Review Article

Heat Stress and Tolerance Mechanisms in (*Triticum aestivum* L.): A Comprehensive Review

Comment [Ma1]: SUGGESTED TITLE: **Understanding Heat Stress and Tolerance Mechanisms in Wheat (Triticumaestivum L.): A Comprehensive Review**

ABSTRACT

Wheat (*Triticum aestivum* L.), a key cereal crop within the Poaceae family, significantly contributes to global agriculture, accounting for about 30% of the world's grain production and half of the grain traded internationally. It serves as a staple food in over 40 countries, providing essential calories to 85% of the global population and protein to 82%. As the global population is projected to reach 9.1 billion by 2050, the Food and Agriculture Organization (FAO) anticipates a need for nearly one billion additional tons of cereal production annually to meet increasing demand. Enhancing crop productivity and production is therefore crucial.Wheat cultivation spans tropical and subtropical regions, where it faces numerous abiotic stresses that severely impact yield, with heat and drought being the primary challenges. Global climate models predict a potential 6°C increase in mean ambient temperature by the end of the century. Wheat exhibits high sensitivity to heat stress; even a 1°C rise in temperature can result in a 6% reduction in global wheat production. Heat stress significantly impacts wheat's physiological, biological, and biochemical processes, including seed germination, grain filling duration, grain number, Rubisco enzyme activity, photosynthetic capacity, assimilate translocation rate, leaf senescence, chlorophyll content, and overall yield.To combat heat stress, wheat has developed diverse tolerance mechanisms, such as the induction of heat shock proteins (HSPs) for proper protein folding and the activation of an antioxidative defense system to detoxify reactive oxygen species (ROS). Traits like Stay Green (SG), chlorophyll fluorescence, and canopy temperature are closely linked to heat tolerance. This review provides a comprehensive analysis of the effects of heat stress on wheat morphology, physiology, and biochemistry, and discusses the mechanisms of heat tolerance. Understanding and improving these mechanisms are imperative to sustain and enhance wheat production to meet future food demands amidst global climate changes.

Comment [Ma2]: Add the impact of heat stress on the plants in general and on wheat

Keywords: *drought, heat stress, HSPs, antioxidative, ROS, productivity and production*

1. INTRODUCTION

Wheat (*Triticum* spp.), a significant cereal crop of the Poaceae family, plays a pivotal role in global agriculture, accounting for approximately 30% of the world's grain production and half of the grain traded internationally [1]. It serves as a staple food in over 40 countries, providing essential calories for 85% of the world's population and protein for 82% [2,3]. With the projected global population reaching 9.1 billion by 2050, the Food and Agriculture Organization (FAO) anticipates a need for nearly one billion more tons of cereal production annually to meet the increasing demand [4]. Consequently, enhancing crop productivity and production is crucial in the 21st century.Wheat cultivation spans tropical and subtropical regions, where it faces various abiotic stresses that severely impact yield [5]. These stresses include heat, drought, salinity, cold, chemical exposure, and excessive water [6]. Among these, heat and drought are the primary challenges affecting wheat production globally [7]. Predictions from global climate models indicate a potential 6°C increase in mean ambient temperature by the century's end [8]. Addressing these challenges is imperative to sustain and enhance wheat production to meet future food demands.

Wheat exhibits a high level of sensitivity to heat stress, with studies suggesting that a mere 1°C rise in temperature can result in a 6% reduction in global wheat production [9]. An increase of 1°C above the average temperature during the reproductive stage can lead to significant losses in grain yield [10,11]. Elevated temperatures significantly impact various physiological, biological, and biochemical processes in wheat [12]. Heat stress adversely affects seed germination, grain filling duration, grain number, Rubisco enzyme activity, photosynthetic capacity, assimilate translocation rate, leaf senescence, chlorophyll content, and ultimately, overall yield [13-21]. Moreover, heat stress influences the starch and protein content in grains by inducing the production of reactive oxygen species (ROS), which in turn affect membrane stability, lipid peroxidation, protein oxidation, and nucleic acid damage [22,23]. Wheat has developed diverse tolerance mechanisms to mitigate the harm caused by heat stress, including the induction of heat shock proteins (HSPs) to ensure proper protein folding, refolding, synthesis, and degradation of protein aggregates [2,24,25]. The antioxidative defense system detoxifies accumulated ROS through enzymatic and non-enzymatic antioxidants [26]. Traits such as Stay Green (SG), chlorophyll fluorescence, and canopy temperature are closely linked to heat tolerance in wheat [20].

2. EFFECT OF HEAT STRESS ON WHEAT

High temperature stress impacts the various growth and development phases of wheat, resulting in significant yield reduction. The influence of high temperature stress on plants is determined by both the duration of heat exposure and the growth stage at which the stress occurs [27,28]. Heat stress leads to negative outcomes such as poor germination, decreased leaf area, premature leaf aging, and damage to the photosynthetic apparatus, all of which contribute to a decline in wheat photosynthesis [12,29,30]. The effects of heat stress on wheat manifest as changes in morphology, physiology, and biochemistry.

2.1 Effect on Wheat Morphology

In a variety of crops, such as wheat, high temperature stress has a negative impact on seed germination and plant establishment [13]. Specifically, temperatures as high as 45°C can harm embryonic cells, leading to improper germination and emergence, ultimately affecting crop stand [31]. Furthermore, high temperatures can also reduce the survivability of productive tillers, resulting in a decrease in yield. For wheat, high temperature stress can cause a significant reduction in grain yield (53.57%) and tiller number (15.38%) [21]. Additionally, heat stress hinders root growth, which in turn affects overall crop production [32]. The detrimental effects of high temperature stress are most pronounced during the reproductive phase [33]. Even a slight increase in average temperature during the reproductive stage, such as 1°C, can lead to considerable losses in grain yield [10,11]. The ideal temperature range for flowering and grain filling in crops like wheat is between 12°C and 22°C [2]. Heat stress during early stages of gametogenesis, such as meiosis, can be particularly damaging [34]. It negatively impacts the development of microspores and pollen cells during floral initiation [35]. The phenomenon of grain development is highly sensitive to high temperature stress, which affects the grain filling rate and duration [36,37]. Wheat's lifecycle is shortened under high temperature stress compared to normal temperature conditions [38]. A rise of 1°C to 2°C in temperature can decrease seed weight due to a reduction in grain filling duration [39]. Brief episodes of heat stress during grain filling can lead to significant losses in grain yield, up to 23% [40]. High temperature stress also adversely affects the number and quality of grains. In high temperature stress conditions, there is a decrease in grain number, resulting in a reduced harvest index [15]. The decrease in assimilate production and remobilization due to heat stress leads to poorer grain quality [41]. Wheat productivity suffers greatly from the harmful effects of high temperatures during the growth process [42]. Exposing wheat to ambient temperatures above 35°C for a short period can lead to substantial losses in grain yield [43].

2.2 Effect on Wheat Physiology

Photosynthesis is a crucial physiological process in plants, greatly impacted by high temperatures. In wheat, the stroma and thylakoid lamellae are particularly sensitive to heat stress [30]. Elevated temperatures around 40°C can lead to permanent changes in RuBisCO, Rubisco Activase, and Photosystem II [44]. Exposure of wheat to high temperatures deactivates the RuBisCO enzyme in less than a week [16]. Breakdown of Rubiscoactivase under heat stress reduces photosynthetic capacity [17]. High temperatures alter the fluidity of the thylakoid membrane and cause the separation of light harvesting complex II from photosystem II [45]. The resulting photosynthetic products must be transported to different parts of the plant for growth. Under heat stress, the rate of assimilate translocation is reduced due to decreased membrane stability [18]. Mobilizing water-soluble carbohydrates to reproductive sinks supports grain development [46]. Limitations in sources or sinks can reduce seed set and filling [47]. In cases of source limitation from heat stress, plants must find alternative ways to transport photosynthetic products to the grain [1]. Carbohydrate remobilization from stem to developing grain increases during pre-anthesis heat stress, aiding in grain starch content during post-anthesis heat stress [48]. High oxygen concentrations promote photorespiration, with changes in gas solubility under heat stress leading to increased photorespiration in wheat flag leaves [49]. Plant senescence is the natural aging process characterized by vacuolar collapse, membrane loss, and cellular homeostasis disruption [50]. Moderate prolonged heat stress leads to gradual senescence, while intense short-term heat stress causes protein denaturation and aggregation, ultimately resulting in plant death [24]. Heat stress during maturity accelerates leaf senescence, with high temperatures above 34°C reducing chlorophyll biosynthesis [19,20]. High temperatures affect plant water content and relation, leading to cell dehydration due to osmotic potential reduction [51]. Canopy temperature influences leaf water content, stomatal conductance, and transpiration rate [2]. Chlorophyll fluorescence is closely linked to yield and can help measure photosynthetic efficiency. Traits like chlorophyll fluorescence and canopy temperature can aid in selecting heat-tolerant genotypes [20]. During drought and high temperatures, canopy temperature is associated with deeper roots [52]. Research by Dhyani et al. on wheat genotypes revealed decreased chlorophyll content and leaf area index in heat-sensitive genotypes under late sown conditions, while proline content increased in heat-tolerant genotypes [53]. Under heat stress conditions, plants generate a significant amount of Reactive Oxygen Species (ROS). These ROS disrupt cellular processes through their detrimental effects on lipids, proteins, and DNA. The oxidative harm induced by heat stress leads to a 54% reduction in membrane stability [54]. Accumulation of ROS under heat stress triggers protein denaturation and the production of unsaturated fatty acids, ultimately resulting in increased permeability of the cell membrane [55].

2.3 Effect on Wheat Biochemistry

Starch, a major component of wheat composed of amylose and amylopectin, plays a crucial role in determining starch quality through its amylose content. Variations in amylose content can influence the characteristics of starch. High temperatures have been linked to an increase in amylose content and the amylose:amylopectin ratio[56]. ADP-Glucose Pyrophosphorylase (AGPase) and starch synthase are important enzymes involved in starch biosynthesis, with Soluble Starch Synthase and Granule-bound starch synthase being two forms of starch synthase[2]. Elevated temperatures have been found to reduce starch content in grain by up to one-third of total endosperm starch due to decreased efficiency of starch biosynthesis enzymes[57]. The activity of soluble starch synthase decreases at high temperatures around 40°C, leading to smaller grain size and reduced starch deposition[58]. Nonetheless, Sharma et al. noted that starch deposition remains unaffected by reduced Soluble Starch Synthase activity up to 30°C, although it does impact starch composition. They also mentioned that high temperatures do not significantly affect the activity of granule-bound starch synthase in wheat[59]. Asthir and Bhatia observed a significant decrease in starch biosynthesis in wheat grain under high temperatures, accompanied by an increase in total soluble sugar and protein[60]. The quality of wheat grain is heavily reliant on protein content and composition. Lizana and Calderini found no significant impact on protein concentration under high temperatures[41]. Conversely, Iqbal et al. reported an increase in grain protein content, essential amino acids fractions, leaf nitrogen content, and sedimentation index under high temperature conditions[4].

3. HEAT TOLERANCE MECHANISM IN WHEAT

Plants exhibit various adaptation strategies to thrive in high temperature conditions. Avoidance, Escape, and Tolerance represent the primary mechanisms enabling plants to endure and flourish in such environments. Heat tolerance, specifically, refers to a plant's ability to not only survive but also grow and yield economically under high temperature stress. Key mechanisms promoting heat tolerance in wheat include the activation of antioxidant defenses, the production of Heat Shock Proteins (HSPs), and the retention of green foliage.

3. 1 Heat shock proteins

Protein function relies heavily on its synthesis and folding processes. Misfolding of proteins significantly impacts cellular operations. High temperature (HS) conditions can disrupt protein folding and synthesis [2]. And its leading to the production of stress-inducing agents within the cell. These agents promptly interfere with key metabolic processes, DNA functions such as replication and transcription, as well as mRNA transport and translation until the cell recovers[61]. To counteract this, plants accelerate the production of Heat Shock Proteins (HSPs) as a protective measure[62]. HSPs are categorized into different families based on their size, amino acid sequences, and roles[63]. These families encompass HSP100, HSP90, HSP70, HSP60, and small HSPs. Each family of HSPs serves distinct functions under HS conditions. Heat Stress transcription factors (Hsfs) are initially inactive in the cytoplasm and act as regulatory proteins in the transcription of genes encoding HSPs. In response to HS, these Hsfs become transcriptional activators[64]. Various mechanisms are involved in the expression of genes encoding HSPs, including temperature sensing, signal transduction to Hsfs, and the binding of Hsfs to heat shock elements (HSE) in DNA to initiate gene expression[65]. During HS, HSPs act as molecular chaperones to prevent protein denaturation and aggregation [24,66].

3.2 Reactive oxygen species and antioxidative defense mechanism

High salinity (HS) impacts the plant through the generation of unfavorable reactive oxygen species (ROS) such as singlet oxygen ($^1O_2$), superoxide (O_2 •–), and hydroxyl radical (•OH) [67,68]. In a typical cell, there is a balance between the creation and elimination of ROS, referred to as redox homeostasis [69]. When the production of ROS surpasses the cell's capability to eliminate them, the cell undergoes stress, known as oxidative stress [70]. Additionally, oxidative stress may arise from a reduction in the cell's ability to scavenge free radicals[71]. The increased production of reactive oxygen species (ROS) induced by heat stress leads to alterations in membrane potential (depolarization), lipid peroxidation, protein oxidation, nucleic acid damage, disruption of enzyme function, and initiation of programmed cell death[22,23,72]. The rise in ROS levels associated with heat stress prompts the activation of antioxidative defense mechanisms by triggering the activity of enzymes involved in scavenging free radicals[73].The detoxification of reactive oxygen species (ROS) through the antioxidative defense system is crucial for protecting plants against oxidative harm [71]. Plants possess a highly efficient antioxidative defense system, which involves various enzymatic and non-enzymatic antioxidants [74]. Enzymatic antioxidants consist of superoxide dismutase (SOD), ascorbate peroxidase, catalase (CAT), glutathione peroxidase (GPX), glutathione reductase (GR), and peroxidase (POX), whereas non-enzymatic antioxidants include substances such as ascorbic acid, glutathione, tocopherols, carotenoids, and phenolic compounds [69,75]. These antioxidants play various roles in scavenging reactive oxygen species (ROS) as indicated in Table 1. The synthesis of different antioxidant enzymes is contingent upon the specific type of stress experienced by the plant. In response to heat stress (HS), there is an elevation in the activity levels of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) [63,76]. Balla et al. have documented that the activity of glutathione S-transferase (GST), ascorbate peroxidase (APX), and CAT is heightened in the cultivar that exhibits resilience to HS [77]. Electron leakage from the electron transport chain is an inevitable occurrence in mitochondria, chloroplasts, and the plasma membrane. Reactive oxygen species (ROS) are generated when leaked electrons are accepted by O_2 or as a byproduct of various metabolic processes specific to different cellular regions[78,79]. The acceptance of the leaked electron by an oxygen molecule leads to the production of superoxide or singlet oxygen. Superoxide radicals can be transformed into hydrogen peroxide through either spontaneous dismutation or through the catalytic action of superoxide dismutase (SOD) or certain metal ions (Fe^{3+} and Cu^{2+}) found within the cell. The hydrogen peroxide can further react to form •OH through the Haber-Weiss reaction, which occurs in two distinct steps. In the first step, the metal ion is reduced by the superoxide radical, while in the second step, the reduced metal ion reacts with hydrogen peroxide to generate •OH, known as the Fenton reaction. •OH molecules exhibit higher reactivity compared to other ROS[26]. There is no enzymatic mechanism known to eliminate •OH, leading to potential cell death from increased •OH production [80]. However, the presence of •OH can be reduced through the scavenging of hydrogen peroxide by peroxidase enzymes such as guaiacol peroxidase, as well as by APX and CAT [81]. Despite the association of reactive oxygen species (ROS) production with oxidative stress, these molecules can also serve as signaling molecules under various abiotic stress conditions, promoting tolerance to such stress. As a result, it is recommended that ROS levels should not be completely eradicated, but rather maintained at a certain level to prevent oxidative damage.

3.3 Stay Green:

The genotype known as Stay Green (SG) plays a crucial role in sustaining photosynthesis and grain filling in high temperature (HS) conditions by delaying the expression of genes associated with senescence [82]. SG serves as a significant mechanism for heat stress tolerance in wheat by preserving the photosynthetic area and enhancing the transfer of nitrogen to the developing grains [81]. As ovaries progress through their growth phases, starch levels decline rapidly; however, under HS conditions, the sugar accumulation decreases due to a decrease in photosynthetic activity, which can lead to seed abortion [82]. The presence of SG results in heightened photosynthetic activity, ensuring a consistent supply of sugar to the developing anthers and pollen, thereby promoting the viability of pollen and ovules [83]. A study was carried out to investigate the relationship between specific gravity (SG) traits and canopy temperature depression (CTD) [84]. It was noted that SG genotypes exhibited a greater CTD (difference between air temperature and canopy temperature) under high temperature stress conditions, leading to the conclusion that there is a strong correlation between SG and CTD. As a result, the SG trait could potentially serve as a selection criterion for wheat genotypes under heat stress conditions [32].

4. CAUSES OF HEAT STRESS

Comment [Ma3]: Consider this section after the introduction part for more clarity

4.1 Climatic Variation:

Based on anticipated temperature fluctuations, it is projected that the average global temperatures will increase by approximately 20 degrees Celsius within the next five decades, impacting various locations where cereals are cultivated [92]. The expected rise in ambient temperature by the end of the twenty-first century is estimated to be between 1 and 6 degrees Celsius[11]. This escalation in worldwide temperatures poses a significant threat to agricultural productivity due to the adverse effects of high temperatures, drought, salinity, waterlogging, and mineral toxicity induced by heat stress. Heat stress is characterized by a sustained increase in air temperature beyond a critical threshold, leading to severe or irreversible harm to plants used in agriculture [21]. Elevated soil temperature due to increasing air temperature and reduced soil moisture exacerbates heat stress, posing a significant threat to the success of crops [16].

4.2 Late sowing:

Multiple studies indicate that postponing the planting process can elevate the likelihood of experiencing terminal heat stress during the grain filling phase, leading to a significant decrease in grain yield. It is recommended to sow seeds between the 15th and 25th of November in order to minimize the impact of high temperatures on wheat crops in the IGP region [20]. Each day of delay presents new challenges, with a daily reduction in crop production of 36 kg/ha observed for wheat sowing after the 30th of November [35]. In general, late seeding is not advisable as it exposes wheat varieties to elevated temperatures, resulting in shortened heading and maturation periods that ultimately affect the final yield and quality of grains[33,28]

Factors affecting wheat growth:

Wheat is categorized within the Poaceae family, specifically belonging to the tribe Triticeae and the genus Triticum. This self-pollinating, annual plant requires a long day to grow. Globally, wheat holds the position as the most important food crop, covering a larger cultivated area than any other crop on Earth [64].

CONCLUSION

The significant role of wheat in global agriculture cannot be overstated, as it serves as a primary food source for a substantial portion of the world's population. However, the increasing challenges posed by heat stress due to global climate change threaten wheat productivity. Heat stress adversely affects wheat at various stages of its growth, impacting morphological, physiological, and biochemical processes. This leads to reduced seed germination, grain filling duration, and overall yield, ultimately threatening food security.Wheat's high sensitivity to temperature variations highlights the urgency for developing and implementing effective heat tolerance strategies. Advances in understanding the molecular and physiological responses to heat stress have identified several key mechanisms that confer tolerance. The production of heat shock proteins (HSPs) plays a critical role in maintaining protein integrity under stress conditions. Additionally, the antioxidative defense system mitigates oxidative damage caused by reactive oxygen species (ROS), thereby preserving cellular function. Traits like Stay Green (SG), chlorophyll fluorescence, and canopy temperature are crucial indicators of heat tolerance and can be used in breeding programs to develop more resilient wheat varieties.To meet the future food demands of a growing population, it is essential to integrate these scientific insights into practical agricultural strategies. This includes breeding heat-tolerant wheat varieties, optimizing planting schedules, and employing agronomic practices that mitigate heat stress. Collaborative efforts among researchers, policymakers, and farmers are imperative to develop sustainable solutions that enhance wheat resilience to heat stress. By addressing these challenges, we can ensure stable wheat production and contribute to global food security in the face of climate change.

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