces photosystem II efficiency and limits Rubisco activity, thereby decreasing photosynthetic carbon assimilation (Hatfield & Prueger, 2015) [5]. Simultaneously, increased respiration rates under heat stress conditions lead to higher energy consumption and reduced availability of assimilates for grain filling (Farooq *et al.*, 2015) [4]. Heat stress also induces excessive production of reactive oxygen species, resulting in oxidative damage to cellular membranes, proteins and nucleic acids (Mittler *et al.*, 2012) [8].

Heat tolerance in maize is a complex quantitative trait governed by multiple genes and their interaction with environmental factors. Plants have evolved several adaptive mechanisms to cope with high temperature stress, including synthesis of heat shock proteins, activation of antioxidant defense systems, maintenance of membrane stability and regulation of stress-responsive genes (Wahid *et al.*, 2007; Mittler *et al.*, 2012) ^[9, 8]. Considerable genetic variability for heat tolerance exists within maize germplasm, offering opportunities for crop improvement through breeding and selection (Cairns & Prasanna, 2018) ^[2]. However, conventional breeding for heat tolerance is challenging due to strong genotype $\times$ environment interactions and difficulties associated with precise phenotyping under field conditions.

In view of the increasing incidence of heat stress under climate change, improving heat tolerance in maize has become a major priority for sustainable crop production. Integrating physiological understanding with molecular breeding, high-throughput phenotyping and climate-smart agronomic practices is essential for developing heat-resilient maize cultivars. Therefore, a comprehensive understanding of the effects of heat stress and the underlying tolerance mechanisms is crucial for designing effective strategies to sustain maize productivity in a warming climate.

2. Heat Stress in Maize: Concept, Thresholds and Occurrence

Heat stress in plants is defined as the rise in temperature beyond a critical threshold for a period sufficient to cause irreversible damage to growth, development and productivity. In maize, heat stress is increasingly recognized as a major abiotic constraint due to rising global temperatures and the increasing occurrence of extreme heat events under climate change scenarios (Hatfield & Prueger, 2015; IPCC, 2021) ^[5, 6].

2.1 Temperature Thresholds for Heat Stress in Maize

Maize exhibits optimal growth and development at temperatures ranging between 25 and 30 °C. Temperatures exceeding this range, particularly above 35 °C, are considered stressful and can negatively affect physiological and reproductive processes (Wahid *et al.*, 2007) ^[9]. Short-term exposure to high temperature may result in reversible effects; however, prolonged exposure during sensitive growth stages leads to permanent yield losses (Farooq *et al.*, 2015) ^[4]. Day temperatures above 35 °C combined with high night temperatures are particularly detrimental, as elevated night temperatures increase respiration rates and reduce net carbon gain. Such conditions are becoming more frequent in major maize-growing regions, especially in tropical and subtropical climates (Lobell *et al.*, 2011) ^[7].

2.2 Stage-Specific Sensitivity of Maize to Heat Stress

The sensitivity of maize to heat stress varies across growth stages. While early vegetative stages show moderate tolerance, the reproductive phase is highly sensitive to elevated temperatures. Heat stress during tasseling and silking is widely reported as the most damaging, as it directly affects pollination and fertilization processes (Barnabás *et al.*, 2008) ^[1].

High temperature stress during flowering reduces pollen viability, disrupts anther dehiscence and accelerates silk drying, leading to asynchronous flowering and an increased

anthesis-silking interval (ASI). A prolonged ASI is strongly associated with poor kernel set and yield reduction under heat stress conditions (Edreira & Otegui, 2012) ^[3]. Grain filling is another critical stage where heat stress shortens the duration of assimilate accumulation, resulting in reduced kernel weight and grain yield (Farooq *et al.*, 2015) ^[4].

2.3 Occurrence of Heat Stress in Major Maize-Growing Regions

Heat stress commonly occurs in maize-growing regions characterized by semi-arid and tropical climates, including South Asia, sub-Saharan Africa and parts of Latin America. In these regions, late sowing, terminal heat stress and combined heat-drought stress are frequent due to delayed monsoon onset and erratic rainfall patterns (Cairns & Prasanna, 2018) ^[2].

Climate models predict a further increase in the frequency of days exceeding critical temperature thresholds for maize, particularly during the reproductive phase. Lobell *et al.* (2011) ^[7] reported that even a small increase in seasonal temperature can lead to significant reductions in maize yield, highlighting the vulnerability of maize-based production systems to warming trends.

2.4 Interaction of Heat Stress with Other Abiotic Stresses

Heat stress in maize often occurs simultaneously with other abiotic stresses, particularly drought. The combined effect of heat and water stress is more severe than either stress alone, as high temperature accelerates soil moisture depletion and exacerbates plant water deficit (Farooq *et al.*, 2015) ^[4]. Such stress combinations complicate management and breeding efforts, emphasizing the need for integrated stress tolerance strategies.

3. Effect of Heat Stress on Growth, Development and Yield of Maize

Heat stress affects maize at all stages of growth, but the magnitude and nature of damage vary with developmental stage, intensity and duration of stress. Elevated temperatures disrupt morphological, physiological and reproductive processes, ultimately leading to significant yield penalties (Farooq *et al.*, 2015) ^[4].

3.1 Effect on Germination and Seedling Establishment

High temperature stress during germination and early seedling stages reduces germination percentage, delays emergence and weakens seedling vigor. Heat stress interferes with enzymatic activity involved in starch mobilization and protein synthesis, leading to poor root and shoot development (Wahid *et al.*, 2007) ^[9]. Seedlings exposed to elevated temperatures exhibit reduced coleoptile length, impaired root elongation and increased membrane leakage, which collectively reduce stand establishment and early crop competitiveness.

3.2 Effect on Vegetative Growth

During vegetative growth, heat stress significantly reduces plant height, leaf area index and biomass accumulation. Elevated temperatures accelerate phenological development, resulting in shortened vegetative growth duration and reduced canopy size (Hatfield & Prueger, 2015) ^[5]. Heat stress also induces premature leaf senescence, chlorosis and leaf rolling, which limit light interception and

photosynthetic efficiency. Reduced chlorophyll content and impaired photosystem II activity under high temperature further restrict assimilate production required for subsequent reproductive growth (Farooq *et al.*, 2015) ^[4].

3.3 Effect on Reproductive Development

The reproductive phase is the most heat-sensitive stage in maize. Exposure to high temperatures during tasseling and silking severely affects reproductive organ development and function. Heat stress reduces pollen viability and germination, disrupts anther dehiscence and shortens pollen shedding duration (Barnabás *et al.*, 2008) ^[1]. Silk growth is also inhibited, leading to silk desiccation and reduced receptivity. One of the most critical consequences of heat stress is the prolongation of the anthesis-silking interval (ASI). An increased ASI under heat stress leads to poor synchrony between pollen shedding and silk emergence, resulting in reduced kernel set and increased barrenness (Edreira & Otegui, 2012) ^[3]. Yield losses during this stage are often irreversible, even if favorable conditions return later.

3.4 Effect on Grain Filling and Yield Components

Heat stress during grain filling shortens the duration of

kernel development and reduces the rate of dry matter accumulation. Elevated temperature accelerates endosperm cell division and maturation, leading to smaller kernel size and lower thousand-kernel weight (Farooq *et al.*, 2015) ^[4]. Increased respiration under high temperature conditions further reduces the availability of assimilates for grain growth. Overall grain yield reduction under heat stress is primarily attributed to decreased kernel number per ear and reduced kernel weight. Several studies have reported yield reductions ranging from 10% to more than 40%, depending on the timing and severity of heat stress (Lobell *et al.*, 2011) ^[7]. Heat stress occurring during reproductive and grain-filling stages has a disproportionately greater impact on yield compared to vegetative-stage stress.

3.5 Combined Effect of Heat Stress on Yield Stability

Repeated or prolonged heat stress events not only reduce yield but also increase yield instability across seasons. Genotypes that maintain reproductive success, kernel set and grain weight under high temperature conditions are considered heat tolerant. Therefore, yield stability under heat stress is a critical selection criterion in maize breeding programs targeting climate resilience (Cairns & Prasanna, 2018) ^[2].

Table 1: Growth Stage-wise Sensitivity of Maize to Heat Stress

Growth stage	Critical temperature (°C)	Major effects	References
Germination	>35	Poor emergence, weak seedlings	Wahid <i>et al.</i> , 2007 ^[9]
Vegetative	>35	Reduced leaf area, early senescence	Hatfield & Prueger, 2015 ^[5]
Tasseling	>35-38	Pollen sterility, poor shedding	Barnabás <i>et al.</i> , 2008 ^[1]
Silking	>35	Increased ASI, silk desiccation	Edreira & Otegui, 2012 ^[3]
Grain filling	>32-35	Reduced kernel weight, yield loss	Farooq <i>et al.</i> , 2015 ^[4]

4. Physiological and Biochemical Responses of Maize to Heat Stress

Heat stress induces a wide range of physiological and biochemical alterations in maize that directly influence growth, development and yield. These responses are primarily associated with disruption of photosynthesis, altered water relations, membrane instability and oxidative damage. Understanding these mechanisms is essential for identifying key traits associated with heat tolerance (Wahid *et al.*, 2007; Farooq *et al.*, 2015) ^[9, 4].

4.1 Photosynthesis and Chlorophyll Stability

Photosynthesis is one of the most heat-sensitive physiological processes in maize. High temperature stress reduces net photosynthetic rate by impairing chlorophyll synthesis, accelerating chlorophyll degradation and damaging the photosynthetic apparatus, particularly photosystem II (PSII) (Hatfield & Prueger, 2015) ^[5]. Heat stress destabilizes thylakoid membranes and reduces the efficiency of electron transport, leading to decreased carbon assimilation. Rubisco activity is also adversely affected by high temperature due to reduced enzyme stability and increased oxygenation reaction, which enhances photorespiration. As a result, less assimilate is available for growth and grain development, contributing to yield reduction under heat stress conditions (Farooq *et al.*, 2015) ^[4].

4.2 Respiration and Carbon Balance

Heat stress increases mitochondrial respiration rates in maize plants. Elevated respiration leads to excessive

consumption of photosynthates, reducing the net carbon gain of the plant. High night temperatures are particularly damaging as they increase respiratory losses without corresponding photosynthetic compensation, ultimately affecting biomass accumulation and grain filling (Lobell *et al.*, 2011) ^[7]. Heat-tolerant genotypes often exhibit lower respiration rates and better carbon-use efficiency under stress conditions.

4.3 Plant Water Relations and Transpiration

High temperature stress increases evaporative demand, leading to excessive transpiration and plant water loss. Heat stress often coincides with reduced soil moisture availability, resulting in stomatal closure and decreased CO₂ uptake. Reduced leaf water potential under heat stress negatively affects cell expansion and metabolic activity (Farooq *et al.*, 2015) ^[4]. Maintenance of favorable plant water status and efficient stomatal regulation are therefore important traits contributing to heat tolerance in maize.

4.4 Membrane Stability and Lipid Peroxidation

Cell membrane stability is a key indicator of heat tolerance. Heat stress increases membrane fluidity and permeability, leading to electrolyte leakage and loss of cellular integrity. High temperature induces lipid peroxidation through the accumulation of reactive oxygen species (ROS), which further damages membrane lipids and proteins (Wahid *et al.*, 2007) ^[9]. Heat-tolerant maize genotypes generally maintain higher membrane thermostability and exhibit lower levels of lipid peroxidation under stress conditions.

4.5 Oxidative Stress and Antioxidant Defense System

Heat stress leads to excessive generation of ROS such as superoxide radicals, hydrogen peroxide and hydroxyl radicals. These reactive molecules cause oxidative damage to nucleic acids, proteins and cellular membranes. To counteract oxidative stress, maize plants activate antioxidant defense systems involving enzymes such as superoxide dismutase, catalase and peroxidase (Mittler *et al.*, 2012) [8]. Heat-tolerant maize genotypes show enhanced antioxidant enzyme activity and better ROS scavenging capacity, which helps in maintaining cellular homeostasis and protecting metabolic processes under high temperature stress (Farooq *et al.*, 2015) [4].

5. Molecular and Genetic Basis of Heat Tolerance in Maize

Heat tolerance in maize is a complex, quantitative trait regulated by multiple genes and their interactions with environmental factors. Molecular and genetic studies have provided valuable insights into the mechanisms governing heat stress perception, signal transduction and stress-responsive gene expression. Understanding these mechanisms is essential for developing maize genotypes capable of maintaining productivity under elevated temperature conditions (Wahid *et al.*, 2007; Cairns & Prasanna, 2018) [9, 2].

5.1 Heat Shock Proteins (HSPs) and Thermotolerance

Heat shock proteins play a central role in plant responses to high temperature stress. These proteins function as molecular chaperones, facilitating proper protein folding, preventing aggregation of denatured proteins and aiding in protein repair under stress conditions. In maize, several classes of HSPs, including HSP70, HSP90 and small heat shock proteins (sHSPs), are rapidly induced in response to heat stress (Mittler *et al.*, 2012) [8]. Enhanced expression of HSPs has been strongly associated with improved thermotolerance in maize. Heat-tolerant genotypes generally exhibit higher and more stable expression of HSPs compared to heat-sensitive ones, enabling them to maintain cellular protein homeostasis under elevated temperatures (Wahid *et al.*, 2007) [9].

5.2 Heat Shock Transcription Factors and Gene Regulation

Heat shock transcription factors (HSFs) regulate the expression of heat-responsive genes by binding to heat shock elements in promoter regions. Under heat stress, HSFs are activated and initiate transcription of HSPs and other protective genes. In maize, several HSF families have been identified and shown to play key roles in heat stress tolerance (Mittler *et al.*, 2012) [8]. Apart from HSFs, other transcription factors such as NAC, WRKY and bZIP families are also involved in regulating stress-responsive pathways. These transcription factors contribute to enhanced antioxidant activity, osmotic adjustment and stress signaling, thereby improving maize tolerance to high temperature stress (Farooq *et al.*, 2015) [4].

5.3 Quantitative Trait Loci (QTLs) Associated with Heat Tolerance

Heat tolerance in maize is controlled by multiple quantitative trait loci (QTLs) associated with morphological, physiological and yield-related traits. QTLs linked to

anthesis-silking interval, pollen viability, membrane thermostability, canopy temperature depression and grain yield under heat stress have been identified using molecular markers (Edreira & Otegui, 2012) [3]. Mapping of these QTLs has facilitated the identification of genomic regions contributing to heat tolerance. Marker-assisted selection based on these QTLs enables more precise and efficient breeding for heat-tolerant maize cultivars, particularly when combined with phenotypic selection under stress environments (Cairns & Prasanna, 2018) [2].

5.4 Role of Candidate Genes and Omics Approaches

Advances in genomics, transcriptomics and proteomics have accelerated the identification of candidate genes involved in heat stress responses. Transcriptomic analyses have revealed differential expression of genes related to protein protection, antioxidant defense, carbohydrate metabolism and hormone signaling under heat stress conditions (Mittler *et al.*, 2012) [8]. Omics-based approaches provide a comprehensive understanding of heat stress response networks and facilitate the discovery of novel genes and pathways associated with thermotolerance. Integration of these approaches with conventional breeding holds significant promise for accelerating the development of heat-resilient maize varieties (Cairns & Prasanna, 2018) [2].

6. Screening and Phenotyping Methods for Heat Tolerance in Maize

Efficient screening and phenotyping of maize genotypes for heat tolerance are essential components of breeding programs aimed at developing climate-resilient cultivars. Heat tolerance is a complex trait influenced by genotype, environment and their interactions, necessitating the use of reliable, repeatable and stage-specific screening methods (Cairns & Prasanna, 2018) [2].

6.1 Field-Based Screening under Natural Heat Stress

Field evaluation under natural heat stress conditions remains the most practical and widely used approach for screening maize genotypes. Late sowing is commonly employed to expose maize plants to high temperature during critical reproductive stages, particularly tasseling and silking (Edreira & Otegui, 2012) [3]. Genotypes are evaluated for yield performance, kernel set and stability across locations and seasons. Key field indicators of heat tolerance include reduced anthesis-silking interval, higher kernel number per ear and stable grain yield under heat stress environments. Multi-location trials are essential to capture genotype × environment interactions and identify broadly adapted heat-tolerant genotypes (Cairns & Prasanna, 2018) [2].

6.2 Controlled Environment Screening

Controlled environment facilities such as growth chambers and greenhouses allow precise imposition of heat stress at specific growth stages. These systems enable evaluation of maize responses to defined temperature regimes, reducing environmental variability. Controlled screening is particularly useful for studying physiological and molecular responses to heat stress and validating field observations (Wahid *et al.*, 2007) [9]. However, controlled environment studies may not fully replicate field conditions, and therefore should be used in conjunction with field-based screening for effective selection.

6.3 Morphological and Phenological Traits

Several morphological and phenological traits are commonly used as indirect selection criteria for heat tolerance in maize. Among these, anthesis-silking interval (ASI) is considered one of the most reliable indicators of reproductive resilience under heat stress. Genotypes with shorter ASI generally exhibit better pollination success and higher grain yield under high temperature conditions (Edreira & Otegui, 2012) ^[3]. Other important traits include stay-green characteristics, tassel size, silk emergence rate and leaf senescence pattern. These traits are relatively easy to measure and show good association with heat tolerance and yield stability (Farooq *et al.*, 2015) ^[4].

6.4 Physiological and Biochemical Indicators

Physiological traits such as canopy temperature depression (CTD), chlorophyll content, chlorophyll fluorescence and membrane stability index are widely used to assess heat tolerance. Lower canopy temperature indicates efficient

transpirational cooling and better water status under heat stress (Hatfield & Prueger, 2015) ^[5]. Biochemical indicators such as antioxidant enzyme activity and electrolyte leakage provide insights into cellular stability and oxidative stress tolerance. These traits are valuable for discriminating heat-tolerant and heat-sensitive genotypes, particularly under controlled screening conditions (Wahid *et al.*, 2007) ^[9].

6.5 High-Throughput Phenotyping and Remote Sensing

Recent advances in phenotyping technologies have enabled high-throughput screening of large maize populations. Remote sensing tools such as infrared thermography, multispectral imaging and unmanned aerial vehicles facilitate rapid, non-destructive assessment of canopy temperature, biomass and stress responses under field conditions (Cairns & Prasanna, 2018) ^[2]. Integration of high-throughput phenotyping with genomic data enhances selection accuracy and accelerates genetic gain for heat tolerance traits.

Table 2: Key Traits Used for Screening Heat Tolerance in Maize

Trait	Indicator of tolerance	Screening method	References
Anthesis-silking interval	Shorter ASI	Field phenotyping	Edreira & Otegui, 2012 ^[3]
Canopy temperature	Lower CTD	Infrared thermometry	Hatfield & Prueger, 2015 ^[5]
Chlorophyll stability	Delayed senescence	SPAD/fluorescence	Farooq <i>et al.</i> , 2015 ^[4]
Membrane stability	Low electrolyte leakage	Lab assay	Wahid <i>et al.</i> , 2007 ^[9]
Antioxidant activity	ROS scavenging	Enzyme analysis	Mittler <i>et al.</i> , 2012 ^[8]

7. Breeding Strategies for Improving Heat Tolerance in Maize

Genetic improvement remains the most sustainable and cost-effective approach for enhancing heat tolerance in maize. Given the complex and quantitative nature of heat tolerance, breeding strategies must integrate conventional selection with physiological, molecular and genomic tools to achieve stable performance under high temperature stress (Cairns & Prasanna, 2018) ^[2].

7.1 Conventional Breeding Approaches

Traditional breeding methods, including mass selection, recurrent selection and hybrid breeding, have played a significant role in improving heat tolerance in maize. Selection is typically carried out under natural heat stress environments using yield and yield stability as primary criteria. Landraces and locally adapted germplasm often serve as valuable sources of heat tolerance traits due to their long-term adaptation to high temperature environments (Farooq *et al.*, 2015) ^[4].

Recurrent selection helps accumulate favorable alleles for heat tolerance over successive cycles, while hybrid breeding exploits heterosis to enhance stress resilience. However, conventional breeding is often constrained by low heritability of yield under stress and strong genotype × environment interactions (Edreira & Otegui, 2012) ^[3].

7.2 Physiological Trait-Based Breeding

Incorporation of physiological traits as indirect selection criteria has improved the efficiency of breeding for heat tolerance. Traits such as shorter anthesis-silking interval, stay-green behavior, canopy temperature depression, pollen viability and membrane thermostability are strongly associated with improved performance under heat stress (Wahid *et al.*, 2007; Farooq *et al.*, 2015) ^[9, 4].

Physiological trait-based breeding allows early-generation selection and reduces dependence solely on yield, which is often highly variable under stress conditions. Combining these traits with yield performance enhances selection accuracy for heat tolerance.

7.3 Marker-Assisted Selection and QTL Introgression

Marker-assisted selection (MAS) enables the identification and introgression of genomic regions associated with heat tolerance into elite maize backgrounds. QTLs linked to traits such as anthesis-silking interval, kernel set and grain yield under heat stress have been successfully identified and utilized in breeding programs (Cairns & Prasanna, 2018) ^[2]. MAS is particularly useful for pyramiding multiple stress tolerance traits and accelerating breeding cycles. However, the effectiveness of MAS depends on the stability of QTL expression across environments, which remains a challenge in heat stress breeding.

7.4 Genomic Selection and Modern Breeding Tools

Genomic selection (GS) has emerged as a powerful approach for improving complex traits such as heat tolerance. GS uses genome-wide marker information to predict breeding values, enabling selection without extensive phenotyping in every generation. This approach is especially advantageous for traits with low heritability under stress conditions (Cairns & Prasanna, 2018) ^[2]. Integration of high-throughput phenotyping with genomic selection enhances prediction accuracy and accelerates genetic gain. GS is increasingly being adopted in international maize improvement programs targeting climate resilience.

7.5 Transgenic and Genome Editing Approaches

Advances in genetic engineering and genome editing technologies have opened new avenues for improving heat tolerance in maize. Manipulation of genes involved in heat

shock protein synthesis, antioxidant defense and stress signaling pathways has shown promise in enhancing thermotolerance (Mittler *et al.*, 2012) ^[8]. Genome editing tools such as CRISPR/Cas enable precise modification of

stress-responsive genes without introducing foreign DNA. Despite their potential, the deployment of transgenic and genome-edited maize varieties is limited by regulatory, ethical and public acceptance issues in many countries.

Table 3: Breeding Approaches for Heat Tolerance

Approach	Key features	Limitations	References
Conventional breeding	Field selection, hybrids	Slow progress	Farooq <i>et al.</i> , 2015 ^[4]
Marker-assisted selection	QTL introgression	Environment sensitivity	Cairns & Prasanna, 2018 ^[2]
Genomic selection	Genome-wide prediction	Cost, infrastructure	Cairns & Prasanna, 2018 ^[2]
Genome editing	Targeted gene modification	Regulatory issues	Mittler <i>et al.</i> , 2012 ^[8]

8. Agronomic Management Practices for Mitigating Heat Stress in Maize

While genetic improvement provides long-term solutions for heat tolerance, agronomic management plays a crucial role in minimizing the immediate impact of heat stress on maize productivity. Adoption of climate-smart agronomic practices can significantly reduce crop exposure to high temperature stress and enhance yield stability under warming conditions (Hatfield & Prueger, 2015) ^[5].

8.1 Adjustment of Sowing Time

Modification of sowing dates is one of the most effective agronomic strategies to avoid heat stress during sensitive growth stages. Early or optimum sowing allows maize plants to complete critical reproductive phases before the onset of peak summer temperatures. Delayed sowing, on the other hand, often exposes maize crops to terminal heat stress during flowering and grain filling, leading to substantial yield losses (Lobell *et al.*, 2011) ^[7]. Region-specific sowing schedules based on climatic forecasts are therefore essential for minimizing heat stress risk and improving maize productivity.

8.2 Irrigation Management

Adequate and timely irrigation helps mitigate heat stress by maintaining favorable plant water status and facilitating transpirational cooling. Supplemental irrigation during tasseling and silking stages is particularly effective in reducing canopy temperature and improving pollen viability and kernel set (Farooq *et al.*, 2015) ^[4]. Efficient irrigation methods such as drip and sprinkler systems enhance water use efficiency and reduce heat-induced moisture stress. Proper irrigation scheduling based on crop water requirements and weather conditions is critical for minimizing combined heat and drought stress.

8.3 Mulching and Conservation Agriculture

Mulching with crop residues or organic materials helps reduce soil temperature, conserve soil moisture and improve soil structure. Residue retention under conservation agriculture systems moderates the soil microclimate and reduces heat stress impacts on maize roots (Hatfield & Prueger, 2015) ^[5]. Conservation agriculture practices, including minimum tillage and crop residue management, improve soil organic carbon and enhance soil water-holding capacity, thereby increasing maize resilience to high temperature stress.

8.4 Nutrient Management

Balanced nutrient management enhances plant vigor and improves tolerance to heat stress. Adequate supply of potassium, calcium and micronutrients strengthens cell

membranes, regulates stomatal function and enhances antioxidant activity under stress conditions (Wahid *et al.*, 2007) ^[9]. Split application of nitrogen reduces excessive vegetative growth and improves nitrogen use efficiency under high temperature conditions. Integrated nutrient management combining organic and inorganic sources further improves soil health and stress tolerance.

8.5 Use of Stress-Reducing Inputs

Application of plant growth regulators, osmoprotectants and anti-transpirants has been shown to alleviate heat stress effects in maize. Compounds such as salicylic acid and proline enhance antioxidant defense and stabilize cellular metabolism under high temperature stress (Farooq *et al.*, 2015) ^[4]. Although these inputs provide short-term benefits, their use should be economically viable and environmentally safe.

9. Future Research Needs and Perspectives

The increasing frequency and intensity of heat stress events under climate change necessitate a reorientation of maize research toward long-term resilience and yield stability. Despite significant advances in understanding heat stress responses, several knowledge gaps remain that require focused research efforts (Cairns & Prasanna, 2018) ^[2].

9.1 Integration of Multi-Stress Tolerance

In natural field conditions, heat stress rarely occurs in isolation and is often accompanied by drought, nutrient stress or high radiation. Future research should prioritize understanding the combined effects of heat and other abiotic stresses on maize growth and yield. Breeding strategies must focus on developing maize genotypes with combined tolerance to heat and drought, as these stress combinations pose the greatest threat to maize production systems (Farooq *et al.*, 2015) ^[4].

9.2 Advancement in High-Throughput Phenotyping

Accurate and rapid phenotyping remains a major bottleneck in heat tolerance breeding. The integration of remote sensing tools, such as infrared thermography, multispectral imaging and unmanned aerial vehicles, should be expanded to improve screening efficiency under field conditions. Linking high-throughput phenotyping data with genomic information will enhance selection accuracy and accelerate genetic gain for heat tolerance traits (Cairns & Prasanna, 2018) ^[2].

9.3 Functional Genomics and Gene Discovery

Although several heat-responsive genes have been identified, the functional characterization of these genes in maize is still limited. Future studies should focus on

validating candidate genes and regulatory networks associated with heat tolerance using transcriptomics, proteomics and metabolomics approaches. Functional genomics will provide deeper insights into stress response pathways and facilitate targeted crop improvement (Mittler *et al.*, 2012) ^[8].

9.4 Precision Breeding and Genome Editing

Precision breeding approaches, including genomic selection and genome editing, offer promising opportunities for improving heat tolerance in maize. Genome editing tools such as CRISPR/Cas enable precise manipulation of key stress-responsive genes, potentially accelerating the development of heat-resilient maize cultivars. However, further research is needed to assess the stability and field performance of edited lines under diverse environmental conditions (Cairns & Prasanna, 2018) ^[2].

9.5 Climate-Smart Agronomy and Policy Support

Future research should also integrate agronomic innovations with genetic improvement to develop climate-smart maize production systems. Decision-support tools based on climate forecasting, along with policy support for the adoption of heat-tolerant varieties and sustainable practices, will be essential for enhancing maize resilience at the farm level (Hatfield & Prueger, 2015) ^[5].

10. Conclusion

Heat stress has emerged as a major abiotic constraint limiting maize growth, development and productivity under changing climatic conditions. Elevated temperatures adversely affect maize at all growth stages, with the reproductive phase being particularly sensitive, resulting in poor kernel set and yield losses. Heat tolerance in maize is a complex trait governed by physiological, biochemical, molecular and genetic mechanisms. Significant progress has been made in understanding heat stress responses, including the role of photosynthesis, antioxidant defense, heat shock proteins and stress-responsive genes. Advances in screening techniques, molecular breeding and genomic tools have improved the efficiency of developing heat-tolerant maize genotypes. However, effective management of heat stress requires an integrated approach combining genetic improvement with climate-smart agronomic practices. Future research should focus on multi-stress tolerance, precision phenotyping and genome-enabled breeding to enhance yield stability. Strengthening these strategies will be crucial for sustaining maize production and ensuring global food security in a warming climate.

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