Chapter

Maize Adaptability to Heat Stress under Changing Climate

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Abstract

The rapidly increasing human population is an alarming issue and would need more food production under changing climate. Abiotic stresses like heat stress and temperature fluctuation are becoming key issues to be addressed for boosting crop production. Maize growth and productivity are sensitive to temperature fluctuations. Grain yield losses in maize from heat stress are expected to increase owing to higher temperatures during the growing season. This situation demands the development of maize hybrids tolerant to heat and drought stresses without compromising grain yield under stress conditions. The chapter aimed to assess the updates on the influence of high-temperature stress (HTS) on the physio-biochemical processes in plants and to draw an association between yield components and heat stress on maize. Moreover, exogenous applications of protectants, antioxidants, and signaling molecules induce HTS tolerance in maize plants and could help the plants cope with HTS by scavenging reactive oxygen species, upregulation of antioxidant enzymes, and protection of cellular membranes by the accrual of compatible osmolytes. It is expected that a better thought of the physiological basis of HTS tolerance in maize plants will help to develop HTS maize cultivars. Developing HTS-tolerant maize varieties may ensure crops production sustainability along with promoting food and feed security under changing climate.

Keywords: corn, exogenous applications, heat tolerance, grain quality, grain yield, changing climate

1. Introduction

Since the turn of the twentieth century, the air temperature has risen, expected to proceed to rise as a result of climatic variability. These rises in temperatures may trigger high-temperature stress (HTS): serious damage to plants [1, 2]. As a result, food and feed security have become a crucial challenge under current prevailing agro-climatic conditions [3–5]. Climate modeling has indicated that high temperature during the day and night is threatening global agriculture production system [6]. The result is that maize crop yield is reduced globally [7, 8]. Maize is one of the important crops being cultivated globally with a wide range of uses, and it is an important food crop in the world [9–11], it has been primarily aimed for increasing yield, quality, and stability under different environments [12–15]. Maize is an important component of human food, animal feed, and biofuel industries [5]. It ranks top among cereal crops globally and becomes raw material of numerous food and feed industries. Among growth limiting factors, heat stress has a major effect on maize growth and nutrient composition at different developmental stages. Since several abiotic stresses occur simultaneously, such as drought stress and heat stress, the development of improved breeding procedures is essential for increasing the maize productivity and quality [16]. There is a crucial need for further research to develop maize genotypes tolerant to high temperature and drought stress.

Various physiological and biochemical processes govern plant growth and yield. Stomatal conductance, for example, regulates water loss as transpiration as well as an influx of CO_2 for its fixation in the Calvin cycle. Several researchers had suggested that the stomatal conductance is an important indirect heat-tolerant selection criterion in crops [17]. Similarly, osmoprotectants and chaperone proteins got an important part in the adaptive reaction of maize to heat stress and combined stresses. Moreover, leaf senescence-related proteins enhance maize tolerance to combined heat and drought stress [18]. Introgression of these traits in locally acclimated maize hybrids through potential donor hybrids helps in developing maize hybrids tolerant to heat and drought stress. Moreover, identification of donor genotypes possessing favorable traits is important in heat stress breeding programs [19]. Therefore, the present review aimed to evaluate the updates on the effect of heat stress on different plant developmental stages, some physiological and biochemical traits, yield and yield traits of maize. Moreover, this review included updates on various strategies used to improve crop tolerance against heat stress including, conventional breeding strategies, management practices, shotgun approaches, and molecular biology-based strategies. Given the critical analysis of success and limitations for improving maize crop productivity under heat stress, future directions for research are also suggested.

2. Adverse effects of heat stress on growth, development, and yield performance of maize

2.1 Morpho-physiological responses

Temperature above 35^0C for a prolonged period is considered unfavorable for crop growth and development and, particularly 40^0C during flowering and grain filling have severe negative impacts on grain yield [5]. Plants under heat stress exhibited significantly reduced stomatal conductance resulting in a reduced rate of photosynthesis. Excessive heat also causes a reduction in net photosynthesis, leaf area, reduced biomass accumulation and seed weight [20]. However, heat-tolerant maize varieties that produced the highest metabolites are not usually high yielding varieties. The heat-tolerant maize varieties are usually characterized by the reduced plant height, leaves plant^{-1}, and leaf area index ultimately reduced the yield. Therefore, several factors should be put into consideration when selecting for heat tolerance in maize. At the cellular level, HTS triggers the appearance of certain genes and increases the accumulation of certain metabolites that may enhance the heat enduring ability of plants [21]. Generally, remarkable genotypic variations in the stomatal conductance were observed [22, 23]. Stomatal conductance, which is a key trait of the photosynthetic leaf, was significantly influenced by abiotic stresses [24]. Delay canopy senescence due to various light interceptions by green leaf area has been reported to be necessary for high productivity of hybrid maize under normal watering and drought stress [16]. The impinging of high-intensity light to plants can lead to permanent damage to membrane structure [20]. The cell membrane is considered the first physiologically sensitive structure to the high temperature and becomes functionally inactive at heat stress [25]. Membrane function and cell wall stretch have inverse relation [26, 27]. Continuous damage in the biological membrane may downregulate the mobility of water, ions, and soluble organic solid molecules within plant cell membranes; hence carbon of production, transport, and accumulation may be affected by these factors. Membrane stability could be used as an assessment of high-temperature tolerance of plants. It is the most appropriate and convenient test; leakages of electrolytes at a high temperature can be measured by this test [28].

Soil plant analyses development (SPAD) value and grain yield have a significant relationship after anthesis, but no positive association has been noticed during the middle and later grain-filling stages [29, 30]. During HTS, the chlorophyll biosynthesis gene gets downregulated [31]. Experimental observation has suggested that the differences among net photosynthetic ratio after exposure to high temperatures were related to the conversion of the chlorophyll “a” into chlorophyll b ratio; due to low chlorophyll “a” and rapid leaf senescence, the photosynthetic rate is negatively affected [32]. HTS induces several metabolic events at the cellular and subcellular levels. The heat stress influences the production of ROS and oxidative stress as well [33–35]. The antioxidative defense system includes both enzymatic and nonenzymatic antioxidants that are shown to participate in response to the development of oxidative stress influenced by heat stress [21].

Scientists showed that rather extreme heat intensity could cause serious tissue damage as well as mortality may arise in a matter of minutes and could ultimately be due to a massive collapse of cell organization [36]. Damages can occur just after deep-term exposures at moderate to maximum heat stress. Informal and gradual damages caused by high temperatures include chlorophyll and mitochondrial destruction of enzymatic activity, protein catabolism impairment, protein deterioration, and cell turgidity looseness [37]. As can be seen in studies, with either the introduction of heat-shocked proteins, plants and animals react to high-temperature pressure [38, 39]. These are intended to avoid species from the harmful impacts of heat stress as well as other sources of pressure [40]. A simple reaction to high-temperature stress is a reduction in regular cellular metabolism. This drop is especially marked at 45°C. The fall in the natural production of protein also goes hand in hand with increased expression and transcription of a fresh set of molecules identified as heat-shock proteins (HSPs) [41]. Previous studies demonstrated that in *Zea mays,* high-temperature stress reduced the protein production and changes the chemical structure of these proteins [42]. Heat stress at the reproduction phase negatively affects the physiology of plants like flower initiation, source-sink relationship, and falling of pods, which ultimately decreases the number of seeds [43]. High-temperature stress is most crucial for the physiological traits of crop plants. High temperature reduced the number of ears, number of kernels, chlorophyll efficiency, firing of leaf, and blasting of the tassel [44]. Climatic stress like high-temperature stress severely reduces the growth and yield of several crops belongs to Leguminosae (Fabaceae). Heat stress severely reduced the physiological growth development and production of *Vigna radiata*. Heat stress reduced dry matter production and other yield attributes [45].

2.2 Effect on seed germination and seedling development

HTS hampers the plant growth; particularly germination and seedling emergence are more sensitive [46]. Stressful environment severely reduces the germination and early seedling growth in several crop plants [47, 48]. However, seeds of sensitive crops exposed to 24 and 48 h moderate heat stress exhibited a higher germination rate. Such an increase in seed germination rate due to short-term exposure to moderate heat stress was attributed to the altered expression of gibberellin and abscisic acid biosynthesis genes [49]. The seedling stage is generally considered as the most sensitive stage to stress in maize development [50]. However, the detrimental impact of water deficit stress on the initial phase of growth and seedling establishment of maize plants cannot be underestimated [51–53].

The appropriate sowing date is important for seed germination and seedling establishment to physiological maturity. The heat-tolerant maize varieties germinated earlier than the non-drought tolerant maize varieties under the critical level of watering. During germination, HTS is associated with an impaired emergency, and a reduced plant stand and plant density [54]. Biochemical components such as soluble sugar and proline increased with increased stress, while starch content and relative water content reduced with increased water deficit [55]. Fluctuations in mean daily temperature (either it is maximum or minimum) disturb seed germination ability [56]. High-temperature stress is the main cause of the reduction in plant yield due to poor germination. [57, 58] studied the impact of high temperature on various developmental phases, especially at seedling emergence in various crop genotypes. Critical periods of stress in maize include seedling establishment stages, rapid growth period, pollination and grain-filling stage. It is proven that in the maize plant with the implementation of stress, not only the leaf area is reduced, but also its growth rate is affected and the appearance of each leaf is delayed [59].

2.3 Grain-filling stage

HTS at the grain-filling stage in spring maize is the main obstacle [60]. Temperature beyond 40°C, mainly during flowering and grain filling has a severe impact on plant grain productivity [5]. Grain filling is highly sensitive to drought and heat, due to the involvement of the array of diverse enzymes and transporters, located in the leaves and seeds [45]. During HTS, the stability of the thylakoid membrane structure is reduced, resulting in degrading chlorophyll, which reduces light energy absorption, transfer, and photosynthetic carbon assimilation, and ultimately photosynthesis is reduced. Inhibited photosynthesis decreases the supply of photosynthates to the grain, leading to a serious reduction of kernel weight and grain yield [60–62]. Delay in the development of reproductive organs might be the result of the reduced cell division and cell elongation processes due to reduced supply of photosynthates and carbohydrate metabolism during the active vegetative growth stages [63].

2.4 Yield components and grain yield

A projection based on the increased daily maximum temperatures concluded that to increase the maize yields by 12% for the period 2016–2035, improved technologies would be needed [64]. Maize plant can face moderate to high temperature, but temperature above 35°C for a long duration is considered unfavorable for crop growth and development, and temperature beyond 40°C, mainly during flowering and grain filling will have a severe impact on plant grain productivity [5]. Meanwhile, early season temperature increases have induced the maize reproductive period to start earlier, developing the risk of water and heat stress. Declines in time to maturation of maize shown of independence of effects to availability of water, the potential of yield which becoming increasingly limited by warming itself [65]. Irrigation regimes were the major determinant of grain yield during the grain-filling stage in maize while significant differences in the number of kernels per row were obtained among irrigation regimes [66]. A large difference in grain yield is caused due to HTS, which is shown in **Figure 1**. Tissue injuries inversely influence the photosynthetic rate during heat stress, which can cause leaf damaging and increase the rate of leaf senescence that largely results in decreasing photosynthetic efficiency [44]. Reduced chlorophyll content, including grain yields and oxidative damages, possibly had a direct correlation under heat stress [5, 67]. Previous research studies indicate that high temperature has a severe effect on the cob growth rate as well as biomass partitioning [68]. Many factors including duration of pollen viability, increased kernel abortion rate, lower the rate of cell division in storage tissue (endosperm), decrease in starch synthesis, downregulate the sink capacity of developing kernel, increased rate of sugar accumulation, kernel development, and less/higher enzyme activities could be responsible for the reduction in kernel per row under heat stress [44, 67]. Stress environment leads to a severe reduction in yield of crop plants probably by disrupting leaf gas exchange properties, which not only limit the size of the source and sink tissues, but the phloem loading, assimilate translocation, and dry matter partitioning are also impaired [46]. Unsuccessful fertilization reduces the seed size and increases flower abortion rate owing to high temperature and it has negative effects on plant reproductive phase [69, 70]. Temperature range 0–35°C, is considered suitable for leaf growth, the temperature range 35–40°C has an inverse relation with leaf growth. Temperature beyond 35-40°C is responsible for lower net photosynthetic rate, which further leads to protein aggregation, enzyme inactivation, inhibition of protein synthesis leading to the degradation of protein synthesis [69, 71]. Eventually, an increase in temperature

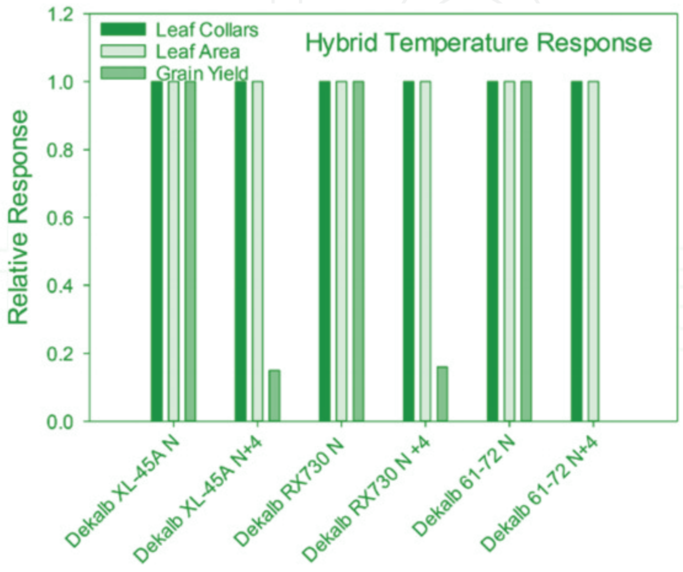

Figure 1.
Differences in total leaf collars, cumulative leaf area, and grain yield of three corn hybrids grown under normal Ames, Iowa temperatures and normal +4°C temperatures.

beyond its critical value leads to generating a heat stress that harms the morphological growth, grain yield, and yield-related attributes of two maize cultivars "Xida 319" and "Xida 889" [72].

2.5 Quality traits of maize

Temperatures higher than 35°C negatively affect maize grain quality. Grain quality, which is governed by factors including the duration and rate of grain filling and the availability of assimilates, is negatively influenced under water deficit conditions. Similar negative effects of stress were reported on the grain weight of wheat [15, 73–75]. Variations in flour quality in a hard-grained crop could be related to changes in protein composition due to heat stress during the grain-filling stage [76]. As per the findings of Mousavi et al. [77], heat stress at the flowering stage greatly reduced the starch content due to the reduction in the photosynthetic activities leading to an increase in the grain protein ratio. Usually, maize quality properties are affected by genotypes, environmental factors, and their interactions (**Figure 2**). Therefore, growth and development of maize are dramatically affected by heat stress leading to reduced grain weight with low starch, crude oil, and protein contents [30]. Grain filling is the most environmentally sensitive phase in maize, which strongly affects grain development quantitatively and qualitatively [7, 15]. Oury and Godin [78] reported a negative correlation between protein contents and grain weight in maize under stress conditions. Association analysis revealed that cob length, thousand-grain weight, and protein contents had a significant relationship with grain yield of maize [79].

In the previous study, the starch content in waxy maize grain was decreased, whereas protein content was increased, resulting in the change of grain quality [80]. However, the activities of enzymes involved in the synthesis of starch and protein are still lacking [81]. The qualitative and quantitative characteristics of grain productivity are mainly influenced by the environmental fluctuation and these changes inversely influence the development and maturing of seed that affect the seed-filling process and deposition of reserves [80]. Generally, high impinging of light affects negatively in plant productivity by causing premature senescence, decreased seed-filling duration, and enhancing remobilization of photosynthates from source to sink [82]. These factors combined, mainly lowers plant biomass and productivity, and finally lowers the assimilate production and mobilization of the reserve to different developing crops [83]. Generally, it is predicted that gene controlling cell division gets downregulated due to water stress, which could be responsible for the decreased cell number in cotyledons along with endosperm. However, further research is required to find out the actual

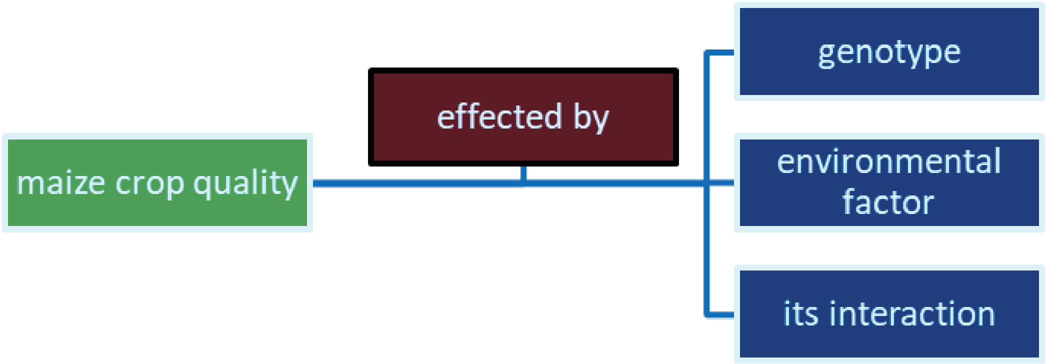

Figure 2.
Quality of maize is influenced by genotype, environment, and their interaction.

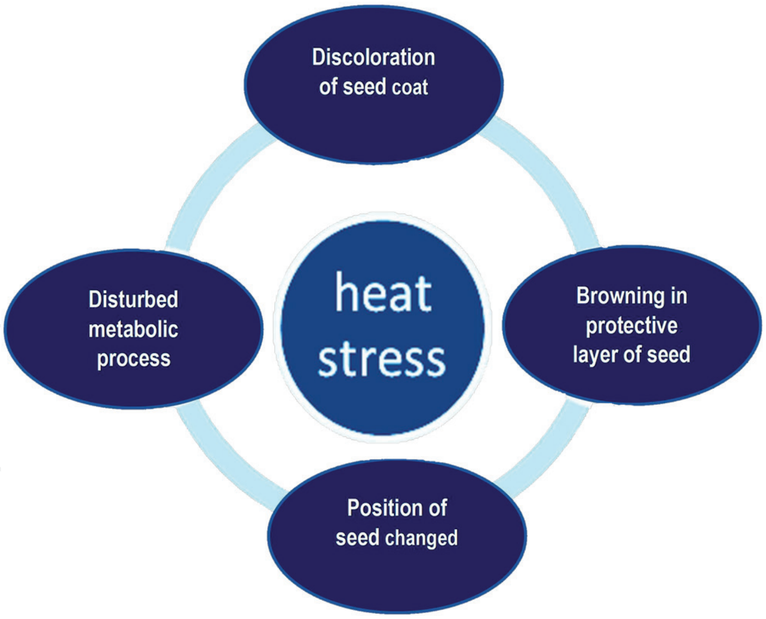

Figure 3.
Quality of maize is deteriorated due to heat stress.

mechanisms controlling these events. Probably due to low enzyme efficiency or high km carbohydrate gene gets downregulated in developing seedling, resulting in limited availability of sucrose, finally producing reduced seed size [45]. The time of seed filling reduced in pea, soybean, and white lupin, resulting in smaller grains [84]. Heat stress during grain filling markedly decreased starch accumulation in wheat [85] and rice [86].

High-temperature stress decreases the protein concentration in the wheat seeds during seed formation stage [76]. Carbon and nitrogen transmission in the seed is improved with the maximum temperature but C transfer is reduced by the daily temperature fluctuations [87]. Temperature variability effects are more visible on the size of seed than seed N contents [87]. Size of seed and protein concentration in the seed are inversely proportional to each other [88]. High-temperature stress reduces seed production, which ultimately declines the seed protein contents [89]. Protein accumulation in the seeds depends upon high-temperature stress [89]. When high-temperature stress occurs at the seed-filling stage it declines the seed protein contents [89]. When wheat crops are exposed to the high-temperature, glutenin protein production is decreased while gliadins protein production remains stable [90]. Seed protein contents of various crops are decreased after imposing the high-temperature stress, but various amino acid concentrations become low [91]. Heat stress damaged the protective layer of seed and food storage tissues of seed, which is why the quality of seed was deteriorated (**Figure 3**).

3. Adaptation and management strategies of maize under heat stress

Enhancement of the antioxidant defense system is an important strategy to scavenge ROS by antioxidant enzymes [92]. Similar to antioxidant defense, phytohormones such as auxin (indole acetic acid, IAA), cytokinins (CKs), abscisic acid (ABA), ethylene (ET), gibberellins (GAs), salicylic acid (SA), brassinosteroids (BRs), and jasmonates (JAs) have key roles in coordinating various signal transduction pathways during the abiotic-stress response [93]. Many studies have shown that altering cultural practices, such as planting rate [94], planting date [95, 96], the phenological variation of crop cultivars [60, 95] soil management [97], nutrient management [60], and irrigation [60] can positively or negatively modify maize yield response to climate change.

3.1 Avoid high-temperature stress by adjusting the sowing date

Advancing or delaying the sowing date may be a potent, farmer-friendly and biologically viable strategy to avoid HTS. Earlier findings reported that earlier sowing dates and longer season varieties have overcome the negative effects of climate warming on spring maize yield [95]. Similarly, other findings reported by [98] showed that by changing sowing date from late April to late May, the mean daily temperature decreased 1.7 and 4.3°C whereas the diurnal temperature increased 4.3 and 3.1°C during grain-filling middle stage (16-45 days after silking) and grain-filling late stage (45 days after silking to maturity), respectively.

3.2 Optimizing irrigation

High air temperatures during the crop growing season can reduce harvestable yields. However, crop varieties with improved heat tolerance traits as well as crop management strategies at the farm scale are thus needed for climate change mitigation. Therefore, to mitigate the negative impact of increased growing season temperatures on crop growth and yield, especially in low latitude regions, heat-tolerant crop varieties, as well as modified farm management practices are needed, especially in the areas when irrigation is needed for crop production and irrigation water depends on the underground aquifers [99]. They also observed that applied irrigation at nighttime through subsurface drip reduced the root-zone soil temperature, which helped plant for improving plant growth and yield of corn. Optimizing irrigation has the potential to improve the water use efficiency of maize leading to enhanced heat tolerance [60]. Soil drought stress and atmospheric high temperature in the vegetative growth period could delay the process of growth of spring maize and shorten the reproductive stage, but those get improved when the soil moisture content in the maize field is maintained 65% field capacity by drip irrigation [100].

3.3 Accumulation of heat-stress defensive phytohormones in plant tissues

Plant growth hormones and exogenous chemicals (e.g., ABA and $CaCl_2$) play important roles in strengthening heat tolerance in maize under HTS [60]. Exogenous ABA induces maize to produce HSPs, strengthening PSII heat tolerance [101]. An exogenous $CaCl_2$ increases the maize cell membrane antioxidant capacity to improve heat tolerance [102]. Phytohormones such as auxin (IAA), cytokinins (CKs), abscisic acid (ABA), ethylene (ET), gibberellins (GAs), salicylic acid (SA), brassinosteroids (BRs), and jasmonates (JAs) have key roles in coordinating various signal transduction pathways during the abiotic-stress response [93].

Auxin or indole-3-acetic acid (Aux/IAA) acts as a chemical messenger to communicate cell activities when crops face different environmental stresses, including salinity, drought, waterlogging, extreme temperatures (heat, chilling, and freezing), heavy metals, light (intense and weak), and radiation (UV-A/B) [92, 103, 104]. Cytokinin (CK) is one of them, which functions solely and or with other hormones to mediate different mechanisms within plants in response to environmental fluctuations. During heat stress, protein denaturation and metabolic imbalance are occurred due to the excessive production of ROS. While to survive against heat stress, plants stimulate heat-shock proteins as a protective measure to prevent protein denaturation [105]. For example, the upregulation of heat-shock proteins in tobacco and bentgrass was recorded due to the enhancement of the antioxidant activity as a result of higher CK in plant cells [106]. Besides this, external application of CK inhibits the damage in photosynthesis under heat stress in maize, rice, and passion fruit [107, 108]. Salicylic acid (SA) is a naturally occurring phenolic compound [109] which plays a crucial part in the regulation of growth and development of the plants, and also a defensive mechanism to survive against abiotic stresses [110]. Similar to SA, abscisic acid (ABA) plays a vital role in plants' physiological adjustments such as against abiotic stresses [111, 112] along with increasing seedling growth, endogenous levels of ABA, and reduced oxidative damage to plants due to heat stress. Similarly, Hasanuzzaman et al. [21] observed that ABA is a signaling molecule and also enhance the number of other signaling molecules such as nitric oxide for thermos-tolerance. Similar to other phytohormones, gibberellic acid (GAs) also interacts with other phytohormones in numerous developmental and stimulus-response processes in plants. GAs have been reported to alleviate the adverse effects of abiotic stress in plants, including rice as reported by Yamaguchi [113]. Brassinosteroids (BRs) is a new group of phytohormones, present in almost every part of the plants [114]. Similar to other phytohormones, BRs have shown tremendous potential against the abiotic stress-induced oxidative stress [103] including high temperature [115].

3.4 Nutrient management

Inadequate and imbalanced nutrients and impaired soil fertility are associated with mineral-nutrient deficiencies and toxicities [116–118]. Adequate nutrition is essential for the integrity of plant structure and key physiological processes. For example, nitrogen (N) and magnesium are a structural part of chlorophyll and these are needed for photosynthesis. Nitrogen plays a very crucial role in temperature stress tolerance. At higher temperatures, the intensity of light is also very high. So, high light intensity, as a function of high temperature, which affects the uptake of mineral nutrients, ultimately influences the plant growth negatively. Since N plays a major role in the utilization of absorbed light energy and photosynthetic carbon metabolism [119, 120]. Whereas phosphorus is needed for energy production and storage; it is a structural part of nucleic acids and potassium is needed for osmotic regulation and activation of enzymes [117, 118]. Maize physiological function decreases under abiotic stress but can be compensated by nutritional management, for example, adequate potassium fertilizer improves cell membrane stability, turgor pressure, water potential in maize under water-deficit conditions [60]. Thus, a strategy to improve heat tolerance in maize at the grain-filling stage is to regulate nutrition.

3.5 Selection of high-temperature stress-resistant varieties

Selection criteria have been proposed in traditional breeding to facilitate the detection of heat-tolerant maize variety. As different varieties respond differently to HTS, breeding heat-tolerant varieties is an effective strategy to improve heat tolerance at the spring maize grain-filling stage [60]. Screening of various cultivars was done to screen the warmness of the plant canopy, stomata behavior of upper most leaf (flag leaf), and photosynthesizing efficiency that are closely related to each other for the production maximum grain production under high-temperature stress conditions [121–123].

3.6 Morpho-physiological mechanisms

Under HT conditions, plants exhibit various mechanisms for surviving, which include long-term evolutionary phenological and morphological adaptations and short-term avoidance or acclimation mechanisms such as changing the leaf orientation, transpirational cooling, or alteration of membrane lipid compositions [92]. Also, high-temperature stress can be avoided by crop management practices such as selecting proper sowing methods, choice of sowing date, cultivars, irrigation methods, etc. It was discussed that combined hotter and drier climate change scenarios cause a greater maize yield reduction than hotter only scenarios. The incorporating drought and heat tolerance into maize germplasm has the potential to offset predicted yield losses and sustain maize productivity under climate change [19].

Tao and Zhao [60] reported that superoxide dismutase (SOD) increased and malonic dialdehyde (MDA) decreased in maize ear leaf for enhancing the stability of cell membrane, which helps to improve photosynthesis for good grain-filling characteristics (long quickly increase period and high mean rate of grain filling). It also produced high kernel weight under HTS [124, 125] leading to reporting of new origins of genetic engineering which exhibited leakage of electrolytes and MSI are the two basic parameters to screen the temperature stress-tolerant cultivars of various crops [126]. Electrical ions were gathered from the affected plants and were washed out with pure water to measure the membrane stability index MSI [127]. Seed production ability and stability index of the membrane were closely related to each other [3]. Mitochondrial tetrazolium is a very useful indicator of HTS sensitivity. Leaves' tissues were dipped in triphenyl tetrazolium chloride chemical mixture during HTS. The spectrographic technique was used to quantify the related rates of triphenyl tetrazolium chloride reduction to formazan and tissues viability [128]. Heat tolerance (HT) of the crop is generally defined as the ability of the plant to grow and produce an economic yield under HS. This is a highly specific trait, and closely related to the species, even different organs and tissues of the same plant, may vary significantly in this respect. Plants have evolved various mechanisms for thriving under higher prevailing temperatures. They include short-term avoidance/ acclimation mechanism or long-term evolutionary adaptations [92]. Many alternative traits related to heat resistance in *Zea mays* have been identified, including leaf kinetics, net photosynthesis rate (Pn), leaf anatomy at seedling stage [129] anther emergence [130], pollen grain viability [131], etc. However, the utility of those traits in stress breeding is not well established to date. Furthermore, most of the research focused on the heat stress on temperate maize, whereas only limited information is available on tropical maize [42].

One of the ways to deal with the adverse effects of heat stress may involve exploring some molecules that have the potential to protect the plants from the harmful effects of HT. In recent decades, exogenous application of protectants such as osmoprotectants, phytohormones, signaling molecules, trace elements, etc., have shown a beneficial effect on plants grown under HTS and these protectants have growth-promoting and antioxidant capacity [21, 92]. Exogenous applications of several phytohormones were found to be effective in mitigating heat stress in plants. Accumulation of osmolytes such as proline (Pro), glycine betaine (GB), and trehalose (Tre) is a well-known adaptive mechanism in plants against abiotic stress conditions including HT [92]. Supplementation with Pro and GB considerably reduced the H_2O_2 production, improved the accumulation of soluble sugars, and protected the developing tissues from heat stress effects. At the field level, managing or manipulating cultural practices, such as the timing and methods for sowing, irrigation management, and selection of cultivars and species, can also considerably decrease the adverse effects of HT stress. In recent decades, exogenous applications of protectants such as osmoprotectants, phytohormones, signaling molecules, trace elements, etc., have shown beneficial effects on plants growing under HT, due to the growth-promoting and antioxidant activities of these compounds [21, 92].

3.7 Molecular markers utilization

The genetic analytical study depends upon the genetic markers. Information about genetic reproduction aids to identify potential gene markers [132]. To mitigate the harmful effects of high-temperature several gene markers like a random polymorphic amplifier, AFLP (amplifier fragmentation length polymorphism), as well as sequenced simple repeats SSR, were used to increase the crop production under heat-stress [133, 134]. During genetic breeding, the SNP marker was used because of its genetic sequence in legumes to identify resistant genotypes against heat stress [135]. QTL chromosome numbers and their origin were very useful to mitigate the effects of heat stress [132]. Different molecular markers are studied in population genomics across the environment in many individuals to find out novel variation patterns and help to find if the genes have functions in significant ecological traits. Genome-wide association study (GWAS) is a powerful tool for understanding the complete set of genetic variants in different crop cultivars to recognize allelic variant linked with any specific [136]. GWASs generally highlight linkage among SNPs single nucleotide polymorphism marker and traits and based on GWAS design, genotyping tools, statistical models for examination, and results in interpretation [137].

3.8 Accumulation of antioxidants and heat-shock proteins

Heat stress disturbed the crop metabolic activities by changing tissue balance. Heat stress directly produced toxic substances in plant tissues call ROS due to which plant suffers from oxidative stress. Moreover, to reduce oxidative damage resulting from heat-induced oxidative stress, plants have developed different adaptive mechanisms, via the biosynthesis of enzymatic and non-enzymatic antioxidants and the sequestering of other materials in crop tissues. Enhancement of antioxidant defense system is an important strategy to scavenge ROS by antioxidant enzymes such as ascorbate peroxidase (APX), ascorbate reductase (AR), catalase (CAT), glutathione reductase (GR), glutathione peroxidase (GPX), and superoxide dismutase (SOD) and with non-enzymatic antioxidants such as ascorbate (AsA), glutathione (GSH), carotenoids, flavanones, and anthocyanins [92]. Furthermore, adaptation to temperature changes, at the molecular level, was accompanied by the degradation of the normal proteins and the synthesis of HSPs involved in the mechanism of defense in plants. Seed germination is the most critical growth stage of the whole plant life cycle because it is the first step to carry out whole-plant growth and development, but heat stress is the main reducing factor of seedling emergence in semiarid areas [138, 139].

4. Conclusion

Heat stress and unprecedented climate changes have become a major challenge for sustainable crop production globally. Plant growth, development, and productivity get compromised due to heat stress. Elucidating maize hybrid for temperature tolerance could be an indispensable step toward a balanced yield. Tolerance and avoidance of stress could be an easy way to boost crop production under a changing climate; for example photosynthetic rate can be improved by targeting candidate traits and candidate genes involved in photosynthesis at a molecular level. It could lead to high assimilates production, more transportation of sugar to grain; finally, it decreases grain-filling rate, improves kernel size, and could be very useful to improve plant productivity. Heat-insensitive maize hybrids can be developed by gene editing *CRISPER-CAS9* system through targeting a gene that is responsible for heat sensitivity. The base of further research should be focused on spring maize crops. Field experiments regarding the sowing date are essential by analyzing the impact of meteorological factors on maize growth and grain yield. Application of osmoprotectants, nanotechnology, and the use of sustainable agriculture agents have become necessary for further research. Further, interdisciplinary studies that include agronomy, animal sciences, and climate modeling are warranted to assess the impact of the feeding of both the HTS-tolerant maize varieties and those grown under heat stress on animal health and production. This review could encourage such interdisciplinary approaches to develop maize hybrids with high nutritional values and are not prone to drastic yield reductions owing to fluctuations in agro-climatic factors (especially temperature) and the outcome may lead to sustainable maize production in the tropics under changing climate.

Conflicts of interest

The authors declare no conflicts of interest.

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