Heat Stress in Maize: Understanding the Physiological and Biochemical Impacts

Abstract

Climate change and global warming ~~are~~ critically impact~~ing~~ agriculture, with rising temperatures significantly threatening crop growth and yields. From 2011 to 2020, the global surface temperature rose by 1.09°C compared to the 1850–1900 baseline, with projections suggesting a further increase, potentially reaching three °C above present levels by 2100. This increase, driven primarily by greenhouse gas emissions, adversely affects crops, including maize (*Zea mays* L.), a critical global food, feed, and industrial crop. Maize is susceptible to heat stress, which leads to significant reduction in yield ~~reductions~~. Research indicates that temperatures above 35°C cause irreversible damage to maize, affecting its nutrient uptake, chlorophyll content, and biomass accumulation. Heat stress during crucial growth stages, particularly the reproductive phase, results in pollen sterility, poor seed set, and grain abortion. Studies have revealed that maize yields decrease by an average of 7.4% for each degree Celsius rise in temperature. Furthermore, heat stress increases oxidative stress and disrupts cellular structures, thereby further impairing plant growth. Future research should prioritise breeding heat-tolerant maize varieties and optimising agronomic practices to mitigate these effects. Advanced genomic tools and biotechnological approaches can accelerate ~~identifying~~ the identification and ~~manipulating~~ manipulation of genes involved in heat tolerance. Additionally, plant growth regulators such as gibberellic acid, abscisic acid, and salicylic acid offer promising avenues for enhancing maize resilience to heat stress by modulating physiological responses and stress adaptation mechanisms. Effective strategies need to be developed by fostering interdisciplinary collaboration and leveraging innovative technologies to ensure sustainable maize production in the face of climate change. Understanding the underlying mechanisms of heat stress responses at molecular, cellular, and whole-plant levels is crucial for developing comprehensive mitigation strategies, thus securing food production for the future.

Keywords: Maize, Heat stress, Global Warming, and Yield loss

Introduction

Climate change and global warming are significantly threatening environmental changes and increased frequency of extreme weather events. The Intergovernmental Panel on Climate Change (IPCC) reports that from 2011 to 2020, the global surface temperature rose by 1.09°C (±0.1°C) compared to the 1850–1900 baseline. The current trend suggests a temperature increase of 0.3°C per decade, potentially reaching three °C above present levels by 2100 [1]. This rise is predominantly driven by human activities, particularly the emissions of greenhouse gases like carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). Agriculture is significantly impacted by rising temperatures, as the growth and development of crops depend on optimal temperature ranges. When temperatures exceed these optimal ranges, crop growth and yield quality decline [2]. A study by the Swiss Re Institute on the economic impacts of climate change estimates that by 2050, climate change could reduce the global economy's total value by 10% [3]. Additionally, several studies have suggested that yields of wheat, rice, maize, and soybean could decrease by 6.0%, 3.2%, 7.4%, and 3.1%, respectively, for every one °C increase in temperature [4,5].

Maize (*Zea mays* L.), often called ‘the queen of cereals,’ is a highly adaptable crop cultivated across diverse climates and utilized for many purposes. As the second most cultivated crop globally, maize includes varieties such as sweet corn, field corn, baby corn, and popcorn. Specific types of field corn encompass quality protein maize, waxy maize, and high-oil maize. Serving as an essential food source for billions, maize also plays a crucial role in feed and industrial applications. According to FAOSTAT [6], global maize production is approximately 1147.7 million metric tonnes from 193.7 million hectares, with an average yield of 5.75 tonnes per hectare. The consumption distribution globally is 61% for feed, 17% for food, and 22% for industrial uses. Notably, maize supports the feed, starch, and bio-fuel industries, accounting for 83% of its production, and contributes to over 3,000 products, making it a significant factor in the global agricultural economy [7]. With increasing demands for animal feed, biofuels, and food, global maize consumption is projected to rise by 23 million tonnes by 2029 [8]. India is a leading maize producer, accounting for about 4% of the global maize area and 2% of the total output [7]. The area under maize cultivation in India expanded from 3.159 million hectares in 1950-51 to 9.892 million hectares in 2020-21, with production increasing from 1,729 tonnes to 33,730 tonnes over the same period, reflecting a nearly 17-fold growth. The average yield improved from 547 kg per hectare in 1950-51 to 3,199 kg per hectare in 2020-21 [9]. Maize exhibits the highest growth rate among cereals in terms of both area and productivity, with a productivity increase of over 50 kg/ha per year since 2010, the highest among food crops. In India, maize is primarily used as poultry feed (47%), followed by livestock feed and food (13% each), industrial purposes (12%), starch production (14%), processed foods (7%), and other purposes including export (6%) [7].

Maize is highly susceptible to the adverse effects of global warming, with yields decreasing by an average of 7.4 ± 4.5% for each degree Celsius increase in global temperature [4]. NASA projections indicate that high greenhouse gas emissions could significantly impact maize production by 2030, potentially reducing yields by 24% and causing severe global repercussions if production drops by 20% [10]. Heat stress is a major challenge for maize, particularly in tropical and subtropical regions, and is exacerbated by climate change. Heat stress affects maize at various developmental stages, particularly during the reproductive phase, leading to issues such as silk desiccation, pollen sterility, poor seed set, and grain abortion. It also reduces photosynthesis, biomass accumulation, and grain filling [11]. Research by Noor et al. [12] on 99 tropical maize inbred lines and 58 hybrids under optimal and heat-stress conditions found that heat stress significantly impacts most traits, with key traits influencing grain yield under heat stress, including the number of cobs per plant, grains per row, chlorophyll content, leaf firing, and tassel blast.

Although maize generally requires relatively high temperatures for optimal growth, temperatures above 35°C cause irreversible damage to various physiological and biochemical processes. This damage includes reduced net photosynthesis, leaf area, poor seedling establishment, decreased biomass accumulation, and test weight [2]. Heat stress also affects nitrogen uptake, nitrate reductase activity, and photosynthetic-nitrogen use efficiency, reducing them by 33.3%, 23.8%, and 44.2%, respectively, compared to control conditions [13]. During the reproductive stage, heat stress leads to reduced pollen viability and shedding, impaired fertilisation and seed set, decreased grain filling and yield, altered gene expression and metabolism, increased oxidative stress and cell damage, and reduced thermotolerance [14]. Noor et al. [12] measured grain yield and 15 other traits in 99 tropical maize inbred lines and 58 hybrids under optimal and heat-stress conditions. The results showed that heat stress significantly impacted most of the traits, including grain yield, ears per plant, kernels per row, chlorophyll content, leaf firing, and tassel blast. Numerous studies have examined the mechanisms of heat stress responses at various levels, ranging from molecular to whole-plant. Hence, this review aims to discuss the impacts of heat stress on various physiological and biochemical aspects of maize.

The impact of heat stress on vegetative growth

Heat stress during seedling establishment poses a severe threat to crops. A three-year study demonstrated that higher temperatures accelerate development rates, resulting in shorter vegetative and reproductive phases and significantly reduced leaf number and area under high-temperature stress [15]. Heat stress treatments in maize hybrids B73 and Mo17 increased ear leaf temperatures by 5.8°C and 5.5°C, respectively, compared to control conditions [16]. Warmer temperatures shortened the vegetative and reproductive phases of maize, with a complete cycle reduced to 30 days [17]. Stomatal conductance and transpiration rates significantly increased during heating, particularly around the silking period, with the most substantial increases occurring from 5 days before to 5 days after silking and from 15 days before silking [18]. High-temperature stress reduced the dry weight of maize hybrids ZD958 and XY335 by 74.10% and 62.80%, respectively, after 12 days of exposure [2]. Year-long experiments showed that heat stress at the V12 stage of maize reduced dry matter by 9.3% and 6.2% in consecutive years, with hybrid XY335 suffering more, losing 14.2% and 15.5% of its dry matter [19]. Maize leaf growth is optimal between 10 and 35°C but slows down above 35°C [20]. Temperatures between 33 and 36°C before and after flowering decreased crop growth rates by 17–29% [21].

Tropical maize experiences significant yield reductions due to heat stress, which causes leaf damage, tassel failure, infertility, and early aging [22]. Heat stress, up to 36°C, significantly reduced radiation use efficiency and nitrogen and carbon metabolism, leading to lower dry matter accumulation [23, 24, 25]. High mean daily temperatures negatively impact coleoptile and seedling growth, with maize growth slowing at 40°C and halting at 45°C [26,4]. High temperatures also shortened the maturity time and days to heading in maize crops, with a study in China showing a decrease in growing duration by 3.2, 6.0, and 3.5 days per decade from 1981 to 2009 [27]. Exposure to 40°C resulted in significant reductions in maize biomass, chlorophyll a and b, carotenoid content, and relative water content (RWC) [28]. High temperatures adversely affected cell size and water status, impairing growth [29]. Extreme heat stress had detrimental effects on maize growth and development, reducing seed vigour and sometimes causing a complete loss of seed viability [30]. It also impaired shoot and root growth at temperatures above 40°C [31], inhibited biomass accumulation in late vegetative stages, affected floret numbers, and disrupted chlorophyll biosynthesis and thylakoid stability [23,32,33,34].

The impact of heat stress on the cellular apparatuses

Maize hybrids showed increased levels of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), with the higher MDA content indicating more severe membrane damage [34]. Shao et al. [2] reported that high temperatures significantly affect MDA levels, as well as the activities of catalase, peroxidase, and superoxide dismutase, particularly at the tasselling stage, with notable changes observed in the ears. Maize plants exposed to high temperatures of 35°C and 42°C showed elevated H_2O_2 content, with a two-hour exposure at 42°C resulting in 1.5 times more H_2O_2 production compared to control plants at 25°C [35]. Heat stress disrupted chloroplast and mitochondrial structures at the 12th leaf stage, leading to increased MDA and reactive oxygen species (ROS) content [19]. Additionally, heat stress significantly inhibited the synthesis of cell wall components, such as hemicellulose and cellulose fractions, during the late vegetative stage [36]. Key enzymes involved in carbon metabolism, including ADP-glucose pyrophosphorylase, starch synthase, and branching enzyme, were also significantly inhibited under heat stress conditions. The accumulation of ROS in the leaves under heat stress accelerated the breakdown of thylakoid components, hastening leaf senescence [37]. Furthermore, heat stress impaired normal cellular metabolism, as evidenced by increased soluble sugar and protein contents in rice [38].

The impact of heat stress on photosynthetic parameters

Maize subjected to heat stress exhibited significantly reduced stomatal conductance by 67.4% and increased leaf temperature by 5.6°C, with genotypes transpiring 19% more under heat stress compared to control conditions. These findings suggest that heat stress may induce stomatal opening as a mechanism for leaf cooling through transpiration [16]. Photosynthesis slowed when leaf temperature exceeded 37.5°C, notably if the temperature rose rapidly. At 45°C, photosynthesis nearly ceased under rapid heat stress treatment but only halved under gradual heat stress, with Fv/Fm dropping below 80% [39].

Maize hybrids experienced a decline in photosynthetic rate following heat stress at the V12 stage, with XY335 showing a more substantial decrease (20%) than ZD958. Heat stress also reduced stomatal conductance by 30% in both hybrids, impacting their transpiration cooling capacity [19]. Photosynthetic traits, such as the quantum yield of photosystem (PS) PSII and PSI, electron transport, and fractions of open reaction centres, decreased under high temperature-induced stress in maize [40]. Heat stress impaired PSII activity in maize, damaging the oxygen-evolving complex at the PSII donor side and hindering electron transfer from QA to QB at the PSII acceptor side. This resulted in PSII inhibition and degradation of the QB-binding (D1) protein, disrupting electron transfer from QA to QB [19]. The CO_2 exchange rate in maize dropped by 17% when temperatures ranged between 33°C and 36°C before and after flowering [41]. Exposure to 45°C led to a severe decline in photosynthesis, malate-inhibited PEPC activity, and complete inactivation of Rubisco in maize [39]. Additionally, the photosynthetic rate decreased when temperatures exceeded 38°C, with sudden temperature rises having a more significant negative impact than gradual ones [42]. Maize plants exposed to heat stress at 35ºC and 42ºC for two hours exhibited a slight reduction in maximum quantum efficiency of photosystem II (Fv/Fm) values, indicating decreased photosynthetic efficiency under high-temperature stress conditions [35, 19]

The impact of heat stress on reproductive growth

Heat stress exerts significant effects on the formation of male and female reproductive organs in plants [43, 44]. In maize, heat stress restricts the growth and emergence of the tassel and panicle, the male and female flower clusters, respectively [45, 46]. For example, panicle growth is inhibited at temperatures as high as 44°C, and ear shoot development is severely impaired [47,36]. The reduced development of reproductive organs is linked to lower sink activity, impacting the ability of plant organs to store sugars [48]. Heat stress prolongs the anthesis-silking interval, with maximum temperatures of up to 42.9°C in the field and 52.5°C in the greenhouse delaying the interval by 10 to 20 days compared to normal conditions [17]. Pollen shedding per plant significantly decreases under heat stress conditions, with reductions observed in various periods before and after silking [49]. Heat stress also diminishes pollen germination rates and pollen tube length in maize varieties, leading to delayed pollen shedding dates [2]. Moreover, heat stress during maize flowering reduces the number and quality of florets, silks, and grains 50]. A rise in temperature causes noticeable changes in the structure of maize pollen grains, affecting their viability and function [51,52]. Additionally, heat stress reduces vegetative biomass accumulation, impacting cob growth and silk emergence [53].

High temperatures above 35°C inhibit the development of maize ovaries and grains, ultimately affecting final yield. Heat stress also shortens the time for tassel emergence and pollen release, increasing the gap between anthesis and silking, resulting in less and weaker pollen [17]. A longer anthesis-silking interval leads to lower yields due to reduced pollination efficiency [18]. Furthermore, heat stress accelerates leaf senescence, shortens the life cycle, and affects grain filling [54]. Lower sink capacity due to heat stress contributes to early leaf senescence and shortened grain-filling duration, further reducing yield [55,56]. Maize reproductive stages advance with increasing temperature, with higher temperatures significantly impacting the anthesis-silking interval, pollen shedding duration, pollen viability, and pollen shape [49].

The impact of heat stress on yield and yield components

Heat stress significantly reduces maize yield, with a 78.9% decrease compared to control plants, accompanied by a 10% reduction in single kernel weight [16]. The duration and timing of heat stress exposure during crucial growth stages profoundly impact yield. For instance, a 15-day heat stress period around silking resulted in an average yield reduction of approximately 25.9%, whereas a 5-day period caused an average reduction of 16.1%. Post-silking periods were more sensitive, with an average yield reduction of 22.1% compared to pre-silking periods [49]. High temperatures during crucial growth stages significantly affect yield components in maize. [2] reported substantial reductions in grain yield (39.19%), 100-seed weight (25-35%), kernel number (30-35%), and cob length and diameter (15-20%) due to high temperatures from the 9th leaf stage to the end of tasselling. Temperatures exceeding 35°C during pollination and grain filling suppress maize fertilization and yield, resulting in substantial daily yield losses [57,58]. Maize grain yield and grain number are significantly reduced when temperatures range between 33°C and 36°C during pre-flowering and post-flowering stages [41]. Similarly, high temperatures during the grain-filling stage led to decreased yields, with potential losses of up to 31% when daytime temperatures exceed 35°C [54]. The reproductive stage of maize is susceptible to high temperatures, with yield decreasing by 1 to 1.7% for every degree Celsius above 30°C [59]. Extended heat stress periods during critical growth stages exacerbate yield losses in maize. For instance, a six °C increase in temperature above normal canopy temperature for three days at the silking stage can cause a 13% yield loss, while exposure to temperatures of 30 to 38°C for 15 days during the tasselling stage can result in a 14 to 17% yield loss [50,60]. High temperatures adversely affect maize productivity, leading to significant reductions in cob biomass, grain biomass, grain number, and stover dry matter [61]. The yield penalty induced by heat stress varies depending on the growth stage and environmental conditions. In greenhouse experiments, yield penalties range from 10 to 26% at the grain-filling stage. In contrast, in field experiments, they can reach up to 15 to 46%, with more significant penalties observed during flowering and lag phases [62,63].

Figure 1: Leaf Rolling in Maize as a Protective Response to High Temperatures

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Figure 2: Improper Grain Filling in Maize Under High-Temperature Conditions

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Conclusion and Future Prospectus

In conclusion, the extensive research underscores the profound impact of high-temperature stress on maize growth and development, affecting physiological, biochemical, and molecular processes. From reduced photosynthesis and leaf area to impaired reproductive success and decreased yield, heat stress exerts a multifaceted and detrimental influence on maize, particularly at temperatures above 35°C. The studies reviewed highlight significant reductions in nitrogen uptake, chlorophyll content, and overall biomass, alongside increased oxidative stress and membrane damage. These findings emphasise the urgency of developing effective mitigation strategies to combat heat stress and ensure sustainable maize production.

Future research should prioritise breeding heat-tolerant maize varieties and optimizing agronomic practices to enhance resilience against high temperatures. Integrating advanced genomic tools and biotechnological approaches can accelerate the identification and manipulation of critical genes and pathways involved in heat tolerance. Additionally, field-level applications of plant growth regulators such as gibberellic acid, abscisic acid, salicylic acid, jasmonic acid, cytokinin, silicon, sodium, and selenium offer promising avenues for improving maize acclimation and stress adaptation by positively influencing physiological responses and stress adaptation mechanisms.

These substances can modulate the expression of stress-responsive genes, antioxidants, and heat shock proteins, further enhancing plant performance under heat-stress conditions. The regulation of phytohormones, signalling molecules, transcription factors, non-coding RNAs, metabolites, and molecular chaperones plays a crucial role in coordinating plants' heat response pathways and networks. By fostering interdisciplinary collaboration and leveraging innovative technologies, we can develop robust solutions to mitigate the adverse effects of heat stress on maize, thereby securing food production in the face of climate change.

Efforts should also focus on understanding the underlying mechanisms of heat stress responses at various levels, from molecular to whole-plant, to develop comprehensive mitigation strategies. This includes manipulating genes encoding heat shock proteins, heat shock transcription factors, enzymes involved in phytohormone biosynthesis or signalling, antioxidant enzymes, and osmoprotectants to enhance plant performance under heat stress conditions. By fostering interdisciplinary collaboration and innovative technologies, we can develop robust solutions to mitigate the adverse effects of heat stress on maize, thereby securing food production in the face of climate change.

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