REVIEW
published: 29 April 2022
doi: 10.3389/fpls.2022.879366

Heat Stress-Mediated Constraints in Maize (*Zea mays*) Production: Challenges and Solutions

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Specialty section:
This article was submitted to Plant Biotechnology, a section of the journal Frontiers in Plant Science

Received: *19 February 2022*
Accepted: *30 March 2022*
Published: *29 April 2022*

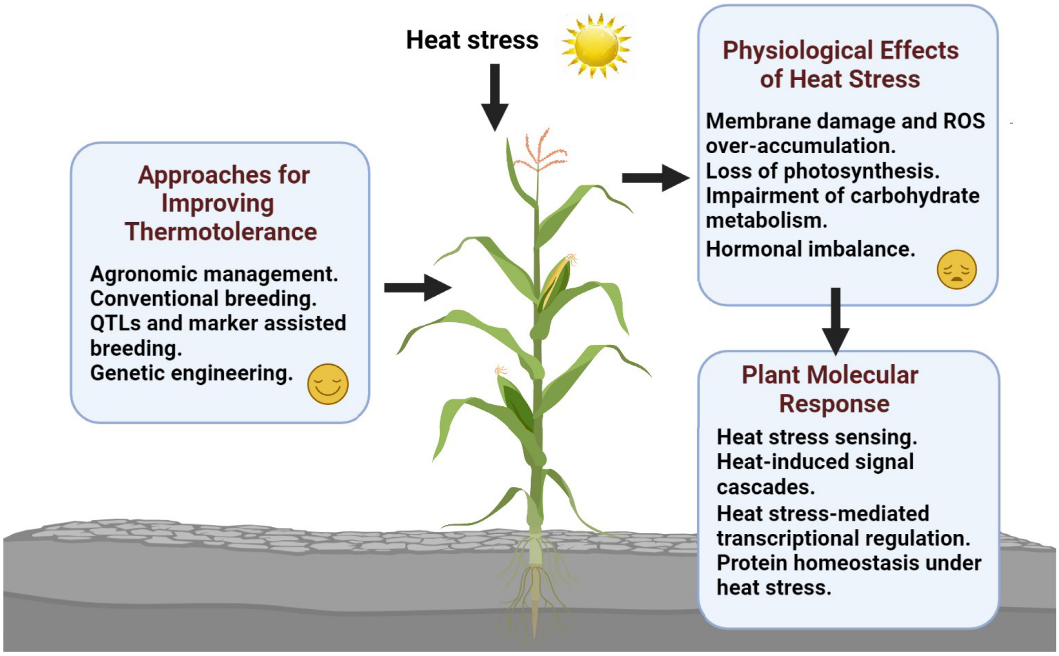
Citation:
El-Sappah AH, Rather SA, Wani SH, Elrys AS, Bilal M, Huang Q, Dar ZA, Elashtokhy MMA, Soaud N, Koul M, Mir RR, Yan K, Li J, El-Tarabily KA and Abbas M (2022) Heat Stress-Mediated Constraints in Maize (Zea mays) Production: Challenges and Solutions. Front. Plant Sci. 13:879366. doi: 10.3389/fpls.2022.879366

An increase in temperature and extreme heat stress is responsible for the global reduction in maize yield. Heat stress affects the integrity of the plasma membrane functioning of mitochondria and chloroplast, which further results in the over-accumulation of reactive oxygen species. The activation of a signal cascade subsequently induces the transcription of heat shock proteins. The denaturation and accumulation of misfolded or unfolded proteins generate cell toxicity, leading to death. Therefore, developing maize cultivars with significant heat tolerance is urgently required. Despite the explored molecular mechanism underlying heat stress response in some plant species, the precise genetic engineering of maize is required to develop high heat-tolerant varieties. Several agronomic management practices, such as soil and nutrient management, plantation rate, timing, crop rotation, and irrigation, are beneficial along with the advanced molecular strategies to counter the elevated heat stress experienced by maize. This review summarizes heat stress sensing, induction of signaling cascade, symptoms, heat stress-related genes, the molecular feature of maize response, and approaches used in developing heat-tolerant maize varieties.

Keywords: abiotic stress, gene signaling cascade, heat stress, molecular response, *Zea mays*

INTRODUCTION

Heat stress is the most devastating abiotic stress factor influencing seasonal growth and spatial variations in various crops (Sallam et al., 2018; Magaña Ugarte et al., 2019). Global warming caused by the increasing growth of the population and the accompanying industrial development has become a concern that cannot be overlooked (Baus, 2017). Also, the average rise in global temperature between 1900 and 2020 was 1.13°C, and it is expected to increase by 1.4–5.8°C in 2100



GRAPHICAL ABSTRACT | This review summarized heat stress-mediated morphological and physiological changes in maize and elucidated the molecular mechanisms responsible for maize response to heat stress. Furthermore, plausible approaches to dissecting the regulatory network associated with heat stress response and improving maize adaptation to global warming have been discussed. This figure was made using BioRender.

(**Figure 1**; Houghton et al., 2001). This gradual increase in global warming and heat waves have become a serious threat to crop productivity (Hoegh-Guldberg et al., 2019). Data published by the Food and Agriculture Organization has revealed the annual relative yield loss in major cereal crops (Faostat, 2019). Also, recent studies have shown that effective heat stress tolerance *via* genetic improvement is the only possible remedy; otherwise, every 1°C temperature rise will cause a 6.0% yield loss of wheat, 3.2% of rice, 7.4% of maize, and 3.1% of soybean (Zhao et al., 2017; Kraus et al., 2022). However, due to increasing population growth, crop yield ought to increase by 70% for sustaining food security to meet the demand of a projected 9 billion population rise in 2050 (Popp et al., 2013; Dawson et al., 2016).

Maize (*Zea mays*) is an important cereal crop that belongs to the Poaceae family (Li et al., 2022) and has ensured global food security with a worldwide production $\geq 1 \times 10^9$ t (10^{12} kg) since 2013 (Faostat, 2017). Maize was initially cultivated in tropical areas under rainfed conditions (Li J. et al., 2021; Maitra et al., 2021). However, there is an increased demand for maize due to its utilization of carbohydrates as biomass for ethanol fuel production, leaves and stem as livestock fodder, grains as raw material in the baking industry, and food and feed crop in many countries (Rooney et al., 2007; Parmar et al., 2017; Dar et al., 2021). Maize is a rich source of starch and calcium in addition to numerous essential minerals, vitamins, and fiber. However, it labors to some nutrients, such as vitamins B12 and C (McKevith, 2004). Iron absorption, particularly the non-heme iron present in maize, can be inhibited by some components of the diet being consumed, such as vegetables, coffee (e.g., polyphenols), tea (e.g., oxalates), milk (e.g., calcium), and eggs (e.g., phosvitin) (Ranum et al., 2014).

Elevated temperature accelerates crop growth but shortens its growing season (Mo et al., 2016; Hu et al., 2017; Ahmed et al., 2018; Ihsan et al., 2019). Additionally, maize growth requires an optimum daytime temperature range of 28–32°C, comparatively higher than the optimum temperature necessary for other cereal crops, such as wheat (*Triticum aestivum*) and rice (*Oryza sativa*) (Sánchez et al., 2014).

The global change resulting from harsh climatic conditions has negatively affected maize crop yields (Lobell et al., 2011; Ahmed et al., 2018; El-Sappah and Rather(eds)., 2022). Also, increased temperature stimulates the over-accumulation of phenolic compounds, resulting in cell necrosis, consequently contributing to maize yield loss (Tebaldi and Lobell, 2018). Furthermore, heat stress (>32°C) causes the deterioration of several metabolic processes in maize plants, including a severe break in photosynthesis, increased surface transpiration rate (Crafts-Brandner and Salvucci, 2002; Sharma et al., 2020), pollen-sterilization at anthesis (flowering stage) (Gourdji et al., 2013), kernels shortening at grain-filling stage (Singletary et al., 1994; Rezaei et al., 2015), cumulatively resulting in a significant yield loss.

The approval of multiple agronomic and breeding alternatives along with advanced genomic tools is inevitable to cope with the deleterious effects of extreme temperatures (Waqas et al., 2021). Several agronomic management practices, such as the management of soil and nutrients, crop rotation, plantation rate, timing, and irrigation, are beneficial for the development of heat

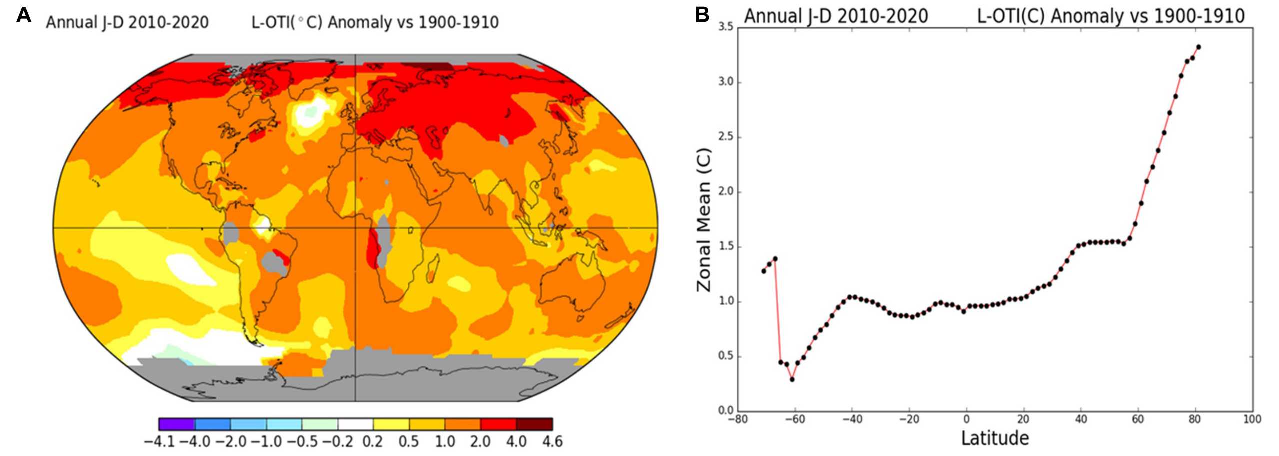


FIGURE 1 | (A) Map of annual mean temperature change (°C) during 1900–1910 and 2010–2020. **(B)** The zonal means plot. Air temperature data of the land surface was retrieved from GHCNv4 (GISS analysis based on global historical climatology network v4), and sea surface temperature data was retrieved from ERSST_v5 (NOAA/NCEI's extended reconstructed sea surface temperature v5). The number at the top right-hand corner of the map plot is an estimate (°C) of the global mean of the calculated area. The maps were made using GISS Surface Temperature Analysis software (https://data.giss.nasa.gov/gistemp/maps/index.html).

tolerance in maize (Sabagh et al., 2020). Genetically modified crops could also be a valuable resource for the development of novel traits that enhance the survival of plants under harsh conditions (Jha et al., 2020). In recent years, the rate of crop improvement has accelerated owing to the rapid progress in plant molecular biology. In several crops, different genetic approaches, including marker-assisted selection (MAS), map-based gene cloning, quantitative trait locus (QTL) mapping, and genome editing (such as RNA interference [RNAi] and CRISPR)/CRISPR-associated-9, Cas9), have been utilized for the selection and improvement of plant traits (Waqas et al., 2021).

This review summarized heat stress-mediated morphological and physiological changes in maize and elucidated the molecular mechanisms responsible for maize response to heat stress. We also discussed plausible approaches in dissecting the regulatory network associated with heat stress response and improving maize adaptation to global warming.

IMPACT OF HEAT STRESS ON DIFFERENT GROWTH STAGES

Vegetative Stage

Technically, the growth of stems, leaves, and roots, usually referred to as vegetative growth, is also known as germination, leaf, and tasseling (Dolatabadian et al., 2010). Heat stress affects the abovementioned growth stages (**Figure 2**) significantly. Also, the optimum soil temperature for maize seeds germination is 21°C, whereas <13°C causes a severe stoppage in germination and <10°C causes a total cessation (Kaspar and Bland, 1992; Towil, 2010; Sánchez et al., 2014). The germination rate of spring sowing of maize seeds cultivated in higher altitudes, such as North Europe and North America, is comparatively low due to low soil temperature (Paul et al., 1996). Early seed germination may expose the crop to freezing temperature, and early flowering leads to short crop duration leading to severe yield loss (Jagadish et al., 2016). However, late cultivation for optimum temperature conditions caused a severe loss in yield due to pest attacks (Rosenzweig et al., 2001). Therefore, only the day-neutral spring maize is favorably cultivated in higher altitudes (Colasanti and Muszynski, 2009).

Notably, the younger seedlings are less susceptible to high temperatures (Sánchez et al., 2014). The overall required temperature range for early maize seedling growth is 30–35°C, and the optimal temperature is around 20°C (Khaeim et al., 2022), 4–6°C higher than the suitable temperature for wheat and barley growth (Sánchez et al., 2014). Importantly, depending upon maize variety and below 20°C, every 0.5°C downfalls in daily temperature resulted in 10–20 days extended crop duration (Rahman et al., 2009). At an average daytime temperature of 15°C may take 200 days for the maturity of maize crop (Wilson et al., 1995).

Maize is susceptible to cold temperature but can recover from its effects if height is less than 15 cm when exposed to cold (Sakai and Larcher, 2012). Temperature below 10°C causes stunted root growth, whereas 17°C temperature results in 1.5 mm root growth per day, and temperature above 40°C inhibits root growth (Ryel et al., 2002). Maize seedlings can recover from constraints of drought stress because it is naturally resistant to drought (Daryanto et al., 2016). In conclusion, maize can recover from adverse climatic conditions if exposed at very early vegetative growth stages. The early cultivation of maize also facilitates the avoidance of pest attacks and the possible development of diseases (Bruns, 2003). So, early sowing of maize is highly recommended.

Reproductive Stage

The fruit setting stage is the reproductive stage that begins with vegetative growth termination and flowering initiation. The stage is susceptible to unexpected fluctuation in temperature, i.e., >32°C temperature, or frost causing severe yield loss (Silim et al., 2006; Siebers et al., 2017). Also, hailstorm adversely affects

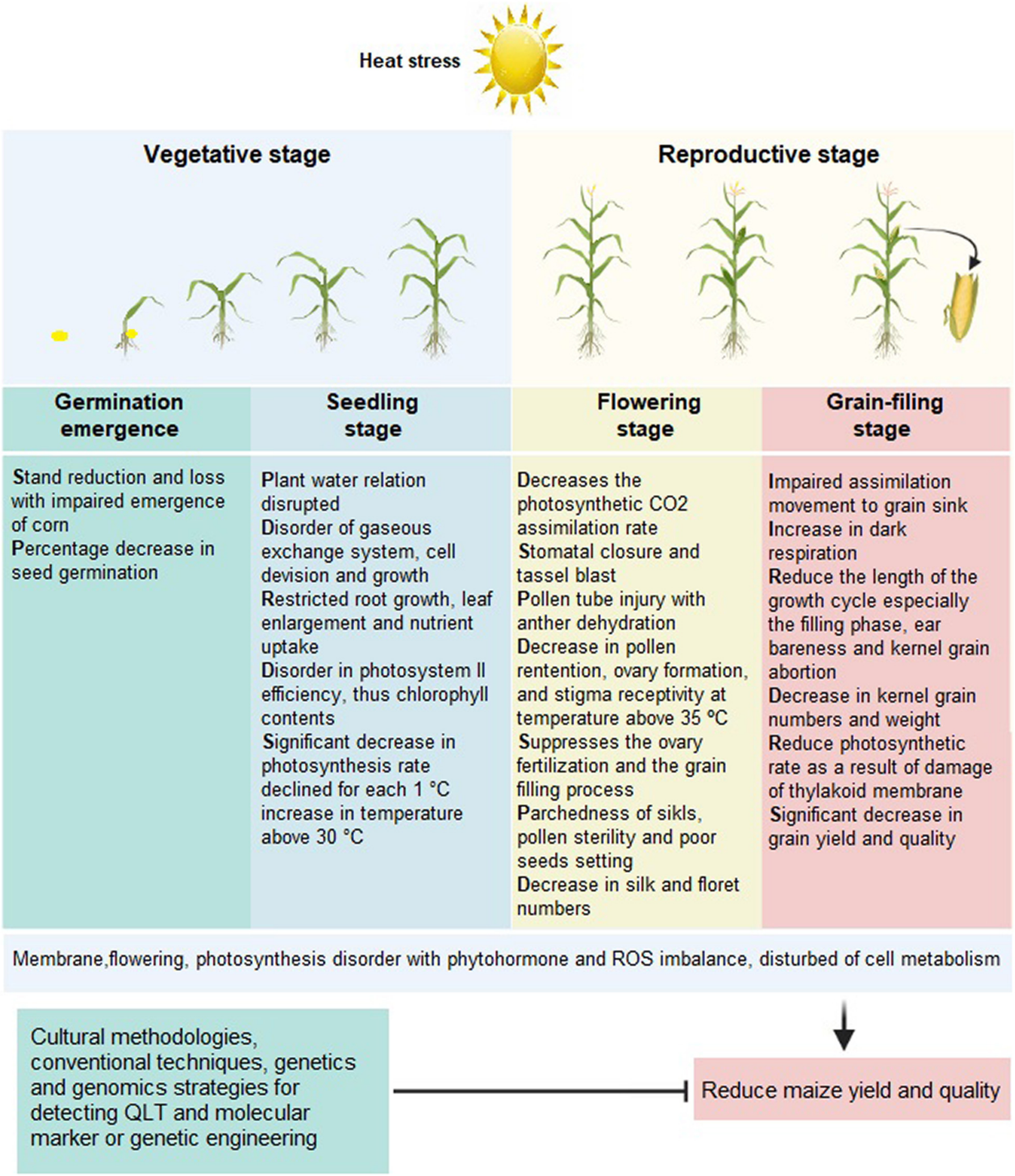


FIGURE 2 | Morphological and physiological characteristics of maize under heat stress. This figure was made using BioRender.

outcomes at the jointing and silking stage (Chen K. et al., 2018). Similarly, soil moisture contents before, during, and after silking result in a severe reduction in yield by 25, 21, and 50%, respectively (Pandey et al., 2000). The optimum temperature at tasseling is between 21 and 30°C (Kiniry and Bonhomme, 1991). Additionally, elevated temperature encourages respiration (Guo et al., 2019) and shortens grain-filling duration, contributing to a significant yield loss (Sánchez et al., 2014). Conversely, low-temperature extends the length of the grain-filling period, the appropriate phase change of photosynthesis to dry matter, and grain filling, resulting in a higher yield (Dordas, 2009; Edreira et al., 2014; Chao et al., 2016). Overall, during pollination and grain filling, temperatures $\geq 35^\circ$C suppress fertilization in maize and decreases its yield by 101 kg/ha per day (Naveed et al., 2014; Dawood et al., 2020).

PHYSIOLOGICAL EFFECTS OF HEAT STRESS

Membrane Damage and Reactive Oxygen Species Over-Accumulation

Heat stress causes cell physiological changes, such as inactivating the photosystem II (PSII) reaction center and the denaturation of the lipid bilayer and embedded proteins in the thylakoid membrane, resulting in the damaging of the cell membrane (Yang et al., 1996; Nijabat et al., 2020). The damaged cell membrane has caused severe retardation of ion exchange, leakage of electrolytes, viscous cytosol due to water loss, toxic compounds production, and homeostasis disruption (Stanley and Parkin, 1991; Demidchik, 2015). Also, these changes have resulted in plant growth cessation through leaf wilt, reduced leaf area, and leaf abscission (Bartels and Sunkar, 2005; Mafakheri et al., 2010). Furthermore, the cell membrane stability varies with plant tissue age, growth stage, growing season, plant species, and heat intensity (Nijabat et al., 2020). Therefore, the plant's retention of its cell membrane stability and water contents under heat stress during the vegetative and reproductive growth period has generated higher yields (Khakwani et al., 2012).

Heat stress stimulates ROS biosynthesis that promotes membranous lipids peroxidation, leakage of cellular contents, protein degradation, enzymatic inactivation, bleaching of chlorophyll pigments, and DNA damage, consequently resulting in necrosis (He and Häder, 2002; Mujahid et al., 2007). Phospholipids-peroxidation causes the production of malondialdehyde (MDA) which causes damage to the cell membrane (Pamplona, 2008; Wadhwa et al., 2012). Additionally, ROS causes polyunsaturated fatty acid peroxidation, leading to chain breakage contributing to increased membrane permeability and fluidity (Catalá, 2009). Notably, the increased accumulation of H_2O_2 causes lipid peroxidation and membrane damage (Banerjee and Roychoudhury, 2018; Yadav et al., 2018). Heat stress-mediated genetic variations have been investigated in several cereal crops, including wheat, barley, rice, and maize (Kumari et al., 2009; Khajuria et al., 2016; Swapna and Shylaraj, 2017). Balanced redox reaction system activation via enzymatic antioxidants, such as superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase, and non-enzymatic antioxidants, such as NADH; NADPH; ascorbic acid, glutathione, and secondary metabolites play a crucial role in heat stress tolerance (Wahid et al., 2007; Foyer and Shigeoka, 2011).

Loss of Photosynthesis

Photosynthetic apparatus is highly vulnerable to damage when exposed to heat stress and intense light (Essemine et al., 2012; Li Y. T. et al., 2020). Therefore, heat stress causes a severe reduction in carbon assimilation, restricts electron transfer, aggravates oxidative damage and photoinhibition of PSII, resulting in significant yield loss (Elferjani and Soolanayakanahally, 2018; Li Y. T. et al., 2020). Heat stress also denatures vital enzymes associated with the Calvin cycle, such as rubisco, and reduces carbon assimilation in C3 plants (Dias and Brüggemann, 2010; Zhang et al., 2020a). However, C4 plants, such as maize, harbor the CO_2 concentration mechanism (Dai et al., 1993; Majeran and van Wijk, 2009), reducing the restriction of photosynthetic carbon assimilation *via* the Calvin cycle (von Caemmerer and Furbank, 2016). Furthermore, Phosphoenol pyruvate carboxylase is the highly thermostable initial enzyme involved in the C4 cycle (O'Leary et al., 2011), suggesting that other photosynthesis pathways contribute to declining photosynthetic carbon assimilation under heat stress in maize (Li Y. T. et al., 2020). Notably, the photosynthetic apparatus acclimatizes to heat stress by improving its antioxidant capacity and changing leaf structure and metabolism (Li Y. T. et al., 2020). However, shock heat stress during flowering causes irreparable yield loss by damaging the leaves, rendering them unable to sprout again due to the completion of vegetative growth (Li Y. T. et al., 2020).

Respiration plays a crucial role in photosynthesis, whereas its inhibition suppresses CO_2 fixation and photoinhibition (Gardeström and Igamberdiev, 2016). However, stomatal closure does not limit the exchange of gases like CO_2 but limits the transpiration rate through leaves. The CO_2 concentration mechanism of C4 plants, such as maize leaves, provides more robust resistance to stomatal restriction than in C3 plants (Markelz et al., 2011). Additionally, the blockage of respiratory electron transfer inhibits photorespiration resulting in PSII photoinhibition (Rochaix, 2011; Zhang et al., 2017). Transpiration through stomata is an important heat-dissipating mechanism, with their closure under heat stress resulting in severe loss in net photosynthetic rate (Pn) (Caine et al., 2019). The lower stomatal conductance (Gs) in maize leaves maintains water-use efficiency but damages photosynthetic apparatus under heat stress. Therefore, the lower Gs due to stomata closure indicates less heat dissipation *via* the transpiration mechanisms in the leaves of C4 plants, such as maize, compared to C3 plants (El-Sharkawy, 2007; Li Y. T. et al., 2020).

Photoinhibition of photosystems (PSI and PSII) in the chloroplast results from the degradation of the light receptors under heat stress contributing to the significant halt in photosynthesis (Zivcak et al., 2015). The oxygen-evolving complex (OEC) of PSII is highly sensitive to heat stress than of high-intensity light, whereas the D1 protein of PSII is more sensitive to high-intensity light instead of heat stress (Vass and Cser, 2009; Tóth et al., 2011). It is reported that heat stress significantly affects the acceptor site of PSII instead of PSI in maize leaves (Yan et al., 2013; Li Y. T. et al., 2020). Accordingly, OEC is the primary site in maize leaf cells affected by heat stress, whereas D1 is the primary site affected by high-intensity light. The over-accumulation of ROS is another cause of D1 protein denaturation (Kong et al., 2013). Therefore, overexpression of OEC and D1 protein and downregulation of ROS *via* genetic engineering and breeding techniques will improve heat tolerance in maize (Li and Howell, 2021).

Imbalance/Deregulation in Primary and Secondary Metabolism

Traditionally, metabolites are divided into primary and secondary/specialized metabolites. Primary metabolites reinforce cell and secondary/specialized metabolites are concerned with an organism's interaction with its environment. Primary metabolism produces precursors for secondary metabolite biosynthesis and plays a direct and central role in plant growth, development, and reproduction. It also produces precursors for secondary metabolite biosynthesis (Medeiros et al., 2021). Secondary metabolites possess functional and chemical diversity (Erb and Kliebenstein, 2020). Thousands of metabolites serve as mediators for the various interactions between plant and the environment (Medeiros et al., 2021). During a stress response, plants fine-tune their metabolic production accordingly; however, the mechanisms, reasons, and regulations for this process are only partially understood.

Leaf metabolites were most affected by long-duration salt, heat, or drought stress treatments compared with the rest of the maize organs. The raffinose pathway metabolites (raffinose and galactinol) and some amino acids such as threonine, tryptophan, and histidine also stood out in the heat stress metabolome profile (Joshi et al., 2021). In the metabolic studies of Joshi et al. (2021), 2,549 genes were upregulated including galactinol synthase (*Zm00001d028931*), stachyose synthase (*Zm00001d039685*), and a putative inositol transporter (*Zm00001d018803*), while 2,587 genes were downregulated as a result of heat stress. Two stress-induced arginine decarboxylase paralogs exhibited a similar dichotomy with drought and heat, inducing *Zm00001d051194*. However, the responses from pairing drought and heat stressors contrasts with the pattern exhibited by the raffinose pathway genes described above where the effects of heat and salt were correlated (Joshi et al., 2021).

Heat stress adversely affects carbohydrate catabolism by denaturing relevant enzymes resulting in the over-accumulation of starch and sucrose (Ruan et al., 2010; Xalxo et al., 2020). Varied expression patterns of genes and proteins involved in carbohydrate metabolism were observed in *Arabidopsis* exposed to heat stress (Kaplan et al., 2004). In addition, heat stress causes over-accumulation of maltose, sucrose, and cell wall-specific monosaccharides (Lima et al., 2013; Sengupta et al., 2015). Additionally, the metabolic profiling of plants exposed to two abiotic stress factors, such as drought and heat, showed over-accumulation of glucose, fructose, sucrose, trehalose, maltose responsible for maintaining cell turgor pressure, stabilizing cell membranes and proteins (Rodziewicz et al., 2014; Kumar et al., 2021). During unfavorable conditions, plants digest starch molecules to get energy as a substitute for glucose; however, extended heat stress causes depletion of all carbohydrate reservoirs and causes plants starvation (Kaplan et al., 2004; Djanaguiraman et al., 2010).

Temperature significantly affects starch biosynthesis in maize kernels, which contributes to the total dry weight of grains (Keeling et al., 1994). Heat stress stimulates the production of osmolytes including fructose, mannose, sucrose, and proline, which plays a vital role in heat stress tolerance (Slama et al., 2015; Sharma et al., 2019). The grain-filling rate and duration are determined by the sucrose contents available in kernels and enzyme activity level (Singletary et al., 1994; Alam et al., 2021). Short interval time series analysis revealed that the "tipping point" for maize metabolome perturbation is lengthened at a >1 day of drought stress, including a combined effect of drought and heat stress (Bechtold et al., 2016). Generally, heat stress causes mechanical changes, whereas drought stress results in the disequilibrium of osmosis in plants cell (Haswell and Verslues, 2015). Therefore, abiotic stress-mediated changes in metabolic responses are probably attributed to adaptations to drought and heat stresses (Kaplan et al., 2004; Khan et al., 2015).

Osmolytes also contribute a crucial role in maintaining membrane structure (Sharma et al., 2019), alleviating proteins degradation, reducing ionic toxicity, protecting cell organelles, scavenging ROS, protecting antioxidant compounds, and maintaining redox equilibrium (Hasanuzzaman et al., 2020). Osmolytes, such as sucrose, fructose, and mannose, are resources of energy, nutrition, structural materials, signaling molecules, and crucially contribute to seed germination and the growth of plantlets (Osuna et al., 2015). Maize (*Zea mays* L.) seedlings exposed to heat stress displayed sudden degradation of glycan contents and upregulated fructose and mannose metabolism (Lieu et al., 2021). The expression of genes involved in fructose, mannose, and sucrose biosynthesis was also upregulated in 21-day-old maize seedlings exposed to heat stress (Stavridou et al., 2021).

The mitochondria and nuclear membrane structure were also disrupted by heat stress, more severe in the heat-sensitive hybrid (Török et al., 2014; Li Y. T. et al., 2020). Also, disruption of mitochondrial membrane structure decreases the efficiency of oxidative phosphorylation, requiring increased consumption of carbohydrates to supply sufficient ATP and further reducing light energy utilization (Li Y. T. et al., 2020). Additionally, many chloroplast proteins are encoded by the nuclear genome; hence, destruction of the nuclear envelope may inhibit the upregulation of photo-protection mechanisms, aggravating the photosynthetic mechanism damage and delaying photo inhibition repair and structural damage (Kumar and Kaushik, 2021). The less grouped PSII units are more sensitive to light, partly explaining the more severe PSII under heat stress (Strasser et al., 2004).

Hormonal Imbalance

Phytohormones, such as auxin/indole acetic acid (IAA), gibberellic acid (GA), abscisic acid (ABA), cytokinin (CTK), ethylene (ET), salicylic acid (SA), brassinosteroids (BRs), strigolactone (SL), and jasmonic acid (JA) importantly regulates cellular processes which are ubiquitous to plant growth under abiotic stress factors (Sharma et al., 2019). Heat stress causes over-accumulation of ABA and the downregulation of CTK, resulting in the improper development of maize kernels (Cheikh and Jones, 1994; Niu et al., 2021). The application of benzyladenine on maize seedlings maintains a proper balance between ABA and CTK, causing an increased heat tolerance

(Cheikh and Jones, 1994). Similarly, the treatment of maize seedlings with Ca^{2+} ions solution and ABA improves the antioxidant enzyme activity, reduces lipid peroxidation, and improves heat tolerance (Hossain et al., 2015; Yang et al., 2021). Similarly, SA, GA, and H_2S stimulate the biosynthesis of proline, betaine, and trehalose, contributing to the enhanced antioxidant activity in maize (Li, 2015; Li Z. G. et al., 2015; Zhou et al., 2018). Overexpression of *ZmbZIP4* induces longer primary roots, more lateral roots, and enhanced biosynthesis of ABA, which cumulatively results in enhanced abiotic stress tolerance (Ma et al., 2018).

MOLECULAR MECHANISMS OF PLANT RESPONSES TO HEAT STRESS

Heat Stress Sensing

Plant cells and organelles harbor an efficient heat sensing mechanism that subsequently stimulates a signaling cascade for rapid adaptive modifications (**Figure 3**; Nievola et al., 2017; Niu and Xiang, 2018). For example, calcium ions (Ca^{2+}) flow through their conducting channels, acting as messengers in a signaling cascade to sense and respond to heat stimuli (Jammes et al., 2011). The plasma membrane is also a primary heat-sensing organelle that contains three types of Ca^{2+} conducting channels, including voltage-dependent Ca^{2+}-permeable channels (VDCCs), voltage-independent Ca^{2+}-permeable channels (VICCs), depolarization-activated Ca^{2+}-permeable channels (DACCs), and hyperpolarization-activated Ca^{2+}-permeable channels (HACCs) (Horváth et al., 2012; Liu et al., 2018). These channels are also known as cyclic nucleotide-gated ion channels (CNGCs), naturally tetrameric cationic, and comprise six transmembrane domains (Urquhart et al., 2011). Notably these CNGCs can be genetically modified as homotetrameric or heterotetrameric to improve their ability to respond to diverse and variable intensities (Ketehouli et al., 2019; Tan et al., 2020).

In maize, 11 plasma membrane-localized CNGC genes were identified, contributing a major role in heat tolerance (Hao and Qiao, 2018). The downregulation of *AtCNGC2*, *AtCNGC6*, *PpCNGCb*, and *PpCNGC* resulted in an increased accumulation of the following heat shock proteins; *Hsp18.2*, *Hsp25.3,* and *Hsp70* (Gao et al., 2012; Finka and Goloubinoff, 2014). Glutamate heat receptor-like channels also stimulated the Ca^{2+} signaling cascade on exposure to heat stress, and the exogenous application of glutamate resulted in improved heat tolerance in maize (Li et al., 2019). Other calcium channel families have been identified as responsible for the heat tolerance capability in maize, such as downregulation of synaptotagmin A that caused the downregulation of HSPs (Yan et al., 2017; Bourgine and Guihur, 2021). Under heat stress, maize annexin, such as *AnxZm33* and *AnxZm35* expression stimulated HACCs in the roots and cytosol (Bassani et al., 2004; Nichols, 2005; Mortimer et al., 2008; He et al., 2019). Phosphoinositide-specific phospholipases C (PLCs) genes, such as *PLC3* and *PLC9* are plasma membrane-localized heat sensors that stimulate phosphoinositide-signaling mediated Ca^{2+} channels (Rupwate and Rajasekharan, 2012; Hayes et al., 2021). For example, *ZmPLC1* encodes a PI-PLC, which plays a major role in maize roots during drought stress (Zhai et al., 2013).

Additionally, heat stress alters the normal working of the chloroplasts and mitochondria membranes, resulting in the over-accumulation of ROS simultaneously stimulating the Ca^{2+} signaling pathway (Li B. et al., 2018; Navarro et al., 2021). ROS, including NADPH-oxidase (NOX) and respiratory burst oxidase homolog, also stimulate signaling cascade for heat tolerance (Sagi and Fluhr, 2006; Takemoto et al., 2007; Chapman et al., 2019). However, the over-accumulation of ROS stimulates a Ca^{2+} based signaling cascade in the cytosol, which then stimulates phosphorylation mediated calcium-dependent protein kinases (CDPKs), causing a direct activation of the respiratory burst oxidase homolog D (RBOHD) (Gao et al., 2014; Marcec et al., 2019). RTH5 family proteins comprise four transmembrane functional domains responsible for membrane embedding and two EF motifs, FAD and NAD, required for Ca^{2+}transport (Lin et al., 2009; Nestler et al., 2014). In maize, RTH5 protein encodes NOX, distributed among all eukaryotic species (Bedard et al., 2007).

Heat-Induced Signal Cascades

Heat-sensitive CNGC gene families comprise the cyclic nucleotide-binding domain and calmodulin-binding domain (CaMBD), facing toward cytosol (Gao et al., 2012; Duszyn et al., 2019). Ca^{2+} sensor-dependent transcription regulation depends upon calcineurin b-like protein (CBL), CDPK, and calmodulin (CaM) (Reddy et al., 2004, 2011; Hashimoto and Kudla, 2011). CDPKs can sense Ca^{2+} to assist their EF-hand domain and transduce Ca^{2+} signals *via* their protein kinase domain (Shi et al., 2018). In maize, 35 CDPKs were identified (Ma et al., 2013), and *ZmCDPK1* has been characterized in cold-stressed roots and leaves (Weckwerth et al., 2015). CaMs bind with the C-terminal of CNGC family genes to activate the heat shock signaling pathway (Hao and Qiao, 2018), as mitogen-activated protein kinase 6 and calmodulin-binding protein kinase 3 (CBK3) (Yan et al., 2017). In maize, the Ca^{2+}–CaM contributes to the activation of ABA-induced antioxidants and nitric oxide (NO) production (Hu et al., 2007; Sang et al., 2008).

Many TFs, such as bZIP, CAMTA, MYB, and WRKY, bind with CaM proteins due to various abiotic and biotic stresses effects (**Table 1**; Yang et al., 2013). Among all, the CAMTA-mediated transcriptional regulation network is dominant, contributing against the diverse environmental stresses, including heat stress, salinity, drought, heavy metals, and exogenous application of hormones (Pandey et al., 2013; Yang et al., 2013; Yue et al., 2015). Additionally, CAMTA genes also play a key role in the mutual induction of regulation in expressing different stress-responsive genes and hormones (Reddy et al., 2000; Yang and Poovaiah, 2002). For example, heat stress induces upregulation of multiple *ZmCAMTA* genes in maize plants (Atkinson et al., 2013). In maize, *ZmCAMTA1*, *ZmCAMTA2*, and *ZmCAMTA3* have been identified, and their expression was upregulated during heat stress (Yue et al., 2015).

Heat stress affects plasma membrane, mitochondria, endoplasmic reticulum, and chloroplasts, resulting in ROS over-accumulation, a critical secondary signaling messenger (Sewelam et al., 2014; Czarnocka and Karpińskiski, 2018).

TABLE 1 | Heat stress-related transcription factor (TF) families in maize.

Family	Gene	Function/stress	References
HSF	*ZmHsf-01*	Heat stress response The upregulation of *ZmHsf-01* is probably with H3K9 hyperacetylation in the promoter region after heat treatment	Lin et al., 2011; Kim et al., 2012; Zhang et al., 2020c
	ZmHsf-03	Heat stress response	Lin et al., 2011
	ZmHsf-04	Heat stress response	Lin et al., 2011
	ZmHsf05	Heat stress response	Jiang et al., 2017
	ZmHsf06	Heat stress response	Li H.-C. et al., 2015
	HSFA6b	Heat stress response Connects ABA signaling and ABA-mediated heat responses	Huang et al., 2016; Gao et al., 2019
	HSFA1	Stimulates immediate expression of different heat shock responsive transcription factors (TFs), including *DREB2A*, *HSFA2*, *HSFA7*, HSFBs, and multiprotein-bridging factor 1C (*MBF1C*)	Yan et al., 2020; Zhao J. et al., 2021
	Hsftf13	Responses to ABA And thermotolerance Activate the Hsp90 and other HSFs	Huang et al., 2016; Li Z. et al., 2020
	ZmHsf-11	Heat stress response	Lin et al., 2011
	ZmHsf-17	Heat stress response	Lin et al., 2011
	ZmHsf-23	Heat stress response	Lin et al., 2011
	ZmHsf-25	Heat stress response	Lin et al., 2011
DREB/CBF	*ZmDREB2A*	Salt, heat, drought, and cold	Qin et al., 2007
AP2/EREBP	*Zm00001d008546*	Heat stress response	Jagtap et al., 2020
MYB/MYC	*ZmMYB-R1*	Cold, salinity, drought, ABA, and heat	Liu et al., 2012
bZIP	*ZmbZIP60 (Zm00001d046718)*	Heat stress bzip28 and bzip60 double-mutant plants are sensitive to heat stress Activates the expression of a type-A HSF, Hsftf13, which, in turn, upregulates the expression of a constellation of HSP genes	Liu et al., 2012; Li Z. et al., 2020
	ZmbZIP17	Drought, ABA, heat, and salt	Jia et al., 2009
	ZmbZIP28	Encodes an ER membrane-associated bZIP transcription factor, contributes to the upregulation of heat-responsive genes and to heat tolerance *bZIP28* binds directly to the promoters of heat-responsive genes	Gao et al., 2008; Zhang et al., 2017
	ZmbZIP4	Heat, cold, salinity, and ABA Contributes to stress resistance in maize by regulating ABA synthesis and root development	Ma et al., 2018
NAC	*Zm00001d010227*	Drought and heat stress	Jagtap et al., 2020
GARP	*Zm00001d044785 (ZmGlk1)*	Heat stress The expression of *ZmGLK1* or *ZmG2* in rice leads to elevated levels of Chl, carotenoid, and xanthophyll cycle pigments and to increased levels of some PSII components	Jagtap et al., 2020; Yeh et al., 2021
WRKY	*ZmWRKY44*	Salt, heat, ABA, and H_2O_2 Have transcriptional activation functions	Kimotho et al., 2019
	ZmWRKY106	Drought, high temperature, ABA, and salt Play a role in the abiotic stress response by regulating stress-related genes through the ABA-signaling pathway Reactive oxygen species (ROS) scavenging	Wang et al., 2018a
	ZmWRKY40	Drought, salinity, heat, and ABA Regulating stress-responsive genes, such as *DREB2B* and *RD29A*	Wang et al., 2018b; Leng and Zhao, 2020
HSP	*ZmERD2*	Heat, salinity, cold, PEG, and dehydration	Song et al., 2016
	ZmERD3	mRNA accumulation	Song et al., 2018
NF-Y	*ZmNF-YA3*	Drought and heat *ZmNF-YA3* is directly bound to the promoter regions of two bHLH TFs (*bHLH92* and FMA) and one bZIP TF (*bZIP45*) involved in the ABA-related pathway	Su et al., 2018; Kimotho et al., 2019

TABLE 2 | Key genes related to heat stress mechanisms.

Genes	Gene description	Function	References
Zm00001d044732 ABA	ABA-induced protein	Acts as a signaling hormone in plants against abiotic stress, but its function in energy homeostasis under heat stress	Cheikh and Jones, 1994
Zm00001d045675 (*AS*)	Asparagine synthetase homolog 1	Elevated maximum daily temperature induces alternative splicing and the roles of SR (serine/arginine-rich) 45a	Li and Howell, 2021
Zm00001d047847 (SR45a)	Serine/arginine-rich splicing factor SR45a	Elevated maximum daily temperature induces alternative splicing and the roles of SR (serine/arginine-rich) 45a	Li and Howell, 2021
GRMZM2G388045 GAMETE EXPRESSED 1 (GEX1)	Encode GAMETE EXPRESSED 1 (GEX1)	Protective roles for reproductive stage under HS	Gao et al., 2019
GRMZM2G377194 CYCD5;1	Encode cyclin D5;1	Protective roles for reproductive stage under HS Increased seed set	Gao et al., 2019
GRMZM2G406715	Encodes a bZIP transcription factor		Gao et al., 2019
GRMZM2G062914 (MPK14)	Expresses a maize mitogen-activated protein kinase, MPK14.	Its Arabidopsis ortholog is *AtMPK1* can mediate and augment ABA signaling	Gao et al., 2019
GRMZM2G059225 (ARF)	Discolored-paralog3 putative ARF GTPase-activating domain protein with ankyrin repeat-containing protein	GTPase activator activity	Gao et al., 2019
Zm00001d028408 (*HSP26*)	Heat shock protein 18 (Heat shock protein 26)	Early heat stress marker gene	Nieto-Sotelo et al., 1990; Abou-Deif et al., 2019
Zm00001d006036 (ZmHSP70)	Heat shock 70 kDa protein	Heat stress response Induced by heat in diurnal temperature cycles	Rashed et al., 2021
Zm00001d003554 (ZmHSP22)	22.0 kDa class IV heat shock protein	Heat stress response Induced by heat in diurnal temperature cycles	Rashed et al., 2021
Zm00001d028557 (ZmHSP17.9)	17.9 kDa class I heat shock protein	Heat stress response Induced by heat in diurnal temperature cycles	Rashed et al., 2021
Zm00001d047542 (ZmHSP17.6)	17.6 kDa class II heat shock protein	Heat stress response Induced by heat in diurnal temperature cycles	Rashed et al., 2021
Hsp18.2	Heat shock protein 18.2	Heat stress response	Borghi, 2010
HSP90	Heat shock protein 90	Induced by heat in diurnal temperature cycles	Marrs et al., 1993
Zm00001d038806 (HSP101)	Heat shock protein 101	Induced by heat in diurnal temperature cycles Play essential roles in both induced and basal thermotolerance and primary root growth	Nieto-Sotelo et al., 2002
Zm00001d014090	Mitochondrial heat shock protein 60	Induced by heat in diurnal temperature cycles	Prasad et al., 1990

(Continued)

TABLE 2 | (Continued)

Genes	Gene description	Function	References
GRMZM2G409658	Encodes a Calcineurin b-like protein-interacting protein kinase (CIPK)	Involved in the stress response process Function in signal transduction	Gao et al., 2019
GRMZM2G116452	Encodes Peroxidase superfamily protein	Involved in the stress response process	Gao et al., 2019
GRMZM2G060349	Encodes a DNA mismatch repair protein, MutS2	Upregulated by high temperature Involved in the stress response process	Gao et al., 2019
GRMZM2G023081	Encodes a cysteine-rich domain-containing protein	Involved in the stress response process	Gao et al., 2019
GRMZM2G061515	Auxin-responsive GH3 family protein expresses an indole-3-acetic acid-amido synthetase	Involved in the stress response process Function in signal transduction Involved in maintaining auxin homeostasis *in vivo* through catalyzing excess IAA conjugation to amino acids	Ludwig-Müller, 2011
GRMZM2G377194	Encodes a D-type cyclin, CYCD5;1	Upregulated by high temperature	Gao et al., 2019
GRMZM2G026892	Encodes a cysteine-rich protein (CRP)	Lose its stability under HS, and thus mean that it is unable to protect the process of seed-set	Gao et al., 2019
GRMZM2G176605	Encodes an ankyrin repeat domain-containing protein	Both pollen tube growth and germination are damaged due to the downregulation of an ankyrin repeat-containing protein	Huang et al., 2006
ZmHSP17.0 and Zm00014a_022730 (ZmHSP17.8)	Heat shock protein 17.2 and Heat shock protein, respectively	Form dodecamers at temperatures lower than heat shock (HS) Protect cellular proteins from aggregation during times of heat stress	Klein et al., 2014
chloroplast sHSP26	Small heat shock protein, chloroplastic	Involved in maize heat tolerance	Hu et al., 2015
Zm00014a018076 ZmHSP16.9	Class I heat shock protein 1	Expressed in root, leaf, and stem tissues under 40°C treatment, which HS and exogenous H_2O_2 upregulate	Sun et al., 2012
Zm00001d028325	brs1;brassinosteroid synthesis1	Confers thermotolerance	Dhaubhadel et al., 1999
Zm00001d029149	Zinc finger protein CONSTANS-LIKE 13	Heat response gene	Jagtap et al., 2020
Zm00001d029892	Metalloendoproteinase 1-MMP	Heat response gene	Jagtap et al., 2020
Zm00001d033805	Glutamate decarboxylase 1 (GAD 1)	Heat response gene Ca2+/calmodulin has been shown to bind GAD and stimulate its activity	Sachs et al., 1996; Jagtap et al., 2020
Zm00001d002597	Rho GTPase-activating protein 3	Heat response gene	Jagtap et al., 2020
Zm00001d003643	L-Ascorbate peroxidase S chloroplastic/mitochondrial	Heat response gene	Jagtap et al., 2020

(Continued)

TABLE 2 | (Continued)

Genes	Gene description	Function	References
Zm00001d006036	Heat shock 70 kDa protein 9 mitochondrial	Heat response gene	Jagtap et al., 2020
Zm00001d041701	Acyl carrier protein 2 chloroplastic	Heat response gene	Jagtap et al., 2020
Zm00001d048592	rca2; RUBISCO activase2: encodes the beta form of RUBISCO activase	Heat response gene	Jagtap et al., 2020
Zm00001d051056	*S*-adenosylmethionine decarboxylase proenzyme	Heat response gene	Jagtap et al., 2020
Zm00001d017729	Serine/threonine-protein kinase MHK	Heat response gene	Jagtap et al., 2020
Zm00001d017992	Metalloendoproteinase 1	Heat response gene	Jagtap et al., 2020
Zm00001d037273	Peptide methionine sulfoxide reductase msrB	Heat response gene	Jagtap et al., 2020
Zm00001d037663	NADH-ubiquinone oxidoreductase 10.5 kDa subunit	Heat response gene	Jagtap et al., 2020
Zm00001d039188	Putative leucine-rich repeat receptor-like protein kinase family protein	Heat response gene	Jagtap et al., 2020
Zm00001d011760	DNAJ heat shock N-terminal domain-containing protein	Heat response gene DNAJ proteins are co-chaperones of the Hsp70 machine, which play a critical role by stimulating Hsp70 ATPase activity, thereby stabilizing its interaction with client proteins	Pegoraro et al., 2011; Jagtap et al., 2020
ZmNIP2-3	Aquaporin NOD26-like membrane integral protein	Heat response gene Differentially phosphorylated under heat stress Encode aquaporins involved in silicon transport	Brusamarello-Santos et al., 2012; Jagtap et al., 2020
Zm00001d045220	Late embryogenesis abundant protein group 2	Heat response gene The LEA proteins are a family of hydrophilic proteins presumed to play a protective role during exposure to different abiotic stresses	Amara et al., 2013; Jagtap et al., 2020
Zm00001d046363	*S*-adenosyl-L-methionine-dependent methyltransferases superfamily protein	Heat response gene	Jagtap et al., 2020
Zm00001d002262	Uncharacterized LOC100502514	High grain yield QTL is related to heat stress	Frey et al., 2016
Zm00001d005002	Carbohydrate transporter/sugar porter/transporter	High grain yield QTL is related to heat stress	Frey et al., 2016
Zm00001d004960	Uncharacterized LOC100281571	High grain yield QTL is related to heat stress	Frey et al., 2016
Zm00001d043407	Uncharacterized LOC100282523	High grain yield QTL is related to heat stress	Frey et al., 2016
Zm00001d013918	Thylakoid lumenal 17.4 kDa protein chloroplastic	High grain yield QTL is related to heat stress	Frey et al., 2016
Zm00001d047096	Beta-expansin 1a	High grain yield QTL is related to heat stress	Frey et al., 2016

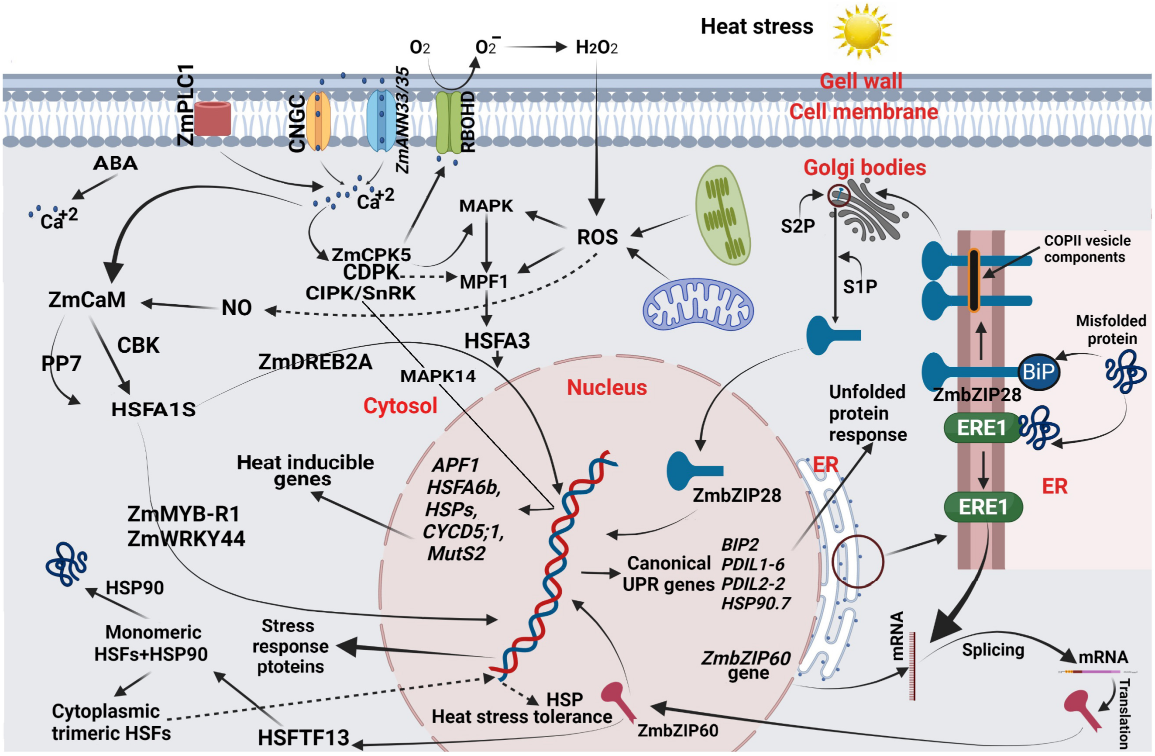


FIGURE 3 | A heat stresses responsive regulatory network in maize. Heat stress damages the cell membrane when exposed to heat stress and promotes the release of apoplastic Ca^{2+}. Heat stress disturbs the plasma membrane's fluidity and permeability, resulting in a loss in function of chloroplasts and mitochondria, higher cytosolic Ca^{2+}, ROS, NO, and over-accumulation of misfolded or unfolded proteins. Increased cytosolic Ca^{2+}, ROS, and NO are secondary messengers and stimulate downstream regulatory networks. Heat stress disrupts protein homeostasis, inducing unfolded-protein response (UPR) and signaling pathways mediated by IRE1-*ZmZIP60* and *ZmZIP28*. The *ZmZIP60* activates the expression of a type-A HSF and *HSFTF13*, which upregulates the expression of HSP genes, i.e., *Hsp90*. The Ca^{2+} signaling is essential in heat tolerance of seed-set in maize under field conditions, where calcium, a critical secondary messenger, converges signals transmitted from high temperature, membrane fluidity, calcium efflux, and ABA (among others), amplifying them through the activation downstream of genes, such as *HSFA6b*, *ABF1*, *CYCD5*;1, *MutS2*, and HSPs during reproductive stage via the MAPK pathway, and eventually enhance maize tolerance to heat stress for seed-set. This figure was made using BioRender.

When maize was exposed to high temperature, the related genes for protein processing in the endoplasmic reticulum (ER) pathway were significantly enriched, which mainly induced heat shock proteins expressions, such as *Hsp40*, *Hsp70*, *Hsp90*, *Hsp100* (**Table 2**), and small HSP (Qian et al., 2019). In response, heat stress response (HSR) genes, such as MYB, AP2/EREBP, NAC, BRs, HSPs, Rubisco, antioxidants (APX and Glutathione *S*-transferase), and kinases are activated to respond to ROS (Khan et al., 2019; Jagtap et al., 2020). ROS, such as H_2O_2 produced by RBOHD, acted as a signaling molecule that directly stimulates mitogen-activated protein kinases, such as MAPK3 and MAPK6, which activate Ca^{2+} or CDPK-mediated phosphorylation *HSFA2* and *HSFA4a* (Luna et al., 2011; Frederickson Matika and Loake, 2014). H_2O_2 also directly activates *HSFA1a*, *HSFA4a*, and *HSFA8* transcription factors, and NO signaling cascade, inducing the binding of heat shock element (HSE) with promoters of HSPs (Miller and Mittler, 2006; Li B. et al., 2018). Phytohormones, such as IAA, CKs, ABA, ET, GA, SA, BRs, and JA, contribute to the signal transduction pathways during heat stress (Eyidogan et al., 2012; Li N. et al., 2021). Several studies indicated calcineurin b-like protein-interacting protein kinase (CIPK) and named sucrose non-fermenting 1-related kinase (SnRK) family members as key players in pollen tube growth seed-set and abiotic stress by perceiving and mediating Ca^{2+} signaling (Yang et al., 2008; Zhou et al., 2015). The Ca^{2+} signaling plays an essential role in the heat tolerance of seed-set in maize under field conditions. In this, calcium, as the critical secondary messenger converges signals transmitted from high temperature, membrane fluidity, calcium efflux, and ABA (among others), amplifies them through activation downstream of genes, such as *HSFA6b*, *ABF1*, *CYCD5;1*, MutS2, and HSPs during reproductive stage via the MAPK pathway (**Figure 3** and **Tables 1**, **2**), and eventually enhancing maize tolerance to heat stress for seed-set (Gao et al., 2019).

Heat Stress-Mediated Transcriptional Regulation

Heat stress stimulates transcription of heat stress factors (HSFs) (**Table 1**) which subsequently results in overexpression of HSPs to mitigate the effect of heat stress (El-Sappah et al., 2012, 2017). However, only HSF or HSP overexpression has no significant role in heat tolerance, indicating that both gene families act synergistically (Wang et al., 2004).

Maize contains 25 HSFs, further divided into A, B, and C subclasses (Lin et al., 2011). Class A HSFs contribute to transcriptional activation, whereas the rest two classes have no specific role in transcriptional activation due to the absence of specific protein motifs (Reddy et al., 2014; Haider et al., 2021). A master transcription activator *HSFA1* stimulates immediate expression of different heat shock responsive transcription factors (TFs), including dehydration responsive element binding protein 2A (*DREB2A*), *HSFA2*, *HSFA7*, HSFBs, and multiprotein-bridging factor 1C (*MBF1C*) (Yan et al., 2020; Zhao J. et al., 2021). Additionally, heat stress stimulates the transactivation of *HSFA1* upon the interaction between *Hsp70* and *Hsp90* (Ohama et al., 2017).

HSFA1 is comprised two alleles; *HSFA1a* and *HSFA1b* (El-Shershaby et al., 2019). *HSFA1* stimulates transcription of ERF/AP2 and *DREB2A* (Mizoi et al., 2012), *HSFA2* acts as a heat-inducible trans-activator of different genes (Chauhan et al., 2013), and *HSFA3* regulates the expression of *DREB2A* and *DREB2C* (Chen et al., 2010). *ZmHsf-6* belongs to class A1, *ZmHsf-1*, *ZmHsf-4*, *ZmHsf-5,* and *ZmHsf-17* belong to subclass A2, *ZmHsf-3*, *ZmHsf-11,* and *ZmHsf-25* belong to class B, all contributing key roles in heat tolerance in maize (**Table 1**; Lin et al., 2011; Zhang et al., 2020b; Jiang et al., 2021). The expression of *ZmHsf-6* was localized in pollens, and its expression was upregulated under heat stress (Jiang et al., 2021). Furthermore, *Hsp70-2* and *Hsp70-4* are downstream targets of *ZmHsf-6* and contribute significantly to abiotic stress response (Li H.-C. et al., 2015). The highest expression of *ZmHsf-1*, *ZmHsf-3,* and *ZmHsf-23* was observed in maize plants exposed to heat stress proving their significant role in maize during heat stress (**Tables 1**, **2**; Lin et al., 2011).

In maize, ZmAP2/ERF is the most prominent TFs family comprised of 292 potential members, out of which 153 belong to the ERF subfamily (Zhou et al., 2012). Also, *ZmDREB2A* plays an essential role in heat tolerance and during drought tolerance in maize plants (Qin et al., 2007) when subjected to heat stress, *DREB2A* regulates transcription of *HSFA3* by stimulating coactivation complex comprised of NUCLEAR FACTOR Y, SUBUNIT A2 (NF-YA2), DNA POLYMERASE II SUBUNIT B3-1 (DPB3-1)/NF-YC10, and NF-YB3 (Schramm et al., 2008). Additionally, heat stress causes the over-accumulation of secondary heat stress-responsive ROS, with *HSFA4a* and *HSFA8* acting as sensors (Cimini et al., 2019; Xu et al., 2021). The maize genome contains 72 MYB TFs, with only 46 playing a key role in abiotic stress response (Du et al., 2012; Chen Y. et al., 2018). Maize plants exposed to abiotic stress factors including heat, salinity, drought, cold, and ABA resulted in overexpression of *ZmMYB-R* (**Table 2**; Liu et al., 2012; Kimotho et al., 2019).

Protein Homeostasis Under Heat Stress

Heat stress interrupts the molecular mechanism of proper protein folding in the ER, which is toxic to ER (Howell, 2013; Fragkostefanakis et al., 2016). Unfolded-protein response (UPR) is an adaptive change in ER that avoids the toxic effect of misfolded proteins (**Figure 3**; Vitale and Boston, 2008); however, prolonged toxicity resulted in programmed cell death (Iurlaro and Muñoz-Pinedo, 2016). UPR also stimulates the signaling cascade to send an ER message to the nucleus to initiate the expression of toxicity-responsive genes (Neill et al., 2019). ER stress activates UPR *via* splicing of *ZmbZIP60* transcripts with the help of kinase (IRE1) and membrane-localized TFs, such as *ZmbZIP17* and a type II membrane protein *ZmbZIP28* (**Figure 3**; Nawkar et al., 2018; Pastor-Cantizano et al., 2020). Both signaling factors bind, producing heterodimers resulting from the upregulation of stress-responsive genes (Gayral et al., 2020). N-terminal domain of *bZIP28* transcription factor face toward cytosol, whereas C-terminal domain face toward the lumen of ER (Liu et al., 2007). From ER, *bZIP28* was first associated with Sar1 GTPase for packaging inside COPII vesicles and then exported to Golgi bodies for modifications by the Golgi site-1 and site-2 proteases (S1P and S2P) (Chung et al., 2018; Pastor-Cantizano et al., 2020). Under heat stress, the N-terminus of bZIP28 is cleaved by S2P, released inside the cytosol, and finally transported to the nucleus. Similarly, IRE1 activates the *bZIP60* transcription factor by splicing and transporting to the nucleus (Reimold et al., 2000; Huang et al., 2017).

The second abiotic stress signaling pathway initiated from ER is comprised of IRE1, a splicing protein, namely kinase/ribonuclease, which activates the *bZIP60* transcription factor *via* proteolysis (Kørner et al., 2015; Pastor-Cantizano et al., 2020). When maize seedlings are exposed to heat stress, the transcript of *ZmbZIP60* is activated by splicing and transferred to the nucleus to induce the expression of HSPs (Li Z. et al., 2018). Another ER-localized *ZmbZIP17* transcription factor is activated under heat and ABA stress and subsequently transported into the nucleus to transactivate HSPs with the help of UPR (Cacas, 2015). HSPs maintain cell metabolites stability under heat stress (Efeoğlu, 2009). Major HSPs which play a key role during heat tolerance in maize are *ZmHSP16.9*, *ZmsHSP17*, *ZmsHSP17.8*, *ZmsHSP26*, *ZmHSP68*, *ZmHSP70*, *ZmHSP90*, and *ZmHSP101* (**Tables 1**, **2**; Sun et al., 2012; Klein et al., 2014; Kumar et al., 2019; Zhao Y. et al., 2021). For example, when maize plants are exposed to heat stress at the reproductive stage, *ZmHSP101* is overexpressed in pollens to prevent their mortality, keep them viable and result in more grains (Gurley, 2000). Generally, transcriptome studies of four heat-tolerant and four heat-susceptible inbred lines, 607 heat-responsive genes, and 39 heat-tolerance genes were identified (Frey et al., 2015).

APPROACHES FOR IMPROVING THERMOTOLERANCE

Agronomic Management

Several agronomic management practices, such as soil and nutrients management, crop rotation, plantation rate, timing, and irrigation, are beneficial in heat tolerance in maize (Sabagh et al., 2020). For example, early sowing of longer season varieties can overcome heat stress in spring maize (Liu et al., 2013). Similarly, nighttime subsurface drip irrigation reduces the root-zone causes in soil temperature, resulting in improved growth and yield in maize (Dong et al., 2016). Additionally, optimized irrigation enhances water use efficiency and aids heat tolerance (Tao and Zhang, 2010). Maize crops exposed to drought and heat stresses during vegetative growth are likely to have shortened reproductive growth stage, resulting in yield loss; however, they can be managed by maintaining soil moisture contents at 65% *via* drip irrigation (Yuan et al., 2004).

Heat stress negatively affects the absorption of adequate concentrations of minerals and nutrients required for normal metabolic and physiological processes (Fahad et al., 2017). For example, nitrogen (N) and magnesium (Mg) are structural parts of chlorophyll, phosphorus (P) is a structural part of nucleic acids (DNA and RNA), and potassium is required for osmotic regulation and activation of enzymes (Waraich et al., 2012; Meena et al., 2020). Additionally, nitrogen plays a key role in utilizing absorbed light, carbon assimilation, and heat tolerance (Meena et al., 2019). Thus, nutrient management can mitigate physiological disorders of maize plants exposed to heat stress, such as applying potassium (K), improving membranes' stability, and maintaining turgor pressure in maize (Tao and Zhang, 2010). Specifically, nutrient management at the grain-filling stage contributes significantly to increased yield. Additionally, applying bioregulators, such as Putrescine and Thiourea, improved heat tolerance in maize seedlings (Yadav et al., 2017).

Exogenous application of plant growth regulators, such as ABA and $CaCl_2$, play a key role in heat tolerance in maize by improving the capability of PSII and stopping the ROS, respectively (Gong et al., 1997; Tao and Zhang, 2010). Artificial application of auxin also improves abiotic stresses, including drought, salinity, waterlogging, heat and cold stress, UV irradiation, and heavy metals tolerance (Vardhini and Anjum, 2015). Similarly, the CK application helps mitigate the denaturation of proteins metabolites due to over-accumulation of ROS and improves the rate of photosynthesis in maize (Zulfiqar and Ashraf, 2021). Additionally, the application of SA and ABA ameliorate the effects of abiotic stress factors, improve seedling growth, mitigate ROS, stimulate the cell-signaling pathway via biosynthesis of NO, resulting in enhanced plant growth and crop yield (Meena et al., 2015). Exogenous application of GA improves the growth and development of plants via mitigating adverse effects of abiotic stresses (Yamaguchi, 2008). The BRs are a newly discovered group of plant hormones with promising potential in abiotic stress tolerance, ROS tolerance, and heat stress tolerance (Arif et al., 2020).

Conventional Breeding

Availability of genetic variations in a population and relationship among traits is base for any successful plant breeding program (Lorenz et al., 2011; Aruah et al., 2012). The exact knowledge of genetic parameters, including population structure, heritability, and genotypic variance among the traits under selection pressure, helps develop efficient breeding lines (Farshadfar et al., 2013). In traditional breeding, selection procedures have been developed to identify and subsequently multiply maize verities with improved heat tolerance (Gong et al., 2015; Gedil and Menkir, 2019). Breeding heat-tolerant varieties is an effective strategy for improving heat tolerance in the spring maize grain-filling stage (Mishra et al., 2021). Many maize cultivars have been screened for canopy structure, flag leaf stomata, and rate of photosynthesis to obtain maximum yield and heat tolerance (Sah et al., 2020). The application of genetic markers accompanied by next-generation sequencing (NGS) has accelerated various development in breeding techniques (Le Nguyen et al., 2019).

Quantitative Trait Locus and Marker-Assisted Breeding

Conventional breeding has significantly improved the selection of heat-tolerant crop varieties (Fu et al., 2012; Bai et al., 2018). During heat stress at the reproductive stage, quantitative trait locus (QTLs) play a major role in pollen production and preservation, receptivity and pollen tube development, proper grain-filling, and post-anthesis leaf senescence (Tiwari and Yadav, 2019). Therefore, the number and origin of QTLs are pivotal to mitigating heat stress (Sharma et al., 2017). Also, the number of QTLs and their roles studied in heat stress-exposed maize seedlings were six during pollen heat tolerance (Tiwari and Yadav, 2019), 11 at two different loci (HSI_{DY} and HSI_{DYA}) during grain-filling located on chromosomes 2, 3, 5, and 9 (Frey et al., 2016) and six during heat susceptibility index (Van Inghelandt et al., 2019). Moreover, 6 and 5 QTLs have been detected associated with pollen tube growth and pollen germination, respectively, using a recombinant inbred population with 45 materials under abiotic stresses, including high temperature (Frova and Sari-Gorla, 1994; Frova et al., 1998). Therefore, these QTLs can be employed in conventional breeding to improve heat tolerance in maize cultivars (Frey et al., 2015). Previously explored maize QTLs can be assessed by exploring the following datasets; http://www.maizegdb.org and http://www.plantstress.com.

Quantitative trait locus are being widely employed in the introgression of favorable alleles in elite maize cultivars *via* backcrossing and confirmation in F1 (Frey et al., 2016; Cerrudo et al., 2018). Molecular markers including simple sequence repeats (SSR), single nucleotide polymorphisms (SNPs), random amplified polymorphic DNA (RAPD), and amplified fragment length polymorphism associated with heat tolerance are also employed in MAS (El-Sappah et al., 2019; Younis et al., 2020). The SNP and SSR are vast in identifying genotypes with maximum heat tolerance (Sabagh et al., 2020). Genome-wide association study (GWAS) is also a valuable tool in identifying novel QTLs responsible for heat tolerance to improve the genetic pool in maize breeding (Wen et al., 2014; Lafarge et al., 2017; Lin et al., 2020). GWAS is also helpful in revealing the linkage between SNPs and specific traits that confers heat tolerance at the flowering stage (Lafarge et al., 2017). GWAS was performed in sub-tropical maize, identifying significant SNPs and haplotype blocks associated with yield contributing traits that help select donor lines with favorable alleles for multiple characteristics, providing insights into heat stress tolerance genetics (Longmei et al., 2021; Seetharam et al., 2021).

Genetic and Metabolic Engineering

Recently, several gene families have been identified and subsequently characterized in maize involved in heat stress response, such as heat shock protein-70 and heat shock factor (Casaretto et al., 2016; Jagtap et al., 2020; Jiang et al., 2021). Additionally, transcriptomic profiling of maize seedlings exposed to heat stress showed several differentially expressed genes employed in developing improved heat-tolerant maize varieties using robust genome editing techniques, such as RNAi and CRISPR/Cas9 (El-Sappah et al., 2021; Razzaq et al., 2021;

Singh et al., 2021). Integration of robust genetic engineering techniques has accelerated conventional breeding of maize by reducing the time of variety development with the application of genetic markers in the early detection of desired traits in F1 (Ahmar et al., 2020). Furthermore, fast growth in NGS has enabled high throughput sequencing of desired traits which is cost-effective, time-saving, reproducible, impossible to achieve *via* conventional breeding (Kulski, 2016).

In maize, several genes have been identified to develop genetically modified (GMO) or transgenic verities with improved heat tolerance (Tiwari and Yadav, 2019; Malenica et al., 2021). For example, overexpression of *ZmVPP1* and *OsMYB55* resulted in increased heat and drought tolerance in maize (Casaretto et al., 2016; Wang et al., 2016). Furthermore, the HSFs gene family plays a pivotal role during heat stress (Haider et al., 2021). Up to 25 HSFs have been reported in several cereal crops, and their key role is confirmed in regulating Hsp genes (Guo et al., 2008). This discovery of identifying and characterizing HSFs and their role in regulating Hsp genes has provided a fundamental basis for the development of GM maize with the highest heat stress tolerance (Ahuja et al., 2010). Furthermore, the overexpression of chloroplast localized 6-phosphogluconate dehydrogenase (6PGDH) PGD3 displayed an over-accumulation of starch in maize endosperm under heat stress improved grain size and weight, whereas, *WPGD1* and *WPGD2* transgenes can increase the number of kernels to mitigate losses in high nighttime temperature conditions (Ribeiro et al., 2020). In the metabolic studies of Joshi et al. (2021), a total of 5,136 genes expression were affected in response to heat stress.

CONCLUSION

Plant growth, development, and productivity are significantly affected by abiotic or biotic stresses because the plants, as sessile organisms, cannot move to favorable environments. Globally, high temperature has become a significant stressor that has accelerated the increase in the air temperature in the recent decades. Maize is a C4 crop species that belongs to the Poaceae family and is moderately sensitive to abiotic stresses, such as temperature. Maize plants are considered to be heat tolerant, but an extended duration of a temperature >35°C is deemed to be unfavorable for the development and growth of crops. In comparison, temperatures above 40°C, mainly during flowering and grain-filling season, will negatively affect the grain productivity of grain in these plants.

Heat stress may alter several physiological processes, namely membrane fluidity, net photosynthesis, respiration rate, hormone levels, osmolytes accumulation, and so on. High temperatures are related to several metabolic events at cellular and sub-cellular levels, leading to the production of ROS and oxidative stress. The anti-oxidative defense system is a prospective mechanism to protect them from ROS damage in plants. Finally, several agronomic management practices, such as the management of soil and nutrients, crop rotation, plantation rate, timing, and irrigation, are beneficial in developing heat tolerance in maize, along with advanced genomic tools. This review summarizes heat stress sensing, the induction of signaling cascade, symptoms, heat stress-related genes, molecular feature of maize response, and approaches to establishing heat-tolerant maize varieties.

FUTURE PERSPECTIVES

Environmental factors affecting maize growth and development include rainfall, light intensity, temperature (heat and cold), relative humidity, heavy metal stress, and wind speed. Drought and heat stress have severe implications for sustainable crop yield. Therefore, it is necessary to develop maize verities having maximum tolerance against drought and heat stress with breeding and genetic engineering. Although substantial efforts had been made to develop heat-tolerant maize verities *via* conventional breeding, it has limitations, such as being laborious, time-consuming, and the possibility of only intra-species gene transfer. However, modern genetic approaches, such as GWAS and genotyping by sequencing, have facilitated inter-species gene transfer to develop maize verities with the highest heat tolerance. Additionally, the complementation of conventional breeding with the development of modern and robust genetic engineering techniques, such as RNAi, CRISPR/Cas9, and TILLING, has accelerated the process of variety development.

AUTHOR CONTRIBUTIONS

AE-S, KE-T, JL, SAR, RRM, and MA: conceptualization. AE-S: writing original draft and collecting the data. AE-S and ASE: draw the figures. AE-S, KY, SHW, MB, QH, ZAD, MMAE, MK, RRM, JL, and KE-T: review, and editing of the manuscript. AE-S, KE-T, and MA: writing final copy. All authors contributed to the article and approved the submitted version.

ACKNOWLEDGMENTS

Many thanks to Prof. Dr. Wang Ling, the President of Yibin University, for her support. At the same time, thanks to Zhou Lei and Jiang Qianwen, the International Office Team, for their continuous help to achieve a suitable environment for research. KE-T would like to thank the library at Murdoch University, Australia, for the valuable online resources and comprehensive databases.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.