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

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This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Wheat (*Triticum aestivum* L.), a vital cereal crop in the Poaceae family, plays a crucial role in global agriculture. It contributes approximately 30% of the world's grain production and constitutes half of the grain traded internationally. Serving as a staple food in over 40 countries, wheat provides essential calories to 85% of the global population and protein to 82%. With the global population expected to reach 9.1 billion by 2050, the Food and Agriculture Organization (FAO) projects that nearly one billion additional tons of cereal will be needed annually to meet increasing demand. Enhancing wheat productivity and production is thus essential. Wheat is cultivated in tropical and

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subtropical regions, where it faces various abiotic stresses that significantly impact yield, with heat and drought being the most critical challenges. Global climate models predict a potential increase in mean ambient temperature by up to 6°C by the end of the century. Wheat is highly sensitive to heat stress; even a 1°C rise in temperature can reduce global wheat production by 6%. Heat stress affects 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. These include the induction of heat shock proteins (HSPs) that assist in 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. Understanding and improving these mechanisms are imperative to sustain and enhance wheat production to meet future food demands amidst global climate changes. This review provides a comprehensive analysis of the effects of heat stress on wheat morphology, physiology, and biochemistry. It also discusses the mechanisms of heat tolerance, emphasizing the importance of developing crop varieties capable of withstanding future climatic conditions. Understanding these mechanisms at physiological, biochemical, and morphological levels is crucial for ensuring future food security.

Keywords: Heat stress; HSPs; oxidative stress; ROS; biochemical; productivity; stay green.

1. INTRODUCTION

Wheat (*Triticum* spp.), a key cereal crop in the Poaceae family, holds a crucial position in global agriculture, accounting for around 30% of the world's grain production and half of the grain traded internationally [1]. It is a staple food in more than 40 countries, supplying essential calories to 85% of the global population and protein to 82% [2-3]. As the global population is expected to reach 9.1 billion by 2050, the Food and Agriculture Organization (FAO) predicts a need for nearly one billion additional tons of cereal production annually to satisfy the increasing demand [4]. Therefore, boosting crop productivity and production is critical in the 21st century. Wheat is cultivated in tropical and subtropical regions, where it encounters various abiotic stresses that significantly impact yield [5]. These stresses include heat, drought [96], salinity [97], cold, chemical exposure [98], and excessive water [6]. Among these, heat and drought are the primary challenges affecting wheat production globally [7-8]. Climate models predict a potential 6°C increase in mean ambient temperature by the end of the century [8]. Addressing these challenges is crucial to sustain and enhance wheat production to meet future food demands.

Wheat exhibits a high sensitivity to heat stress, with studies indicating that a 1°C rise in temperature can cause a 6% reduction in global wheat production [9]. A 1°C increase above the average temperature during the reproductive stage can lead to significant grain yield losses [10-11]. Elevated temperatures adversely affect various physiological, biological, and biochemical processes in wheat [12]. Heat stress impacts seed germination, grain filling duration, grain number, Rubisco enzyme activity, photosynthetic capacity, assimilate translocation rate, leaf senescence, chlorophyll content, and 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 affect membrane stability, lipid peroxidation, protein oxidation, and nucleic acid damage [22-23]. Wheat has developed diverse tolerance mechanisms to counteract 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]. The challenge of climate change necessitates a deep understanding of these tolerance mechanisms. Wheat's ability to withstand heat stress through physiological, biochemical, and morphological adaptations is critical for developing resilient crop varieties. Enhancing these traits will be vital for ensuring sustainable wheat production and meeting the global food demand in the face of increasing temperatures. This review delves into the comprehensive analysis of heat stress impacts on wheat and discusses advanced strategies for improving heat tolerance to secure future food supplies.

2. EFFECTS OF HEAT STRESS ON WHEAT

High temperature stress affects various growth and development stages of wheat, leading to substantial yield reductions. The impact of heat stress on plants depends on both the duration of heat exposure and the specific growth stage at which the stress occurs [27-28]. Heat stress results in negative outcomes such as poor germination, reduced leaf area, premature leaf senescence, and damage to the photosynthetic apparatus, all contributing to a decline in wheat photosynthesis [12,29-30]. The effects of heat stress on wheat are evident through changes in morphology, physiology, and biochemistry. During germination, high temperatures can inhibit seedling establishment, resulting in poor germination rates and weak seedlings. This early stage stress can set back the crop's development, reducing overall plant vigor and yield potential. As wheat progresses to the vegetative stage, heat stress can limit leaf expansion, reduce leaf area, and accelerate leaf aging, which diminishes the plant's photosynthetic capacity [12]. Premature leaf senescence, triggered by heat, further compounds this issue by shortening the duration of active photosynthesis, thus reducing the overall energy available for growth and grain filling [29]. Fig. 1 illustrated various Impacts and responses of plants to heat stress.

At the biochemical level, heat stress affects several critical processes in wheat. It disrupts the activity of key enzymes such as Rubisco, which plays a vital role in carbon fixation during photosynthesis. This disruption reduces the plant's photosynthetic efficiency and carbon assimilation rate, leading to lower biomass accumulation and grain yield. Heat stress also induces the production of reactive oxygen species (ROS), which cause oxidative damage to cellular components, including lipids, proteins, and nucleic acids [22-23]. This oxidative stress can impair cellular functions and lead to cell death if not mitigated by the plant's antioxidative defense mechanisms [26]. Furthermore, heat stress affects the reproductive stage by reducing pollen viability, affecting fertilization, and leading to a lower number of grains per spike. High temperatures during grain filling can shorten the grain filling period, reduce grain size, and alter the starch and protein composition of the grains, impacting both yield and quality [13,21]. To combat these adverse effects, wheat has evolved various tolerance mechanisms. Additionally, traits such as Stay Green (SG), chlorophyll fluorescence, and canopy temperature are closely linked to heat tolerance and are being explored for breeding heat-resistant wheat varieties [20]. In summary, understanding the multifaceted impact of high temperature stress on wheat's growth, development, and biochemical processes is essential for developing strategies to enhance heat tolerance. This knowledge is crucial for ensuring sustainable wheat production in the face of rising global temperatures and securing future food supplies.

2.1 Effect on Wheat Morphology

High temperature stress poses significant challenges to crop growth and productivity, particularly impacting seed germination and plant establishment across various crops, including wheat [13]. Elevated temperatures, reaching up to 45°C, can adversely affect embryonic cells, leading to poor germination and emergence, thereby reducing crop stand and early growth [31]. Furthermore, high temperatures contribute to decreased survivability of productive tillers in wheat, resulting in diminished grain yield and tiller numbers by 53.57% and 15.38%, respectively [21]. The inhibition of root growth under heat stress further exacerbates these effects, affecting overall crop production capabilities [32]. The reproductive phase of wheat is particularly vulnerable to the detrimental effects of high temperature stress [33]. Even slight increases in average temperatures during this critical phase, such as 1°C, can significantly reduce grain yield [10,11]. For optimal flowering and grain filling in wheat and similar crops, temperatures ideally range between 12°C and 22°C [2]. Heat stress during early stages of gametogenesis, such as meiosis, can disrupt microspore and pollen development, crucial for successful floral initiation and subsequent grain formation [34,35].

The impact of high temperature stress extends to the grain development stage, affecting both the rate and duration of grain filling [36-37]. Wheat's lifecycle is accelerated under high temperatures compared to normal conditions, with a rise of 1°C to 2°C shortening seed filling duration and reducing seed weight [38,39]. Even brief episodes of heat stress during grain filling can lead to substantial yield losses of up to 23% [40]. Moreover, high temperature stress negatively affects grain number and quality, contributing to a reduced harvest index due to decreased

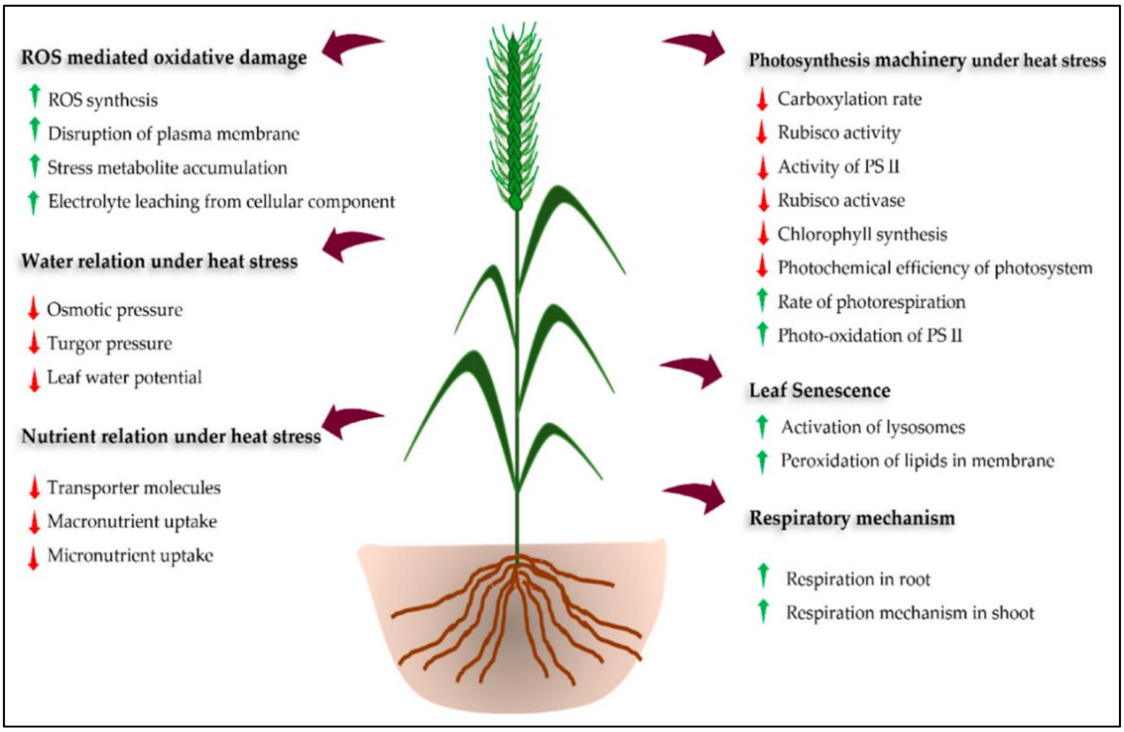

Fig. 1. Impacts and responses of plants to heat stress [94]

assimilate production and remobilization [14,15,41]. The overall productivity of wheat is significantly impaired by exposure to high temperatures throughout its growth stages [42]. Short-term exposure to ambient temperatures exceeding 35°C can cause severe reductions in grain yield, highlighting the sensitivity of wheat to heat stress episodes [43]. Ensuring wheat resilience to high temperature stress is crucial for sustainable agriculture, necessitating continued research into breeding heat-tolerant varieties and implementing adaptive agricultural practices. Addressing these challenges is essential to safeguarding global food security in the face of climate change.

2.2 Effect on Wheat Physiology

Photosynthesis, a fundamental physiological process in plants, plays a critical role in plant growth and development but is significantly influenced by elevated temperatures. In wheat plants, the impact of heat stress on photosynthesis is profound, particularly affecting the stroma and thylakoid lamellae, which are sensitive to thermal fluctuations [30]. Exposure to temperatures nearing 40°C can induce irreversible changes in key enzymes such as RuBisCO, Rubisco Activase, and Photosystem II, essential for carbon fixation and energy transfer [44]. Notably, the deactivation of RuBisCO occurs swiftly, within a week of high-temperature exposure, impairing carbon assimilation [16]. Additionally, the breakdown of Rubisco activase under heat stress further diminishes the plant's photosynthetic capacity [17]. High temperatures also disrupt the thylakoid membrane fluidity, causing dissociation between light harvesting complex II and Photosystem II, crucial for efficient light energy conversion [45].

In response to heat stress, plants must redistribute photosynthetic products to support various growth processes throughout different parts of the plant. However, the rate of assimilate translocation is hampered by reduced membrane stability under high temperatures, impacting overall plant productivity [18]. Effective mobilization of water-soluble carbohydrates to reproductive sinks becomes crucial to support grain development under stress conditions [46]. Limitations in either source (photosynthetic capacity) or sink (demand for assimilates) can lead to reduced seed set and impaired grain filling [47]. Plants facing source limitation due to heat stress must adapt by alternative mechanisms to ensure efficient transport of photosynthates to developing grains [1]. Particularly, carbohydrate remobilization from stems to developing grains increases during pre-anthesis heat stress, facilitating grain starch accumulation under post-anthesis heat stress conditions [48]. The physiological impacts of high temperatures extend beyond photosynthetic efficiency to include increased photorespiration due to elevated oxygen concentrations and altered gas solubility in wheat flag leaves [49]. Moreover, plant senescence, characterized by vacuolar collapse, membrane deterioration, and disruption of cellular homeostasis, progresses differently under moderate prolonged heat stress compared to intense short-term heat stress [24,50]. Accelerated leaf senescence and reduced chlorophyll biosynthesis are evident under heat stress conditions above 34°C during maturity, further complicating plant responses [19,20]. Heat stress also affects plant water relations by reducing osmotic potential, leading to cellular dehydration and impacting physiological processes like stomatal conductance and transpiration rates [51]. Monitoring canopy temperature becomes crucial as it influences leaf water content and provides insights into plant stress responses, aiding in the selection of heat-tolerant genotypes [2,20]. Traits such as chlorophyll fluorescence, which correlates closely with yield, and canopy temperature are pivotal in identifying and breeding for heat-tolerant plant varieties [20,52].

Studies on wheat genotypes have shown varying responses to heat stress, with heat-sensitive genotypes exhibiting decreased chlorophyll content and leaf area index under late sown conditions, while heat-tolerant genotypes show higher proline content, indicative of stress tolerance [53]. Furthermore, under heat stress conditions, plants accumulate Reactive Oxygen Species (ROS), which disrupt cellular integrity by affecting lipids, proteins, and DNA. This oxidative damage leads to a significant reduction in membrane stability and increased cell membrane permeability, exacerbating stress effects [54,55]. In summary, understanding the intricate responses of plants to heat stress is crucial for developing strategies to enhance heat tolerance in crops. The multifaceted impacts on photosynthesis, plant water relations, senescence, and cellular integrity underscore the complexity of plant responses to environmental stressors like high temperatures. Continued research into these mechanisms will be vital for sustaining agricultural productivity in the face of climate change challenges.

2.3 Effect on Wheat Biochemistry

Starch, a pivotal component of wheat grain, consists of amylose and amylopectin, whose proportions determine starch quality. High temperatures have been associated with alterations in amylose content and the amylose to amylopectin ratio, affecting starch characteristics [56]. The enzymes ADP-Glucose Pyrophosphorylase (AGPase) and starch synthase play crucial roles in starch biosynthesis, encompassing forms like Soluble Starch Synthase and Granule-bound starch synthase [2]. However, elevated temperatures can diminish starch content in wheat grain by as much as one-third due to reduced efficiency of these biosynthetic enzymes [57].Specifically, the activity of soluble starch synthase declines notably at temperatures around 40°C, leading to smaller grain size and decreased starch accumulation [58]. Up to 30°C, reduced activity of Soluble Starch Synthase affects starch composition without significant impact on overall starch deposition. Moreover, they noted that granule-bound starch synthase activity in wheat remains largely unaffected by high temperatures [59]. Decline in starch biosynthesis in wheat grain under heat stress conditions, concurrent with increased levels of total soluble sugars and proteins [60].

Protein content and composition are critical determinants of wheat grain quality. Lizana and Calderini found no substantial changes in protein concentration under high temperature conditions [41]. In contrast, Iqbal et al. reported an increase in grain protein content, essential amino acids, leaf nitrogen content, and sedimentation index in wheat exposed to high temperatures, highlighting varied responses in protein synthesis under different heat stress regimes [4]. In conclusion, understanding the intricate interactions between high temperatures and biochemical processes like starch and protein synthesis in wheat is crucial for developing strategies to mitigate the impacts of climate change on crop productivity and grain quality. Continued research into the molecular mechanisms governing these processes will be essential for enhancing heat tolerance and ensuring food security in the face of changing environmental conditions.

3. HEAT TOLERANCE MECHANISM IN WHEAT

Plants employ diverse adaptation strategies to thrive amidst high temperature conditions. These strategies encompass Avoidance, Escape, and Tolerance, each playing crucial roles in enabling plants to not only endure but also flourish in challenging environments. Heat tolerance, a pivotal aspect of these adaptations, denotes a plant's capacity not just to survive but also to sustain growth and achieve economic yield under conditions of elevated temperature stress.

In wheat, several key mechanisms contribute to enhancing heat tolerance. Firstly, plants activate robust antioxidant defenses to counteract oxidative stress, a common consequence of high temperatures that can damage cellular structures and impair physiological functions. Additionally, the induction of Heat Shock Proteins (HSPs) serves as a protective mechanism, assisting in protein folding, stabilization, and cellular repair under heat stress conditions. Moreover, the retention of green foliage amidst high temperatures supports sustained photosynthetic activity, crucial for maintaining energy production and biomass accumulation despite environmental challenges. These adaptive responses highlight the complex interplay of biochemical, physiological, and morphological adjustments that enable plants, including wheat, to thrive in high temperature environments. Understanding these mechanisms is essential for developing strategies to enhance crop resilience and productivity in the face of climate change and evolving environmental conditions. Continued research into these adaptation strategies will be pivotal in ensuring global food security and agricultural sustainability in the future.

3.1 Heat Shock Proteins

Protein function hinges significantly on the processes of synthesis and folding, crucial for proper cellular operations. Misfolding of proteins can severely disrupt these functions, impacting essential cellular processes. High temperature (HS) conditions exacerbate this issue by destabilizing protein folding and synthesis [2], leading to the accumulation 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 cellular homeostasis is restored [61]. To mitigate the detrimental effects of HS, plants employ a defense mechanism involving the accelerated production of Heat Shock Proteins (HSPs) [62]. HSPs are classified into distinct families based on their size, amino acid sequences, and functional roles [63], including HSP100, HSP90, HSP70, HSP60, and small HSPs. Each family of HSPs serves specific protective functions under HS conditions. Initially inactive in the cytoplasm, Heat Stress transcription factors (Hsfs) act as regulatory proteins in the transcription of genes encoding HSPs. Upon HS induction, these Hsfs become transcriptional activators [64]. Several mechanisms orchestrate the expression of genes encoding HSPs, involving temperature sensing, signal transduction pathways leading to Hsfs activation, and the binding of Hsfs to heat shock elements (HSE) in DNA to initiate gene expression [65]. During HS, HSPs function as molecular chaperones, crucial for preventing protein denaturation and aggregation, thereby preserving cellular function and integrity [24,66]. In summary, the induction of HSPs represents a critical adaptive response of plants to high temperature stress, safeguarding protein functionality and cellular viability. Understanding these mechanisms provides insights into enhancing crop resilience against environmental challenges, crucial for sustainable agriculture in a changing climate.

3.2 Reactive Oxygen Species and Antioxidative Defense Mechanism

High salinity (HS) imposes significant stress on plants by triggering the generation of reactive oxygen species (ROS) such as singlet oxygen, superoxide, and hydroxyl radical [67,68]. Normally, cells maintain a balance between ROS production and elimination, known as redox homeostasis [69]. When ROS production exceeds the cell's antioxidant capacity, oxidative stress occurs, leading to damage in lipids, proteins, nucleic acids, disruption of enzyme function, and potential initiation of programmed cell death [22,23,72]. Heat stress exacerbates ROS production, causing membrane depolarization, lipid peroxidation, protein oxidation, and nucleic acid damage [22,23,72]. This stimulates the activation of antioxidative defense mechanisms to counteract oxidative damage [73]. Plants possess a sophisticated antioxidative defense system comprising enzymatic and non-enzymatic antioxidants [74]. Enzymatic antioxidants include superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPX), glutathione reductase (GR), and peroxidase (POX). Non-enzymatic antioxidants encompass substances such as ascorbic acid, glutathione, tocopherols, carotenoids, and phenolic compounds, all of which play vital roles in scavenging ROS [69-70,75].

Under heat stress conditions, there is an increase in the activity levels of antioxidative enzymes such as SOD, CAT, and POX [63,76]. Certain cultivars exhibiting resilience to heat stress show heightened activity of glutathione Stransferase (GST), APX, and CAT [77]. Electron leakage from cellular organelles like mitochondria and chloroplasts generates ROS when leaked electrons react with oxygen molecules [78,79]. Superoxide radicals are converted into hydrogen peroxide either spontaneously or enzymatically by SOD or metal ions like Fe3+ and Cu2+. Hydrogen peroxide can further react to form highly reactive hydroxyl radicals (•OH) through the Fenton reaction, which poses a significant threat due to its high reactivity and lack of specific enzymatic detoxification mechanisms [26,80]. However, peroxidase enzymes such as guaiacol peroxidase, APX, and CAT can scavenge hydrogen peroxide, thereby indirectly reducing •OH levels [81]. Despite their damaging potential, ROS also function as signaling molecules under various abiotic stress conditions, aiding plants in adapting and developing tolerance mechanisms. Therefore, maintaining optimal ROS levels is crucial for balancing stress responses and minimizing oxidative damage without compromising signaling functions that promote stress tolerance [26]. In summary, understanding the intricate dynamics of ROS production and antioxidative defense mechanisms is essential for developing strategies to enhance plant resilience to environmental stresses like heat and salinity, ultimately ensuring sustainable agricultural productivity in challenging climates.

3.3 Stay Green

The Stay Green (SG) genotype plays a pivotal role in enhancing heat stress tolerance in wheat by delaying the onset of senescence-related gene expression, thereby sustaining photosynthesis and grain filling under high temperature (HS) conditions [82]. This genotype preserves the photosynthetic area and facilitates efficient nitrogen transfer to developing grains, crucial for maintaining yield potential [81]. In HS environments, wheat ovaries experience rapid starch depletion, while sugar accumulation declines due to reduced photosynthetic activity, potentially leading to seed abortion [82]. SG genotypes counteract this by maintaining heightened photosynthetic activity, ensuring a steady supply of sugars to developing anthers and pollen, thereby promoting pollen and ovule viability [83]. Research has explored the association between SG traits and canopy temperature depression (CTD), a measure of plant cooling under HS conditions [84]. SG genotypes have been observed to exhibit greater CTD, indicating lower canopy temperatures relative to ambient air temperatures. This correlation underscores the potential of SG as a valuable selection criterion for wheat genotypes under heat stress, aiding in the identification and breeding of heat-tolerant varieties [32]. In summary, the SG genotype in wheat represents a significant adaptation strategy against HS, facilitating sustained photosynthesis, efficient nutrient allocation, and improved reproductive success. Incorporating SG traits into breeding programs could enhance wheat resilience to increasingly challenging climatic conditions, ensuring stable agricultural productivity in the face of climate change [85]. An increase in leaf area, rate and duration of grain filling and photosynthetic competence, water use efficiency, leaf anatomy, have been found to be a characteristic for the SG trait (Fig. 3) [95].

4. CAUSES OF HEAT STRESS

Heat stress in agriculture arises primarily from climatic variations characterized by sustained increases in air and soil temperatures beyond critical thresholds. Projections indicate a potential rise in average global temperatures by as much as 1 to 6 degrees Celsius by the end of the twenty-first century, posing substantial risks to cereal crop cultivation worldwide [90,91]. This escalation not only exacerbates heat stress but also amplifies challenges related to drought, salinity, waterlogging, and mineral toxicity, all of which contribute to reduced agricultural productivity [92,93].

Late sowing practices further exacerbate heat stress impacts on crops, particularly evident during the grain filling phase of cereals like wheat. Studies emphasize that delaying planting increases the likelihood of encountering terminal heat stress, significantly diminishing grain yields [94,95]. For instance, each day of delay in sowing after optimal dates in regions like the Indo-Gangetic Plain results in observable reductions in crop productivity [95]. Such delays expose crops to elevated temperatures during critical growth stages, accelerating maturation and potentially compromising final yield and grain quality [96,97]. Understanding these climatic and agronomic factors is crucial for implementing effective agricultural management practices and breeding strategies aimed at enhancing crop resilience to heat stress. Addressing these challenges requires proactive measures to mitigate the impacts of climate change and ensure sustainable food production in a rapidly evolving environment [86-87].

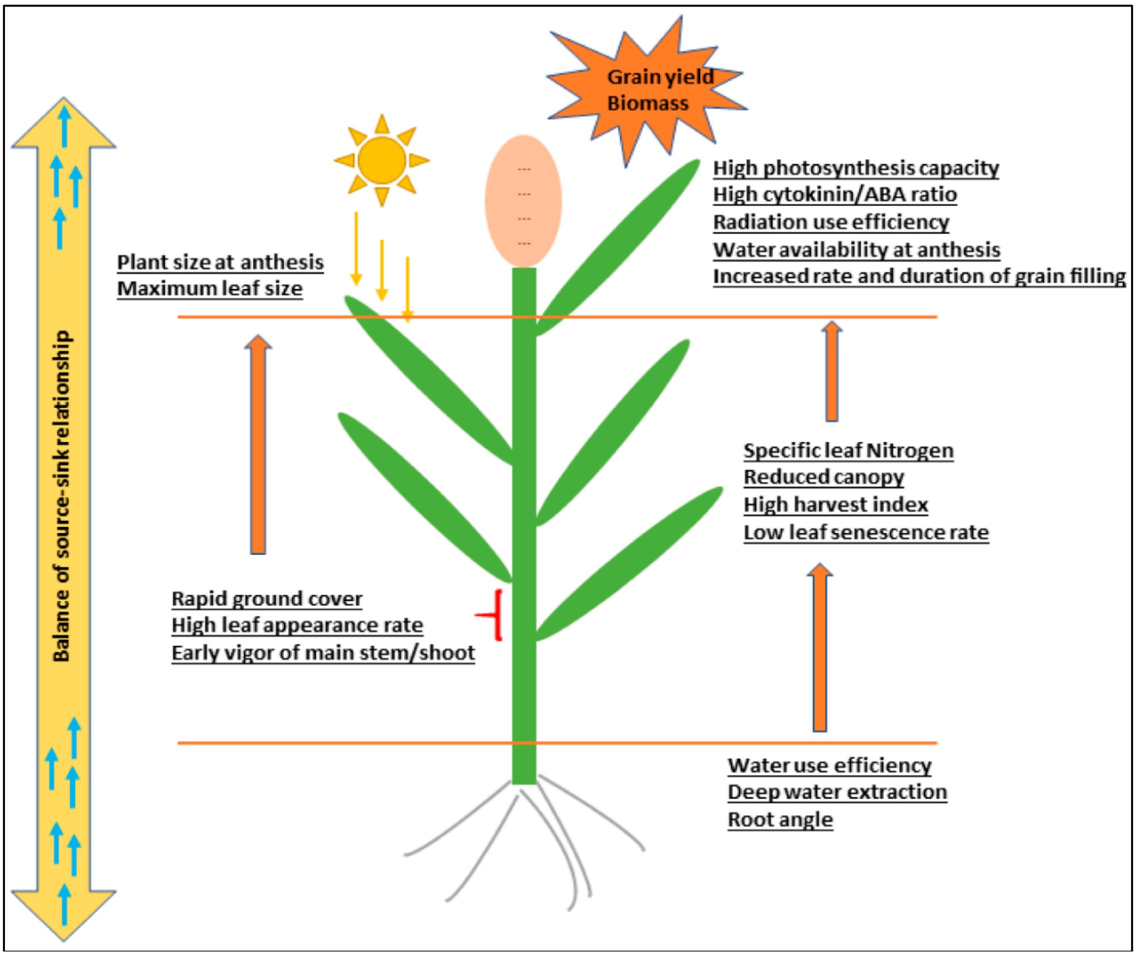

Fig. 2. The physiological features of the stay-green plants including photosynthesis, transport of photosynthates and source-sink relationship [95]

4.1 Climatic Variation

Anticipated temperature fluctuations indicate a projected increase of approximately 20 degrees Celsius in average global temperatures over the next five decades, impacting cereal cultivation across diverse geographical locations [90]. By the end of the twenty-first century, it is anticipated that ambient temperatures could rise by 1 to 6 degrees Celsius [91]. This global temperature escalation poses a significant threat to agricultural productivity, exacerbated by the adverse impacts of high temperatures, drought, salinity, waterlogging, and mineral toxicity associated with heat stress. Heat stress occurs when sustained increases in air temperature surpass critical thresholds, causing severe or irreversible damage to crops used in agriculture [92]. Furthermore, elevated soil temperatures resulting from higher air temperatures and reduced soil moisture levels intensify heat stress, posing a substantial risk to crop success [93].

4.2 Late Sowing

Numerous studies have highlighted that delaying the planting process increases the risk of encountering terminal heat stress during the critical grain filling phase, which consequently leads to a notable decline in grain yield. To mitigate these risks, it is recommended to sow seeds between the 15th and 25th of November to minimize the impact of high temperatures on wheat cultivation in the Indo-Gangetic Plain (IGP) region [94]. Each day of postponement beyond this optimal window presents escalating challenges, with documented reductions in crop productivity amounting to 36 kg/ha per day for wheat sown after the 30th of November [95]. Generally, late seeding exposes wheat varieties to prolonged periods of elevated temperatures, resulting in shortened periods for heading and maturation, thereby compromising the final yield and quality of grains [96,97].

4.3 Factors Affecting wheat Growth

Wheat, classified within the Poaceae family and specifically belonging to the tribe *Triticeae* and genus *Triticum*, is a self-pollinating annual plant that thrives under long-day conditions [99]. Globally, wheat holds a paramount position as the most vital food crop, occupying a larger cultivated area than any other crop on Earth [98]. Essential qualities determining wheat's suitability for flour production include its protein content, milling yield, and rheological properties crucial for bread-making [100]. These traits are largely influenced by genetic factors and the intricate interactions between genotype and environment, which can significantly impact the size and overall performance of wheat varieties [101]. Understanding these genotype-environment interactions is pivotal for optimizing agricultural practices. Factors such as soil quality, atmospheric conditions, and specific plant habitats play significant roles in wheat cultivation [88]. The selection of wheat cultivars is critical for sustainable agricultural management and effective economic planning. Crop yield is subject to various uncontrollable factors, with climate conditions being among the most critical. Meteorological parameters such as cloud cover, diurnal temperature fluctuations, precipitation patterns, average temperatures, and humidity levels are pivotal considerations [89]. Wheat cultivation is not continuous throughout the year in any country, and seasonal and regional variations must be carefully considered, particularly in regions like Pakistan where agricultural practices are sensitive to climate changes. Adapting to evolving climate factors is essential for maintaining and enhancing wheat production efficiency amidst changing environmental conditions.

5. FUTURE ASPECTS OF HEAT STRESS AND TOLERANCE MECHANISMS IN WHEAT

Understanding and mitigating the impacts of heat stress on wheat (Triticum spp.) remains a critical challenge in agriculture, particularly in the context of climate change. As temperatures rise globally, the frequency and intensity of heat stress events are projected to increase, posing significant threats to wheat production worldwide. This review explores current research on heat stress and tolerance mechanisms in wheat and outlines future directions for research and application to ensure food security in a changing climate.

5.1 Genetic and Breeding Strategies

Genetic diversity plays a crucial role in determining the heat tolerance of wheat varieties. Future research should focus on identifying and harnessing genetic markers associated with heat tolerance traits such as stay-green phenotypes, enhanced antioxidant capacity, and efficient photosynthesis under high temperatures. Advanced genomic technologies, including genome-wide association studies (GWAS) and marker-assisted selection (MAS), offer promising avenues to accelerate the breeding of heat-tolerant wheat varieties [71]. Integration of genomic information with phenotypic data from field trials under heat stress conditions will enable breeders to develop wheat cultivars that maintain high yields and quality under challenging environments. Furthermore, exploring wild relatives of wheat for novel heat tolerance genes and traits could expand the genetic base of cultivated wheat and enhance resilience to future climate scenarios.

5.2 Physiological and Molecular Mechanisms

Elucidating the physiological and molecular mechanisms underlying heat stress tolerance in wheat is essential for targeted breeding efforts. Key mechanisms include the regulation of heat shock proteins (HSPs), antioxidants, and osmoprotectants to mitigate oxidative stress and protein denaturation under high temperatures [72]. Future research should focus on understanding the interplay between these mechanisms and their integration into metabolic pathways that support growth and reproduction under heat stress. Advances in omics technologies, such as transcriptomics, proteomics, and metabolomics, provide powerful tools to unravel complex gene networks and metabolic pathways involved in heat stress response. Integrative analyses of multi-omics data will enhance our understanding of wheat's adaptive responses to heat stress and facilitate the identification of molecular targets for genetic improvement.

5.3 Climate-Smart Agricultural Practices

Adopting climate-smart agricultural practices is crucial for mitigating the impacts of heat stress on wheat production. Future research should emphasize the development and adoption of agronomic strategies that enhance soil health [103], water-use efficiency, and resilience to extreme weather events [102]. Practices such as conservation agriculture, precision irrigation, and crop diversification can help buffer wheat crops against heat stress while promoting sustainable intensification of agricultural systems. Furthermore, leveraging digital agriculture technologies, including remote sensing, unmanned aerial vehicles (UAVs), and predictive modeling, can provide real-time data on crop health and environmental conditions. Integrating these technologies with decision support systems will enable farmers to make informed management decisions, optimize resource allocation, and mitigate the risks associated with heat stress.

5.4 Climate-Resilient Crop Management

Effective crop management practices tailored to specific agro-ecological zones and climatic conditions are essential for enhancing wheat resilience to heat stress. Future research should focus on optimizing planting dates, cultivar selection, and nutrient management strategies to minimize heat stress impacts on crop development and yield [104]. Implementing heat-tolerant cultivars in combination with adaptive management practices can enhance the resilience of wheat production systems to climate variability. Additionally, exploring alternative cropping systems, such as relay cropping and intercropping, that enhance resource use efficiency and reduce temperature extremes can contribute to sustainable wheat production under changing climatic conditions. Integrated pest and disease management strategies should also be integrated into climate-resilient crop management plans to mitigate secondary stresses that exacerbate the impacts of heat stress on wheat [106].

5.5 Policy and Socioeconomic Considerations

Addressing the challenges posed by heat stress in wheat production requires coordinated efforts across multiple stakeholders, including policymakers, researchers, farmers, and consumers. Future research should prioritize socioeconomic assessments of climate change impacts on wheat production systems, including economic modeling of yield losses, market dynamics, and food security implications [105]. Policy interventions that support investment in climate-resilient agriculture, research and development, infrastructure development, and capacity building are essential for fostering adaptive capacity and enhancing the resilience of wheat farmers to climate change. Promoting inclusive agricultural policies that prioritize smallholder farmers and vulnerable communities will be critical for ensuring equitable access to technologies and resources that enhance heat stress resilience in wheat production [107-108].

In conclusion, addressing heat stress in wheat requires a multidisciplinary approach that integrates genetics, physiology, agronomy, and socioeconomics. Future research should focus on advancing genetic and breeding strategies, elucidating physiological and molecular mechanisms, promoting climate-smart agricultural practices, optimizing crop management strategies, and advocating for supportive policies. By leveraging technological innovations and collaborative partnerships, we can enhance the resilience of wheat production systems to heat stress and ensure global food security in a changing climate.

6. CONCLUSION

Wheat plays a crucial role in global agriculture by serving as a primary food source for a significant portion of the world's population. However, the escalating challenge of heat stress, exacerbated by global climate change, poses a serious threat to wheat productivity. Heat stress adversely affects wheat across various growth stages, impacting its morphology, physiology, and biochemistry. This results in decreased seed germination, shortened grain filling periods, and ultimately reduced yields, endangering food security. Wheat's high sensitivity to temperature fluctuations underscores the urgent need for effective strategies to enhance heat tolerance. Recent advancements in understanding the molecular and physiological responses to heat stress have identified key mechanisms that confer tolerance. Heat shock proteins (HSPs) play a critical role in maintaining protein integrity under stressful conditions. Furthermore, the antioxidative defense system counters oxidative damage induced by reactive oxygen species (ROS), thereby safeguarding cellular functions. Traits such as Stay Green (SG), chlorophyll fluorescence, and canopy temperature serve as vital indicators of heat tolerance and are instrumental in breeding programs aimed at developing resilient wheat varieties. To meet the future food demands of a growing global population, it is imperative to translate these scientific insights into practical agricultural strategies. This includes breeding heat-tolerant wheat varieties, optimizing planting schedules, and implementing agronomic practices that mitigate heat stress. Collaborative efforts involving researchers, policymakers, and farmers are crucial for developing sustainable solutions that bolster wheat resilience to heat stress. By addressing these challenges, stable wheat production can be ensured, thereby contributing significantly to global food security amidst climate change. Looking ahead, the prevalence of heat stress in wheat is expected to increase on a global scale due to ongoing global warming trends. Heat stress profoundly affects various aspects of wheat production, influencing grain development, duration, rate, quality, and ultimately yield. These effects are genotype-specific and are influenced by the severity, timing, and duration of the stress. Consequently, cultivating heat-tolerant wheat varieties is indispensable for mitigating the detrimental impacts of heat stress. Plants respond to heat stress by synthesizing various metabolites, including antioxidants and heat shock proteins (HSPs). Investigating these metabolites at the molecular level is pivotal for comprehending the underlying mechanisms governing stress tolerance in plants. This research provides essential insights for developing effective strategies to enhance wheat resilience to heat stress, thereby ensuring sustainable agricultural productivity in a changing climate.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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