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Maize under heat stress in lowland tropics: Learnings and the way forward

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Abstract

The two main factors contributing to heat stress are higher temperatures and low relative humidity at high temperatures. Growing almost year-round, maize crops in the lowland tropics are exposed to rising temperatures, negatively affecting crop productivity, especially under rainfed conditions. Studies have identified several morphological, biochemical, and physiological changes in field crops, including maize under heat stress. Among these, a few changes enable plants to adapt to heat stress (stress-adaptive traits), while others exhibit adverse effects of stress (stress-responsive traits). At the biochemical level, heat stress results in increased levels of superoxide dismutase (SOD) and catalase enzyme activities in cells, as well as elevated levels of Heat Shock Proteins (HSPs). Options have been identified to mitigate the effects of heat stress on maize crops, such as suitable planting time to avoid a high-temperature regime coinciding with critical crop growth stages, furrow sowing, and frequent irrigation to maintain a vital minimum relative humidity in the air. Efforts on genetic improvement for heat tolerance in maize resulted in the development of new heat-tolerant maize hybrids, which can thrive at temperatures beyond threshold limits for tropical maize and suffer relatively less under heat stress. However, the challenge remains mainly due to low genotypic variability for stress in elite maize germplasm and strong genotype-by-environment interaction under heat stress, resulting from varying vapor pressure deficits (VPD) at high temperatures. Therefore, diving deeper and exploring local landraces and wild accessions is necessary to explore wider genotypic variation for heat stress tolerance in tropical maize. Recent advances in genomics-assisted breeding may help identify genomic regions associated with heat stress tolerance in maize and target the introgression of validated genomic regions into elite maize germplasm to develop the next generation of maize cultivars with improved, stable performance under heat stress conditions. In this article, we reviewed the progress and key findings on various aspects of research on heat stress in field crops, with an emphasis on tropical maize, which may help refine the approaches of research programs working on heat stress and aiming to develop crop varieties with improved tolerance to heat stress.

Keywords: Maize; Heat stress; Climate change; Vapor pressure deficit; High temperature.

Abbreviations: Doubled haploidy (DH); Genome-wide association studies (GWAS); Harvest Index (HI); Heat shock factor (HSF); Heat Shock Proteins (HSPs); Heat-shock element (HSE); Late embryogenesis abundant (LEA); Radiation use efficiency (RUE); Rapid-cycle genomic selection (RC-GC); Reactive oxygen species (ROS); Relative humidity (RH); Ribulose-bisphosphate carboxylase (RUBISCO); Superoxide dismutase (SOD); Vapor pressure deficits (VPD); Water use efficiency (WUE).

Introduction

Global climatic change has brought several biotic and abiotic stresses to the forefront of sustainable agri-food systems due to their impeding effects on the productivity of field crops, particularly in the lowland tropics of the global South. The global rise in mean surface temperature (Fig. 1) and increased frequency of drought stress are prominent concerns for crop production in many areas worldwide. In lowland tropics, temperatures are predicted to exceed even the most extreme seasonal temperatures (Battisti et al., 2009; Tesfaye et al., 2017; IPCC, 2016). Climate studies have projected that a temperature rise of 1.0°C may cause a substantial decrease in maize grain yield in the lowland tropics (Jodage et al., 2017; Deryng et al., 2014). The tropics and subtropics of sub-Saharan Africa and South Asia are identified as global hotspots for the effects of climate change and climate variability (Aryal et al., 2020). Many areas in the lowland tropics are already experiencing soaring high temperatures above the threshold limit for tropical maize, along with shifts in relative humidity in the air, which increases the VPD. Weather pattern analysis for the past ten years (2014-2023) during the reproductive stage of maize crops (starting from anthesis to early grain-filling stage) in main maize growing seasons revealed that there is a gradual increase in VPD, i.e., drying power of the air, in both sub-Saharan Africa and South Asia (Fig. 2). Therefore, dedicated efforts are needed to adapt or mitigate the projected adverse impacts of heat stress to sustain the food supply of the world population (Rivero et al., 2022).

Heat stress is commonly defined as the condition where temperatures rise above a certain threshold for an extended period, significantly affecting crop growth and development (Zaidi et al., 2023). It is a complex abiotic stress, as its effects involve more than one environmental covariate, including temperature, relative humidity at Tmax, solar radiation, and soil moisture; therefore, it requires multidimensional regulations in plants (Djalovic et al., 2024). Nevertheless, heat stress combines at least two challenges: high day and nighttime temperatures and plant water deficit due to increased VPD (Zaidi et al., 2020). Therefore, heat stress is relatively more harmful to crop production under abiotic stress as global warming continues due to climate change (Mittler et al., 2012; Schonberger et al., 2017). Due to increased VPD under heat stress, plants face an excess heat load and cannot dissipate the resulting excess temperature, which involves a range of physiological and biochemical pathways. The impaired plant functions eventually lead to reduced growth and development, tissue damage, and even plant death in severe cases (Zaidi et al., 2023). It results in several physiological, anatomical, biochemical, and molecular changes in crop plants (Wahid et al., 2007; Zhang et al., 2023).

Around the world, maize is cultivated for human consumption, as well as a significant source of animal feed and fodder, and more recently for bioethanol production (Erenstein et al., 2022). Heat stress, in combination with soil water deficit, can cause a significant reduction in grain yield (Lobell et al., 2013; Siebert et al., 2014). In general, maize is susceptible to heat stress, as a 1.0°C increase in temperature may cause a 7% drop in grain yield (Tigchelaar et al., 2018). Therefore, heat with or without drought stress has emerged as a significant production constraint for maize in lowland tropics (Cairns et al., 2013; Zaidi et al., 2023). A temperature of ≥35°C at the reproductive stage caused a daily grain yield reduction of 101 kg ha^{-1} (Smith, 1996), which might result in up to 42% reduction in final grain yields (Khodarahmpour et al., 2011).

In the South Asian tropics, maize crops are grown in three seasons: winter, summer-rainy, and spring. The summer-rainy maize covers the most significant area, accounting for nearly 70%, and is primarily cultivated as a rainfed crop (Prasanna et al., 2022). The summer-rainy maize is prone to face contingent drought with or without heat stress at various growth stages, especially during the reproductive stage of the crop. The late planting of maize crops in the Spring season exposes the reproductive stages of the crop to severe heat stress (Alam et al., 2017; Zaidi et al., 2020). Heat stress during the reproductive stage has a relatively greater negative impact on grain yield (Rezaei et al., 2015; Noor et al., 2019). The losses in grain yield due to heat stress are found to be associated with an overall reduction in growth, reduced leaf area due to leaf scorching, increased anthesis-silking interval (ASI), tassel blast, tassel sterility, and low viable pollen production, and reduced length of grain filling period (Zaidi et al., 2016; Hussain et al., 2019; Vinayan et al., 2019).

Climate change-induced increases in temperatures during the main cropping season of maize cultivation underscore the need to develop a deeper understanding of maize's response to heat stress, including high temperatures and physiological drought. While mitigation options can be explored to minimize the heat load on popular varieties, targeted breeding of the next generation of maize cultivars is needed to combine high yield and heat stress resilience (Mukaro et al., 2023) and other desirable agronomic traits. The major challenge in understanding the effects of heat stress on maize crops is to encompass the various types of heat stress environments that are influenced by other prevailing weather conditions, such as relative humidity at high temperatures, soil moisture, and soil type (Vinayan et al., 2019). Therefore, genotypic responses may vary significantly at different locations, depending on the prevailing humidity in the air under the same temperature regimes, which is expressed in terms of VPD. Data from maize trials from four heat stress phenotyping sites showed that two sites (Hyderabad and Raichur) behaved as hot-dry locations. The other two sites (Ludhiana and Sabor) were warm-humid sites under similar high temperature (Tmax) regimes (Fig. 3). The variation in the level of VPD at similar Tmax was reflected in terms of mean yield of the maize trials at these locations. Generally, trials exposed to high VPD environments resulted in poor yields, whereas grain yield was higher under low VPD environments. Interactions between genotype and prevailing environmental conditions expressed in plant phenology and function need to be better understood at the plant, tissue, and cellular levels (Barnabás et al., 2008; Vinayan et al., 2021). The status of progress on various aspects of maize under heat stress, as well as the way forward to develop the next generation of maize that can thrive under present and future climatic conditions, are discussed in this article.

Response of maize to heat stress

Temperature is one of the key weather parameters that governs the geographic distribution of plants and the rate of their growth and development under different agroecologies (Li et al., 2018). Plants' responses to heat stress are complex, as they undergo a cascade of events at different plant organs, and their interactions ultimately determine crop yield under stress (Barnabás et al., 2008). Maize grows best at maximum temperatures ranging from 25 to 33 °C (Zaidi and Singh, 2005). A constant or even transitory heat stress can cause morphological, anatomical, physiological, and biochemical changes in maize plants. At temperatures above 38°C, maize plants cannot maintain adequate moisture in the system as evaporation of moisture from soil and plants' transpiration increases, which compounds the effects of heat stress and simultaneously (physiological) drought stress (Weaich et al., 1996; Pingali and Pandey, 2001).

An increase in temperature affects the life cycle of plants by hastening seed germination and early flowering, reducing the vegetative growth period, and disrupting the seasonal growth of particular species (Fitter and Fitter, 2002). Crops grow at an accelerated rate with an increase in temperature, mainly because of faster accumulation of growing degree days (GDD). The plant life cycle becomes shortened due to reduced leaf area growth, active photosynthesis duration, and shorter grain-filling period (Boote et al., 2018). Although some studies have opined that C4 over C3 plant systems have advantages, it has been proven that crop species with more stable photochemistry, particularly at photosystem II (PSII), perform better under heat stress (Dwyer et al., 2007). Heat stress influences plant processes and functions like seed germination, transpiration, protein synthesis, respiration, photosynthesis, assimilate translocation, etc. When elevated temperatures exceed the threshold limit of a plant species, stress responses can induce damage to the light-harvesting complex of leaves and impair carbon fixing enzymes, thereby affecting the yield attributes, including seed set, grain fill rate, and decreased grain fill duration.

Plant growth and development

Heat stress affects various phenological aspects and, therefore, morphological characteristics of maize plants (Table 1). The significant effect of vegetative stage heat stress in maize was reduced elongation rate of the first internode and overall shoot growth (Weaich et al., 1996). Temperatures above 35 °C can reduce leaf area (Thiagarajah et al., 1982), plant height, number of leaves, stem diameter, dry matter yield, ear characteristics, and fewer kernels per plant (Traore et al., 2000). The reduced rates of leaf expansion with increased air temperature could be a direct result of high temperatures on the meristematic region and physiology of the leaf (Watts, 1971). Low chlorophyll stability, leaf firing, tassel blast, and sterility in both male and female flowers were also frequently observed in maize plants exposed to heat stress (Kilen and Andrew, 1969). The primary cause of the trade-off between stress and growth is attributed to the reduced energy supply, which significantly affects growth and development when a plant detects a stress signal (Zhao et al., 2024).

The maize crop shows high heat stress sensitivity between tassel emergence and the early grain-filling stage (Cairns et al., 2013; Zaidi et al., 2023). Heat stress reduces the pollen shedding duration, and the interval between anthesis and silking is much longer, resulting in poor pollination and fertilization (Struik et al., 1986; Noor et al. 2019). Heat stress can delay anthesis and damage most male flowers (tassels), resulting in little or no pollen production and/or male sterility (Zaidi et al. 2016). Heat stress may also cause silk sterility due to desiccation; however, this effect may vary with the intensity and duration of the heat stress (Zaidi et al., 2016; Dass et al., 2010). The effect of heat stress on the anther was expressed in terms of reduced pollen production, poor pollen germination on the stigma, and limited pollen tube elongation (Fahad et al., 2015, 2016).

Pollen viability is as crucial as the quantity of pollen production for adequate pollination, fertilization, and kernel set. The tetrad phase of pollen development and anthesis are the most sensitive stages to heat stress, as a brief exposure to temperature spikes at low humidity during this period can lead to severe damage (Jain, 2020; Ly et al., 2024). Heat stress affects the development of pollen primordia inside the anther (Bots et al., 2005). Fonseca and Westgate (2005) found that the pollen grains remain viable longer at low temperatures. At the same time, under heat stress, dehiscence and viability are severely compromised, and therefore, the seed set might be drastically reduced (51 to 80%). It was also observed that pollen desiccation and subsequent loss of viability is a function of three major environmental components - air temperature, relative humidity at Tmax, and the timing of exposure to stress. Pollen water potential has been reported to be the significant component heat stress affects (Schoper et al., 1986). Heat stress also causes a reduction in silk solute potential; however, this parameter was not found to affect seed set (Schoper et al., 1987). Hence, it is essentially the sensitivity of pollen grains to heat stress that fails fertilization (Dupuis and Dumas, 1990). Furthermore, genotypes with heat-tolerant pollen are characterized by a high germination percentage (Fig. 4) and improved pollen tube development, facilitating adequate fertilization (Herrero and Johnson, 1980).

Plant functions

Heat stress was closely associated with key physiological processes of maize plants, such as reduced radiation use efficiency (RUE), water use efficiency (WUE), net photosynthesis (Pn), and harvest Index (Traore et al., 2000; Karim et al., 2000). It causes reversible declines in the rate of photosynthesis during moderate stress, while causing irreversible damage with an increase in stress severity. Higher photosynthetic rates have been reported in maize plants grown at optimal temperatures compared to those at elevated temperatures (Wang et al., 2000). Almost all the key aspects of the photosynthetic process are sensitive to heat stress, including thylakoid membrane fluidity, electron transport, photochemical reactions, photophosphorylation, and the Calvin cycle (Wang et al., 2018; Cai et al., 2022; Chen et al., 2022; Viljevac et al., 2022; Lakshmi et al., 2023). A rapid decline was observed in the maximum quantum yield (Fv/Fm) in Photosystem II (PS-II) under heat stress, suggesting it is the most sensitive photosynthetic apparatus to heat stress (Crafts-Brandner and Salvucci, 2002; Sinsawat et al., 2004). The abrupt decrease in Fvs/Fms of photosynthesis might be related to the heat-induced changes in chloroplast thylakoids (Chen et al., 2010). The adaptive response of the photosynthetic apparatus to high-temperature stress is expressed through the production of compatible solutes for osmotic adjustment and the maintenance of redox potential and homeostasis (Mathur et al., 2014). This helps in adenosine triphosphate (ATP) homeostasis formation and maintains an energy balance across the thylakoid membrane, preventing irreversible damage under heat stress (Sharkey and Zhang, 2010).

Heat stress causes chlorosis or leaf senescence due to decreased chlorophyll concentration (Rossi et al., 2017). It also affects the activities of specific key photosynthetic enzyme complexes, such as ribulose-bisphosphate carboxylase (RUBISCO) activity (Perdomo et al., 2017). Heat stress causes damage to the chloroplast, inactivates RUBISCO activase (RCA) (Scafaro et al., 2016), and downregulates critical chloroplast components (Wang et al., 2017; Wang et al., 2018), which lowers photosynthetic efficiency (Fatma et al., 2021; Mustafa et al., 2021), redox imbalance (Mustafa et al., 2021), and cellular death in severe cases (Distéfano et al., 2017). The effect of heat stress was nominal on phosphoenol pyruvate carboxylase (PEPC) activity, while pyruvate phosphate dikinase was not affected by high temperature, suggesting that RUBISCO was the primary constraint limiting photosynthesis rate under heat stress (Crafts-Brandner et al., 2002).

Maintenance of PSII photochemistry (Fv/Fm) to maximize quantum yields, cell membrane stability, and lower leaf temperature collectively contributed to heat tolerance in maize (Yadav et al., 2015). A reduced photosynthesis rate due to heat stress during the lag phase of grain filling primarily resulted in kernel abortion and a severe yield penalty. In contrast, stress at the active grain-filling stage affected chlorophyll content and rate of photosynthesis, which was expressed in terms of reduced kernel weight and, eventually, grain yields. During active grain filling, both current photosynthate production and stored assimilates in vegetative parts of the plants contribute to kernel development (Badu-Apraku et al., 1983). Hence, the effect of heat stress on maize grain yield can partly be mitigated through an efficient source-sink relationship (Hunter et al., 1977).

Membrane thermostability

Heat stress-induced change in membrane fluidity is an immediate consequence of the stress as it is one of the most potent sites of perception of increased temperature (Sung et al., 2003). The thermostability of plant cell membranes plays a crucial role in heat stress tolerance, and it could be utilized as a target in maize breeding for enhanced heat stress tolerance. Heat stress-induced loss of plasma membrane integrity caused leakage of solutes and loss of other cellular content (Nagarajan et al., 2005). The unsaturation of membrane lipids (Gombos et al., 1994) is thought to play a pivotal role in protecting the photosynthetic apparatus from heat damage. However, information regarding membrane stability conferring tolerance to heat stress in maize is scant. The lipid profile of heat-stressed maize plants showed a substantial increase in phosphatidic acid in heat-tolerant genotypes, indicating a significant role of this membrane component in thermostability (Premachandra et al., 1991; Chen et al., 2010). Moreover, the accumulation of osmoprotectants, such as glycine betaine, also confers protection against the heat destabilization of membranes in maize under heat stress (Yang et al., 1996). However, the accumulation of glycine-betaine might invite other complications, such as increased incidence of some insect pests like aphids by increasing their survival and reproduction (Araya et al. 1991) and stimulating the growth of microbial diseases such as Fusarium (Pearce et al., 1976).

Hormonal balance

Plant hormones have a significant impact on crop growth, development, and productivity (Zhou and Leul, 1999). A heat stress-induced decrease in cytokinin content affects ear formation, floret fertility, pollen production, and viability, ultimately reducing kernel size and ultimately affecting grain yield (Wu et al., 2016). Increased abscisic acid (ABA) content in anthers and kernels, along with decreased gibberellin content, which contributed to floret abortion under heat stress. Heat stress disrupts maize kernel development by affecting the phytohormone homeostasis in kernels. Abscisic acid is associated with the maturity and growth of maize kernels (Cheikh and Jones, 1994). Maize lines tolerant to heat stress have been reported to have higher levels of ABA (Jones and Brenner, 1987) and cytokinins during kernel development (Cheikh and Jones, 1994). These studies suggest the importance of the two hormones in increasing thermotolerance and providing yield stability for maize. However, the relationship between change in phytohormone homeostasis under heat stress and the development of maize ears needs to be studied.

Cellular and molecular changes

The effects of heat stress on various morphological, physiological, and biochemical aspects result from crosstalk between several cellular and molecular processes induced or repressed under heat stress. Heat stress affects a broad spectrum of cellular components, pathways, and plant metabolism, and the severity of stress depends on the rate of change in temperature, intensity, and duration.

At the transcriptional level, several genes have been identified as regulating physiological and biochemical changes in response to various stresses, including heat stress (Yamaguchi-Shinozaki and Shinozaki, 2006). Among these, transcription factors play a crucial role. In maize, endosperm makes up to 80% of mature kernel weight and, thus, is considered most important in the overall grain-filling process. DNA endo-reduplication has been observed in the endosperm of maize (Kowles and Phillips, 1985), and it was found to be involved in increased gene expression for endosperm development and kernel filling (Kowles et al., 1992). Studies have shown a correlated decline in DNA endo-reduplication and kernel fresh weight at elevated temperatures (Engelen-Eigles et al., 2000), indicating a significant role of endo-reduplication in maize grain yield under heat stress. Hence, the stability of DNA endo-reduplication is essential in optimizing maize yields under heat stress. In response to heat stress, a reduction in the synthesis of ribulose-bis-phosphate carboxylase (RUBISCO) and protein in the kernel (Zein) were observed (Monjardino et al., 2006), indicating post-transcriptional regulation of heat response in maize. In response to heat stress shocks, an up-regulation of protein synthesis genes has also been reported in maize (Qin et al., 2007). Inductions of heat-inducible genes are attributed to the binding of heat shock factors to a conserved heat-shock element (HSE) in the promoter region of the genes. In maize, at least three heat shock factors (HSF) genes - HsfA, HsfB, and HsfC, have been found (Gagliardi et al., 1995), and most of them are heat-inducible, indicating transcriptional control of their synthesis. However, despite extensive studies on Hsfs, no immediate upstream factors to Hsf in heat signal transduction have been identified (Sung et al., 2003). DREB2A, a transcription factor, is associated with drought- and salt-stress response in Arabidopsis thaliana and heat-shock (HS) related genes (Sakuma et al., 2006). Similarly, a DREB2 homolog from maize - ZmDREB2A was found to upregulate some genes related to HS and detoxification in addition to genes encoding late embryogenesis abundant (LEA) proteins in maize seedlings (Qin et al., 2007), enhancing thermo-tolerance in transgenic plants. Unlike Arabidopsis, DREB2A and ZmDREB2A produced two forms of transcripts designated as ZmDREB2A-L and ZmDREB2A-S, which can function as transcriptional activators without any post-translational modification. Under heat stress treatment, the heat shock transcription factor AtHsfA3 (At5g03720) was upregulated, whereas it was absent under normal optimal temperature conditions. Promoter analysis showed that AtHsfA3 contains two DRE sequences in its promoter region, suggesting that this gene is a direct target of ZmDREB2A.

Heat stress affects starch biosynthesis, which accounts for about 70% of the maize kernel (Greene and Hannah, 1998). Studies have shown that heat-induced yield loss in maize is related to heat susceptibility of ADP-glucose pyrophosphorylase (AGP) activity, a major enzyme involved in starch biosynthesis (Hannah et al., 1980). Since AGP is an essential enzyme in starch biosynthesis, its temperature sensitivity likely causes a significant limitation to dry weight production during kernel development in maize under heat stress. A single point mutation in the Shrunken2 (Sh2) gene, which encodes the larger subunit of AGP, was reported to increase the stability of maize endosperm AGP through enhanced subunit interaction (Greene and Hannah, 1998). The heat-stable variant of AGP (Sh2hs33) may facilitate effective carbon flux into starch in maize kernels, and thus, may play a crucial role in minimizing heat-induced yield losses in maize. The study showed that inserting a cysteine in the N-terminus of the small sub-unit provided a 70-fold increase in heat stability in AGP at 55°C (Linebarger et al., 2005).

Catalase plays a significant role in defending plant functions by breaking down hydrogen peroxide (H_2O_2) into water and oxygen (Scandalios et al., 2000) and protects from oxidative stress caused by elevated temperatures. Within one second, this enzyme can convert 83,000 molecules of H_2O_2 into H_2O and O_2. Under severe heat stress, scutellar catalase activity is reduced in maize. Due to diminished levels of the Cat2 transcript, catalase activity declined under heat stress, primarily attributed to a decrease in the amount of Cat2 isozyme. The relative levels of Cat1 transcript were slightly higher in heat-tolerant maize lines with increased temperatures, indicating that the accumulation and/or stability of Cat1 mRNA in the stressed seedlings may compensate for the absence of other catalases. Hence, Cat1 might play a significant protective role in response to heat stress.

The production of reactive oxygen species (ROS) increased under heat stress, damaging PSII and PSI, hindering electron flow, and circumventing photosynthetic pigments, ultimately inactivating Calvin cycle enzymes (Zahra et al., 2023). These effects are related to the impact of heat on plastoglobuli formation, swelling of the thylakoid membrane, decrease in grana lamellae, degradation of photosynthetic proteins, and dissociation of DI and D2 protein turnover. The enzyme superoxide dismutase (SOD) protects against injuries caused by reactive oxygen species (ROS) and suppresses the production of free radicals (Fujii et al., 2022). The active SOD repairs oxidative damage by converting reactive oxygen species into water.

Generally, protein synthesis in plants quickly responds to environmental changes. Under heat stress conditions, maize synthesizes a few novel proteins termed heat shock proteins (HSPs) which enable the survival of plants under such adverse conditions (Cooper and Ho, 1983; Diogo-Jr et al., 2023). Heat shock proteins protect cells from stress-induced injury by acting as molecular chaperones, stabilizing other proteins and preventing them from denaturation and aggregation under stress (Ellis, 1987; Schirmer et al., 1996). In maize, HSPs have a potential role in maintaining normal membrane-associated processes during heat stress, as they have been associated with different organelles (Cooper and Ho, 1987). At elevated temperatures, HSP synthesis is tissue-specific (Cooper and Ho, 1984); thus, elongating portions of the primary root exhibit a stronger heat shock response than the more mature parts. Pollen is more sensitive to heat stress than female tissues (Alam et al., 2017). It might be related to the observation that under heat stress, the synthesis of a typical set of HSPs is found only in the female tissues, whereas no heat-shock response was detected in the mature pollen (Dupuis and Dumas, 1990). Even vegetative and sporophytic tissues of maize, including young shoots and pre-meiotic tassels, produce abundant quantities of all typical heat shock proteins (HSPs) in response to heat stress. However, the maize pollen exposed to the same temperatures during germination did not synthesize these specific HSPs (Hopf et al., 1992). The ability of the HSPs to synthesize upon exposure to heat stress was gradually lost during maize pollen development and the germination of pollen grains. The heat-shock response is associated with micro-gametophytic developmental stages, with uninucleated microspores eliciting the most potent response (Frova et al., 1989). The members of several prominent HSP gene families were expressed at the protein level close to the first pollen mitosis at normal temperature, indicating a possible involvement of these proteins in the first pollen mitosis during pollen development. However, later stages of pollen development, i.e., mid-tricellular and mature pollen, do not exhibit heat-induced accumulation of HSP70 transcripts. The defective heat shock response of maize pollen is attributed to an inefficient induction of heat shock gene transcription, resulting in a specific block in accumulating sufficient transcript levels for HSP (Hopf et al., 1992).

Mitochondrial HSP22 is suggested to protect mitochondria during heat stress in maize. It was suggested that while HSP22 is involved in organellar signaling of heat stress damage, HSP70 and cpn60 are constitutively expressed proteins (Lund et al., 1998). Similarly, four

Table 1. Effect of heat stress on various morphological and physiological traits of maize plants.

Traits associated with heat stress	Reaction/ Response	Source
Seedling vigor	Reduction	Noor et al., 2019
Seedling germination	Poor	Xue et al., 2021
Plant height	Reduction	Longmei et al., 2023; Yang et al., 2023
Leaf firing	Increase	Alam et al., 2017; Noor et al., 2019
Silking date	Increase	Alam et al., 2017; Noor et al., 2019; Longmei et al., 2023
Anthesis Silking interval	Increase	Alam et al., 2017; Noor et al., 2019; Longmei et al., 2023
Pollen viability/germinability	Reduced	Lohani et al., 2020; Zinn et al., 2010
Tassel sterility	Increase	Liu and Huang, 2000
Tassel Blast	Increase	Noor et al., 2019; Longmei et al., 2023
Pollen viability	Reduced	Vinayan et al., 2019; Liu and Huang, 2000; Fahad et al., 2015, 2016
Seed set	Poor	Gao et al., 2019, Fonseca and Westgate, 2005; Yang et al., 2023
Membrane Stability	Reduced	Yadav et al., 2005; Nagarajan et al., 2005
Lipid profile in fatty acid	Increase	Djalovic et al., 2024
Chlorophyll content	Reduced	Alam et al., 2017; Noor et al., 2019
Rubisco activity	Reduced	Scandalios et al., 2000
Heat Shock Proteins (HSPs)	Increase	Dupuis and Dumas, 1990; Cooper et al., 1984
Reactive oxygen species	Increase	Wang et al., 2018

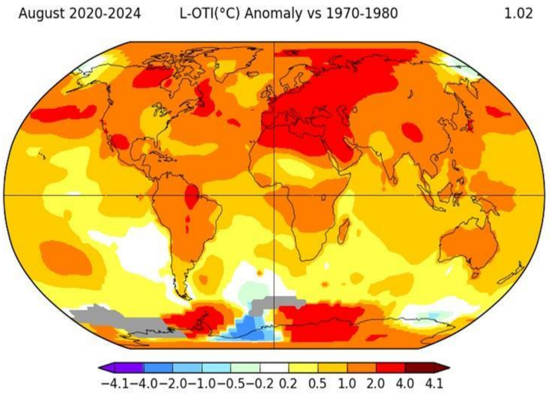

Fig 1. The average air temperature changes between 2020 and 2024 compared with the 1970-1980 average. Source: NASA, (https://data.giss.nasa.gov/gistemp/).

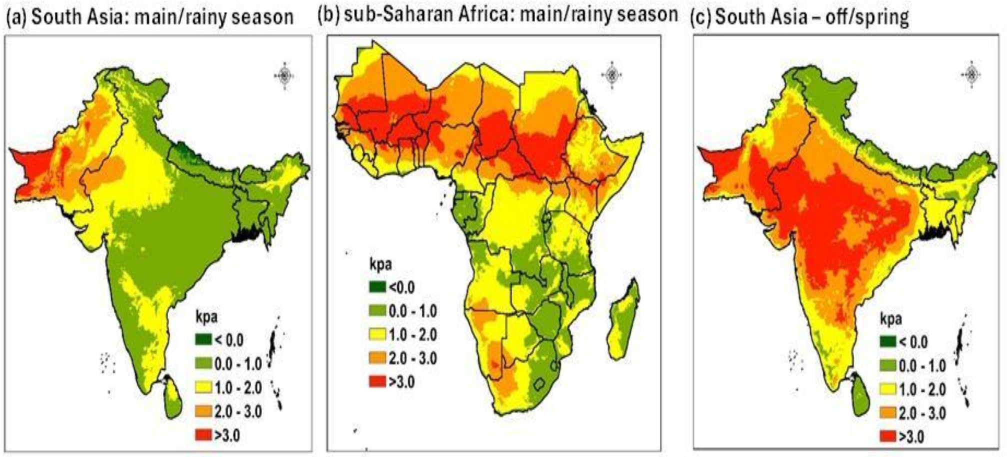

Fig 2. Change in vapor pressure deficit (VPD) at Tmax over the past 10 Years (2014-2023) during the reproductive growth stage for maize crop (anthesis to early grain-filling) in South Asia and sub-Saharan Africa.

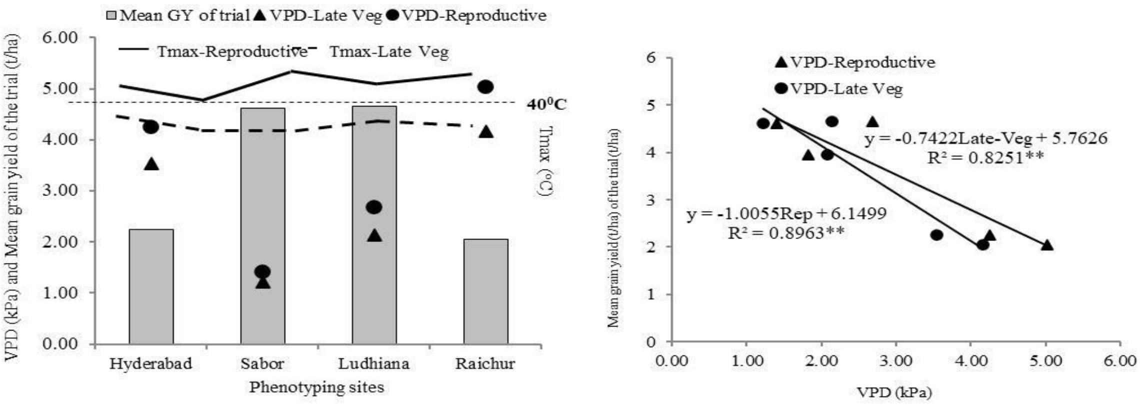

Fig 3. (a) Genotypic response of maize at different locations of heat stress phenotyping sites with similar maximum temperature (Tmax, 39.4±1.7 ∘ C) and varying vapors pressure deficit (VPD). (b) relationship between grain yield and VPD of the site at similar high-temperature regimes at vegetative and reproductive stages.

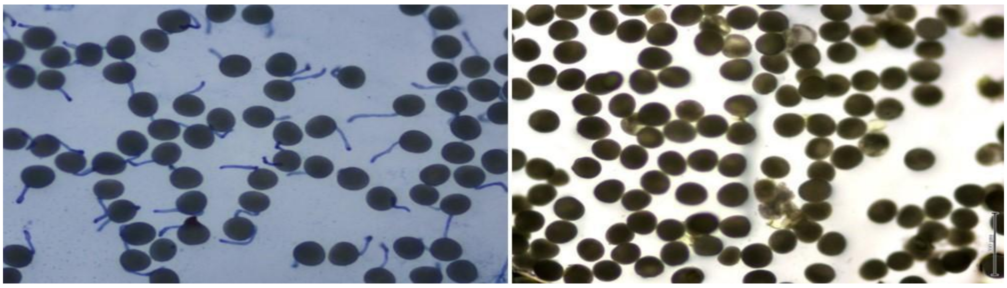

Fig 4. Genotypic variability for pollen viability in maize under heat stress, expressed in pollen germination in (a) heat tolerant and (b) heat susceptible inbred lines.

forms of HSP22 were found in mitochondria produced with the results of phosphorylation and differential intron splicing (Lund et al., 2001). Specific HSP genes encoding cytosolic and mitochondrial molecular chaperones must be steadily activated to adapt to chronic mitochondrial malfunction (Kuzmin et al., 2004). The study concluded that the expression of the mitochondria-dependent HSP gene differs from normal reactions to heat shock, indicating new signaling routes and induction processes. In the absence of external stress, establishing constitutive expression of HSP genes may be essential for cell defense and adaptation to long-term respiratory insufficiency.

Managing the impact of heat stress on maize

Integrating genetic enhancement with climate-smart cultural practices is necessary to manage various abiotic stresses, including heat stress (Wahid et al., 2007).

Crop management

Several crop management practices are recommended to mitigate heat stress. These include planting in furrows within a ridge-furrow system and applying irrigation using a sprinkler or misting irrigation system, which helps increase humidity around the crop canopy and reduces the heat stress effect on plants (Bal et al., 2022). Sowing time can be carefully chosen to avoid the coincidence of critical phases of reproductive stages with severe heat stress periods. In the case of large-area plantings, staggered sowing can be employed, which prolongs the duration of pollen availability (Dass et al., 2010). High radiation levels can lead to elevated soil temperatures for the crop. However, choosing a suitable variety with vigorous growth in the initial stages and a strong root system to penetrate quickly through the upper 20 cm of the soil profile might better tolerate high soil temperatures (Lal, 1974). Mulching can be used for water conservation and to improve the physical environment of seed beds during heat-stress conditions (Dalmago et al., 2004; Sidiras and Pavan, 1986). A 52% increase in the grain yield of maize was reported after using rice straw or forest litter as a source of mulch (Lal, 1954). Plots with and without mulch have been shown to differ in temperature by up to 8°C at a depth of 5 cm. According to a simulation study, employing surface mulching as an ameliorative management technique significantly reduced soil evaporation and the hardness of topsoil as a barrier to maize seedling establishment. (Weaich et al., 1996). Zero tillage, i.e., planting in untilled soil, is suggested to mitigate heat stress in maize, as no-tillage causes higher stability in the soil thermal regime than the conventional system (Dalmago et al., 2004).

Genetic improvement of heat stress tolerance

A successful breeding plan for heat stress tolerance requires a deeper understanding of the genetic inheritance, as heat stress is a complex trait. Effective selection for heat tolerance in maize requires assessing genotypes in replicated trials across diverse environments, as heat tolerance is a quantitatively inherited trait (Bai, 2003). Dominance gene action is predominant for various traits, including seedling emergence and vigor, morphophysiological and reproductive traits, and ultimately grain yield under heat stress (Tassawar et al., 2007). Non-additive gene action for yield and yield-contributing characters under heat stress in maize was also reported (Akbar et al., 2008). The non-additive genes influenced cell membrane thermostability, stomatal conductance, transpiration rate, turgor potential, and days to tasselling, whereas the additive genes predominantly affected days to physiological maturity under both normal and heat-stressed conditions (Akbar et al., 2009). The dominant gene action for most traits associated with heat stress tolerance implicates an inbred-hybrid breeding strategy to improve heat tolerance in maize (Mukaro et al., 2023). Population improvement can increase the frequency of favorable heat-tolerant genes in improved populations, thereby deriving new maize inbred lines with enhanced heat tolerance levels. These new inbred lines can then be used in the development of new hybrid combinations with even greater heat tolerance levels (Hosamani et al., 2020).

The secondary traits that were identified to be associated with heat stress tolerance (Alam et al., 2017) are governed by multiple genes/loci (Parrado et al., 2020). Genotypic variability must exist for traits of interest, such as heat stress, to facilitate selection and targeted breeding. Extensive screening of elite maize germplasm for identifying potential sources of heat stress tolerance yielded limited success, as genotypic variation is limited in elite maize cultivars (Nelimor et al., 2020). Using conventional breeding methods, which involve selecting heat-tolerant lines based on phenotype, breeders have had limited success due to significant genotype × environment interaction effects and low heritability of grain yield under heat stress (Hussain et al., 2006; Rahman et al., 2013, 2015). Moreover, selection based on key secondary traits and grain yield under stress helped identify maize lines with heat stress tolerance (Longmei et al., 2021, 2023). Understanding stress-adaptive and stress-responsive secondary traits helps decide the selection direction for each trait during the phenotyping of maize genotypes under heat stress (Alam et al., 2017; Noor et al., 2019). The identified lines with heat tolerance traits could be used in backcross breeding to transfer stress tolerance traits into elite genetic backgrounds. However, as introgression typically occurs within existing maize germplasm, it may not necessarily help improve yields under heat stress.

Despite identifying many genes involved in tolerance to various abiotic stresses, including heat stress tolerance in maize, a clear understanding of the gene resources and molecular mechanisms that enable withstanding exposure to stress is lacking compared to other model plant species (Yang et al., 2023). By revealing the molecular mechanism underlying maize plants' ability to balance growth and heat stress tolerance, genetic resources can be developed to create new heat-stress-tolerant cultivars using contemporary breeding techniques (Zhao et al., 2024). To make well-informed selection decisions and introduce heat tolerance into elite genetic backgrounds, recent developments in genomics, molecular breeding techniques, and phenomics have enhanced our understanding of the genetic underpinnings of maize's response to heat stress (Seetharam et al., 2021; El-Sappah et al., 2022). Using genome-wide association studies (GWAS) and advanced mapping populations, several genes/QTLs have been identified for different traits under heat stress (Seetharam et al., 2021; Diolovic et al., 2024). However, no QTLs/haplotypes with large effects could be discovered (Seetharam et al., 2021), and therefore, breeding for heat stress tolerance in maize is primarily handled as a quantitative trait (Zaidi et al., 2023). Crop improvement programs must prioritize novel traits, genes, and haplotypes and employ targeted introgression into elite genetic backgrounds to improve heat stress tolerance. New generations of maize lines with enhanced performance under heat stress-vulnerable agroecologies can be developed by introducing validated genomic regions into elite genetic backgrounds. A precise selection of heat-tolerant maize germplasm may be aided by the trait-associated markers from multiple studies in the expanding pan-genome sequence data. CIMMYT maize program in Asia implemented a targeted population improvement for heat stress tolerance using three cycles of rapid-cycle genomic selection (RC-GC). Maize lines were extracted from advanced cycles of the improved populations using doubled haploidy (DH), and those DH lines were evaluated as test crosses under managed heat stress in the field conditions. Best-performing crosses were advanced using the stage-gate process, which resulted in the identification of improved heat-tolerant hybrids that were licensed to seed partners (Fig. 5). The new heat-tolerant hybrids were officially released/registered by partners and deployed in over 50,000 ha in heat stress vulnerable ecologies in South Asian countries (Zaidi et al., 2023).

The challenge, however, remains to cope with unpredictable weather extremes. High temperatures with heat waves in lowland tropics are breaking their records year after year (Dailidien et al., 2023). Global warming gradually leads to global drying, as indicated by an increase in potential evapotranspiration in the South Asia region and an increasing risk of drought stress (Aadhar et al., 2020). Therefore, maize germplasm with further enhanced levels of heat stress resilience needs to be developed to keep pace with the changing climate and associated extreme weather conditions, including high temperatures and low humidity.

Conclusions

Climate change effects, such as recurring heatwaves and sporadic droughts, pose a significant challenge to agricultural production, especially for rain-fed crops like maize. Heat stress causes a double-sided water deficit: supply-side due to depleted soil moisture due to increased surface evaporation at high temperatures, and demand-side drought with decreased moisture in the air. With both effects coming together, plants are often exposed to severe water deficits, with no relief from the soil or air. A recent study from South Africa reported that nationwide maize yield variability was relatively higher due to heat waves (35%) than drought events (25%) (Simanjuntak et al., 2023). These studies underscore the need for dedicated and concerted efforts to develop maize technologies, including climate-smart agronomics and the next generation of maize varieties that combine high yields with stress resilience, thereby offsetting the predicted significant yield losses. There is a need to look beyond the available genotypic variability within working/elite maize germplasm in breeding programs in lowland tropics and explore wider genetic diversity through pre-breeding efforts on local landraces and wild accessions to identify potential heat-responsive source germplasm (Würschum et al., 2022). Of course, pre-breeding efforts on landraces require a core subset with adequate variation for the desired traits (Würschum et al., 2022) . Genomic-assisted selection may help identify new sources of trait donors with further enhanced heat tolerance levels for maize breeding programs in the lowland tropics.

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