



Review

Heat and Wheat: Adaptation strategies with respect to heat shock proteins and antioxidant potential; an era of climate change



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ABSTRACT

Extreme changes in weather including heat-wave and high-temperature fluctuations are predicted to increase in intensity and duration due to climate change. Wheat being a major staple crop is under severe threat of heat stress especially during the grain-filling stage. Widespread food insecurity underscores the critical need to comprehend crop responses to forthcoming climatic shifts, pivotal for devising adaptive strategies ensuring sustainable crop productivity. This review addresses insights concerning antioxidant, physiological, molecular impacts, tolerance mechanisms, and nanotechnology-based strategies and how wheat copes with heat stress at the reproductive stage. In this study stress resilience strategies were documented for sustainable grain production under heat stress at reproductive stage. Additionally, the mechanisms of heat resilience including gene expression, nanomaterials that trigger transcription factors, (HSPs) during stress, and physiological and antioxidant traits were explored. The most reliable method to improve plant resilience to heat stress must include nanobiotechnology-based strategies, such as the adoption of nano-fertilizers in climate-smart practices and the use of advanced molecular approaches. Notably, the novel resistance genes through advanced molecular approach and nanomaterials exhibit promise for incorporation into wheat cultivars, conferring resilience against imminent adverse environmental conditions. This review will help scientific communities in thermo-tolerance wheat cultivars and new emerging strategies to mitigate the deleterious impact of heat stress.

1. Introduction

Wheat (*Triticum aestivum*) is one of the most important cereal crops safeguarding global food security. However, there is a need to produce an additional 190 million tons of wheat grain to feed the estimated 10 billion people by 2050 [1]. Climate change-induced abiotic stresses significantly reduce wheat grain yields worldwide. As per a past report, the spatiotemporal interaction of distinct climatic factors affects the growth and production of the crop and hence it is very important to understand the impact of climatic factors like drought and heat stress [2].

Climate change is a big concern for wheat production, with and decline of 6 % its production due to heat stress, especially the rising temperatures because wheat being a temperature is very sensitive to heat stress [3]. About 6 % of the total agricultural land area is affected by the heat stress problem and this is expected to increase in the

upcoming years resulting in a predicted US\$12 billion annual loss in agricultural production. Within the next two decades, the Earth's average global temperature is predicted to rise by 1.5 °C. Analysis by the Goddard Institute for Space Studies and other academic organizations revealed a 1.04 °C rise in the average global temperature between 1880 and 2019 [4].

Wheat has severe biochemical and developmental changes as a result of the heat stress (HS) brought on by this high temperature, which lowers grain production and grain quality [5]. Because wheat is more susceptible to the impacts of high temperatures during the flowering stage, it is less likely to bounce back if harmed during this vital period [6]. The minimum, and optimum temperatures during germination, heading, anthesis, and grain filling stages range between 20 and 25 °C, 14 and 18 °C, 20 and 24 °C, and 25 and 27 °C, respectively. During the anthesis stage, wheat is particularly susceptible to high-temperature stress but can withstand it with proper management [7]. High

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temperature or heat stress can influence wheat development and improvement by changing physicochemical processes like anti-oxidative enzymes, stress-induced hormone activity, oxidative damage, photosynthesis, proteins, respiration, the relation of water and nutrient, and yield parameters (biomass, grain size, and number, tiller count) upon contact with heat stress and plant reactions to abiotic stress are varied and dynamic. When exposed to temperatures above the ideal range, wheat can experience HS by changing physiological and biochemical processes like photosynthesis, oxidative damage, stress-induced hormone activity, and anti-oxidant enzymes, i.e. SOD, CAT, POD as well as yield-producing parameters (tiller count, grain number, and size of grains) [6–8]. (See Tables 1, 2, 3.)

Moreover, the impact varies depending on the degree and duration of stress. [20]. Because of this, focus on the sustainability of wheat yield via highlighting resistant genotypes and upgrading breeding strategies should be done that aid in enhancing heat stress resistance and protecting wheat yields from heat stress [3]. A better knowledge of nanoparticles as agronomic management, agronomical assisted breeding and gene editing linked with heat stress tolerance has practical applications for planning countermeasures. For example, the identification of certain tolerance approaches and their role in coping mechanisms. An effective way to improve and enhance wheat yield, sustainable crop protection is through the use of nanomaterials is new emerging and ecofriendly technique. Genome mapping in wheat, governing physiological parameters aids in gene identification assuring tolerance from heat stress, and provides a superior foundation for marker-assisted breeding for heat tolerance [21,22]. The growth and development of such cultivars will help to address issues with food and nutritional security in non-conventional areas. Certain traditional breeding approaches, such as germplasm screening and selection and molecular breeding, are helpful genetic techniques for wheat cultivar growth [23]. Additionally, various biotechnological approaches like gene editing, besides with latest advanced omics tools can aid in making heat stress-tolerant cultivating

Table 1
Variables of climate change and heat stress.

Variables	Characteristics	References
Temperature	Exploring heat injury, the adaptations, and the role of hormones particularly in response to high temperatures.	[9,10]
	Climate change impacts wheat productivity by 6 % per degree rise, requiring effective management strategies like screening germplasm, molecular duplicate or selection assisted by markers to increase productivity and sustainability.	[11,12]
Rainfall	Forest ecology focuses on plant growth and survival, ignoring global change's impact associated with rainfall on seed production. Understanding masting is crucial for predicting trends in seed predation and pollination.	[13]
	The US Acid Rain Program reduced sulfur dioxide emissions but also reduced ambient sulfate levels, causing crop revenue losses of \$1–\$1.5 billion annually and decreased land value.	[14,15]
Global warming	Climate change causes global warming impacts grapevines, affecting wine quality and sustainability. Grapevines adapt to global warming associated with high temperatures, requiring heat-stress-adapted genotypes or stress-tolerant germplasm for viticulture.	[16]
	The study highlights the need for enhanced understanding of plant heat stress responses to predicted global temperatures, recommending the integration of heat stress experiment results and breeding programs.	[17,18]
	Global warming threatens agricultural production by inhibiting plant development and improvement, particularly among chloroplasts, that are heat-stress sensitive and are essential for activating nuclear heat-response genes.	[19]

Table 2
Wheat growth stages under different thermal ranges.

Stages	Optimum temperature (°C)	Minimum temperature (°C)	Maximum temperature (°C)
Seed germination	20–25 ± 1.2	3.5–5.5 ± 0.44	35 ± 1.02
Root growth	17.2 ± 0.87	3.50 ± 0.73	24.0 ± 1.21
Shoot growth	18.5 ± 1.90	4.50 ± 0.76	20.1 ± 0.64
Leaf initiation	20.5 ± 1.25	1.50 ± 0.52	23.5 ± 0.95
Terminal spikelet	16.0 ± 2.30	2.50 ± 0.49	20.0 ± 1.60
Anthesis	23.0 ± 1.75	10.0 ± 1.12	26.0 ± 1.01
Grain filling duration	26.0 ± 1.53	13.0 ± 1.45	30.0 ± 2.13

Table 3
Various heat shock proteins (HSPs) and their roles in plant heat tolerance.

HSPs	Characteristics	References
Small HSPs	Class 1 and 2, Aids in the folding back of disordered proteins, eliminating heat aggregation.	[136,137]
HSP10	Familiar in chloroplast chaperons, helps in protein folding in chloroplast	[138]
HSP20	This subset of sHSPs, characterized by their alpha-crystalline domain, protecting enzymes and structural proteins from heat-induced denaturation.	[139]
HSP40	After the synthesis of fully refolded protein, HSP40, HSP70, and HSP100 generate small HSPs associated with refolding.	[140]
HSP60	Aids in protein refolding and prevents the buildup of denatured proteins.	[141]
HSP70	Allows for correct protein folding and helps to stabilize newly synthesized proteins by preventing aggregation formation.	[140]
HSP90	Modulates heat stress-relationship signal transduction	[142]
HSP100	Aids in stress tolerance and protein aggregation degradation	[143]
HSP101	Aids in cell protection from hydrolysis and thermo-tolerance	[136]

varieties [24]. However, the limited accomplishment of wheat in the improvement of intensity stress strength can be credited to the absence of joint difficult work by agronomists, biotechnologists, physiologists, and plant breeders. Henceforth, the acceptance of a rounded multidisciplinary technique integrating the consequences of nanotechnology in agronomical management, genome, gene editing, and breeding options is required to provide practical explanations.

The study discussed how heat stress affects several physio-biochemical and molecular pathways in wheat and described a number of approaches i.e., genetic techniques, and new emerging techniques, nanotechnology to improve the antioxidant, yield, carbohydrate metabolism, physiological parameters i.e. anthesis stage and others classical methods, agronomic methods are explored. If the plants are unable to withstand the global warming, all the improvements in wheat quality have been or will be for naught. Although abiotic stress has received sufficient research, there is little information available on the common HS in crops. Thus, the main areas that are concerned with heat stress and plant adaptation are outlined in this review. The development of stress-tolerant wheat varieties has also been discussed, along with a number of pertinent and recent research articles and effective methods. The plant scientific community will undoubtedly find our review article to be of interest because it reviews current stress tolerance techniques and fosters new insights into wheat engineering for heat stress tolerance.

2. Sensitive stages and heat stress in wheat

Wheat is more defenseless with the impacts of heat stress (HS) at the time of its reproductive stages, preventing the creation of pollen tubes and affecting embryo development [25]. During the reproductive

season, high temperatures might result in a 44 % reduction in the total biomass of wheat [5]. Seed germination, which requires ideal humidity and temperature levels, is significantly impacted by HS, an abiotic stress. [26], in their research, study that under HS conditions, two wheat cultivars, DBA Aurora and L6, had lower germination indices and germination potential. Moreover, [27] presented that MiRNA expression and epigenetic modifications in wheat seedlings may be important elements in maximizing seed vigor for improved breeding under heat stress. High-vigor seedlings are more efficient in radiation and resource utilization, but they do not affect vegetative and reproductive phases over generations [28].

Heat stress (HS) poses a danger to wheat productivity throughout the reproductive and grain-filling periods [29]. When compared to vegetative stages, HS has a more detrimental impact on grain and crop condition, decreasing grain yield by up to 30 %, as reported by [30]. 12–24 °C is the optimal temperature range for anthesis and grain filling, with the most sensitive period being eight to six days before anthesis [31]. Results from 30 wheat crop models demonstrate that artificial heating reduces grain production in the majority of sites [32].

Past review directed by [33], for a temperature increase of 2 °C, rising temperatures are projected to have a variety of effects on falling wheat yields ranging from 1 % to 28 %, and for a temperature increase of 4 °C, it ranges from 6 % to 55 %. Wheat grows with fewer spikelets, grains per hundred, and a slower rate of seed germination when the nighttime temperature is high (HS) [34]. High temperature (HS) influences the development of pollen tubes, which results in aberrant ovary development and decreased cereal production, making harvest index (HI) the most important factor in wheat. High nighttime temperatures can lower grain production, HI, 1000-grain weight, as well as the amount of grain per spike, especially during grain filling [26]. For wheat breeders to improve wheat's ability to tolerate high nighttime temperatures, this research provides important features.

2.1. Effect of heat stress on the morphology and yield

Raised temperature conditions negatively impacts plant establishment and seed germination in wheat, causing improper germination, emergence, weak crop stands, and reduced tiller survival [12]. However, wheat under heat stress has decreased tiller count and grain production, affecting crop output [35]. It also reduces root development, leading to inefficient nutrient uptake and decreased crop output. The optimal temperature range for blossoming and filling of grains is somewhere in the range of 12 °C and 22 °C [36]. High temperature (HS) is increased during the grain loading process is quicker, reducing seed weight and leading to a loss of up to 23 % in grain production [35]. High temperature (HS) also affect the grain quantity and quality, as well as growth, lowering the harvest index and causing reduced assimilate production and remobilization [37]. Wheat production is significantly decreased due to high temperatures, and exposure to ambient temperatures for a short period may significantly suffer, grains are already posing significant challenges. [25]. According to these studies, apparently raised temperatures have an effect at the time falling of grain stage reduces tillers and grain size as well as number.

2.2. Effect of heat stress on the physiology of wheat

Photosynthesis, the primary significant physiological movement in plants, is significantly impacted by high temperatures [16]. Wheat is especially defenseless against heat pressure in the stroma and thylakoid lamellae, where the rubisco enzyme becomes inactive in less than seven days [38]. Heat pressure causes the thylakoid film to turn out to be less liquid, making the light-reaping complex II distinct from the photosystem II [5]. Photosynthetic products must be transported to other plant components, and the rate of assimilate translocation is slowed down due to reduced membrane integrity [39]. Water-soluble carbohydrates mobilized to the reproductive sink stimulate grain growth and

development. Heat stress-induced source constraints limit seed set and seed filling, and the plant must find an alternative method to transfer the photosynthetic product into the grain [5]. The impact of post-anthesis heat stress on grain starch content are reduced by pre-anthesis high temperature, which enhances the remobilization of carbohydrates are transported from the stem to the growing grain.

Photorespiration is encouraged by the presence of high oxygen concentrations, leading to increased photorespiration in flag leaves in wheat [40]. Senescence is the process of aging in plants, with hallmarks such as vacuolar collapse, loss of membrane integrity, and altered cellular homeostasis [41]. High temperatures (above 34 °C) hasten leaf senescence and canopy temperature influences transpiration, leaf water content and conductance of stomatal cells [42]. Plants create a lot of reactive oxygen species (ROS) when they are stressed disrupting cellular function and reducing membrane thermo-stability [43]. within heat stress, ROS build-up, promoting protein denaturation and unsaturated fatty acid production, ultimately enhancing cell membrane permeability [44]. HS increase photorespiration and decreases the membrane stability.

2.3. Effect of heat stress on the biochemistry

Amylose content is the key quality standard for wheat starch, which is composed of amylose and amylopectin [11]. Heat pressure can prompt a loss dependent upon 33 % of endosperm starch content because of a shortcoming in starch, which is an essential source [45]. At 40 °C, the activity of soluble starch synthase diminishes, this leads to the formation of smaller grains and reduction in starch deposition [46]. High temperature does not significantly impact granule-bound starch synthase activity, in any case, wheat grain starch creation diminishes under heat stress, while the amount of protein and sugars that dissolve increase [47,48]. Protein composition and content significantly impact wheat grain quality, which increments with protein focus, fundamental amino acids, precipitation record and leaf nitrogen levels [49,50]. These studies demonstrate the outcomes of heat stress that decreases starch production due to loss of the endosperm starch content.

3. Stress and various response mechanisms in wheat

3.1. Morphological and phenological responses

Heat stress impacts plant development and advancement, influencing several processes like germination, seedling emergence, and grain quality. As a result, good monitoring and management are required for the best crop yields [12]. A past survey by [51] presented the unfavorable impact of HS on morphological as well as yield components of wheat. The impact varies depending on exposure intensity, genotypes, soil moisture state, and atmospheric carbon dioxide concentration [17]. High temperatures cause poor seedling establishment, reduced root and shoot growth, leaf wilting, flower abortion, and terminal HS, which severely reduces wheat dry matter accumulation and grain quality revealed by [25,52]. To sustain wheat yields, more attention should be given to regulating terminal HS.

3.2. Response at the physiological and molecular level

Temperature-sensitive physiological action in plants are crucial for expansion and development. Heat shock (HS) decreases photosynthetic efficiency, affecting plant development and biomass production. This decrease is associated with increased non-photorespiratory activities and a decrease in soluble proteins, Rubisco, as well as Rubisco binding proteins [53]. Different research experiments give evidence that heat stress resulted in decreased leaf region, less compelling photosynthetic hardware, before the time leaf senescence, extreme creation of receptive oxygen species (ROS), disturbance of the thylakoid layer, adjusted compound activity, and denaturation of intensity shock proteins (HSPs),

all of which diminish wheat efficiency [54–56]. The plant's water status is basic under HS, as water admission and happening can upgrade the temperature of plant tissue [17]. Covering temperature altogether affects leaf relative water content, leaf water potential, pace of happening, and stomatal conductance [5,57]. Due to increasing evapotranspiration rates, larger vapor pressure deficiencies result in lower LWRC and LWP values [58]. However, little proof exists about what HS means for the yield's supplement status. Nitrogen uptake and transport in wheat decline under high temperature because of diminished nitrate reductase action [59]. The elements phosphorus, potassium, sulfur, and sodium work together to preserve cell membranes and maintain a redox state [60]. These nutrients sustain photosynthetic electron transport activity, minimizing ROS and maintaining a redox state. HS causes significant oxidative damage to plants, generating superoxides, hydroxyl radicals, and hydrogen peroxide [61]. During the stress plant's response system, consisting of transcription factors (TFs) and HSPs, helps clear accumulated ROS and sustain metabolic activities and production. Signal transduction molecules like calcium-dependent protein kinases, mitogen-activated protein kinases (MAPKs), sucrose, and phytohormones are involved in the stress reacting [62] shown in Fig. 1. In addition, [63] reported that during HS, sensitive genes, lead to bringing down LWRC and LWP values because of expanded evapotranspiration rates. These findings indicate that using advanced genetic tools coupled with eco-physiology can identify novel genes that are promising to tackle grain filling during heat stress.

3.3. Mechanisms of heat tolerance

Plants have three main adaptation mechanisms for heat stress: evasion, departure, and resilience. High temperature tolerance in wheat involves antioxidant defense, heat shock protein production, and maintaining greenness [64]. These mechanisms enable plants to survive, thrive, and return profits in high-temperature environments. Sessile plants evolve defense systems, such as immediate avoidance strategies and long-term evolutionary tolerance mechanisms, to deal with environmental challenges. These defense and repair systems provide plants

with HS tolerance by preserving and repairing damaged proteins and membranes.

3.4. Mechanisms and role of ROS

Plants under heat pressure produce responsive oxygen species (ROS), like singlet oxygen, superoxide, and hydroxyl radical ($\bullet\text{OH}$), that disturb the harmony between the age and searching of ROS in ordinary cells [61]. This leads to oxidative stress when the amount produced exceeds the cell's capacity to scavenge them. Increased ROS generation triggers free radical scavenging-related enzymes to stimulate the antioxidative protection system [65]. To shield plants from oxidative harm, a cell reinforcement protection mechanism should detoxify ROS. Enzymatic cell reinforcements, for example, superoxide dismutase (Turf), ascorbate peroxidase, catalase (Feline), glutathione peroxidase (GPX), glutathione reductase (GR), and peroxidase (POX), assume an essential part in searching ROS [66]. The different level of stress influences the synthesis of antioxidant enzymes such as SOD, CAT, and POX activity increasing during heat stress. Singlet oxygen or superoxide is synthesized when an oxygen molecule receives a [67]. Superoxide radical reduces metal ions in cells through spontaneous dismutation or catalytic activity of SOD [68]. The Haber-Wiss reaction changes hydrogen peroxide into $\bullet\text{OH}$, controlled by two phases. $\bullet\text{OH}$ is particularly reactive and can cause cell death [67]. However, by scavenging hydrogen peroxide with peroxidases like guaiacol peroxidase or APX and CAT, $\bullet\text{OH}$ can be reduced [69]. Oxidative stress and ROS production are related, however ROS may also act as a molecule of signaling under diverse abiotic conditions and promote resistance [70] Fig. 2. Therefore, ROS should not be destroyed and kept to minimize to the greatest extent possible oxidative damage. These studies indicate that SOD, and GPX, play a significant influence in the scavenging of ROS during stress conditions and enhanced defensive mechanisms at the time oxidative stress.

3.5. Antioxidant defense system mechanism

Cell organelles generate ROS and membranes in small quantities, and

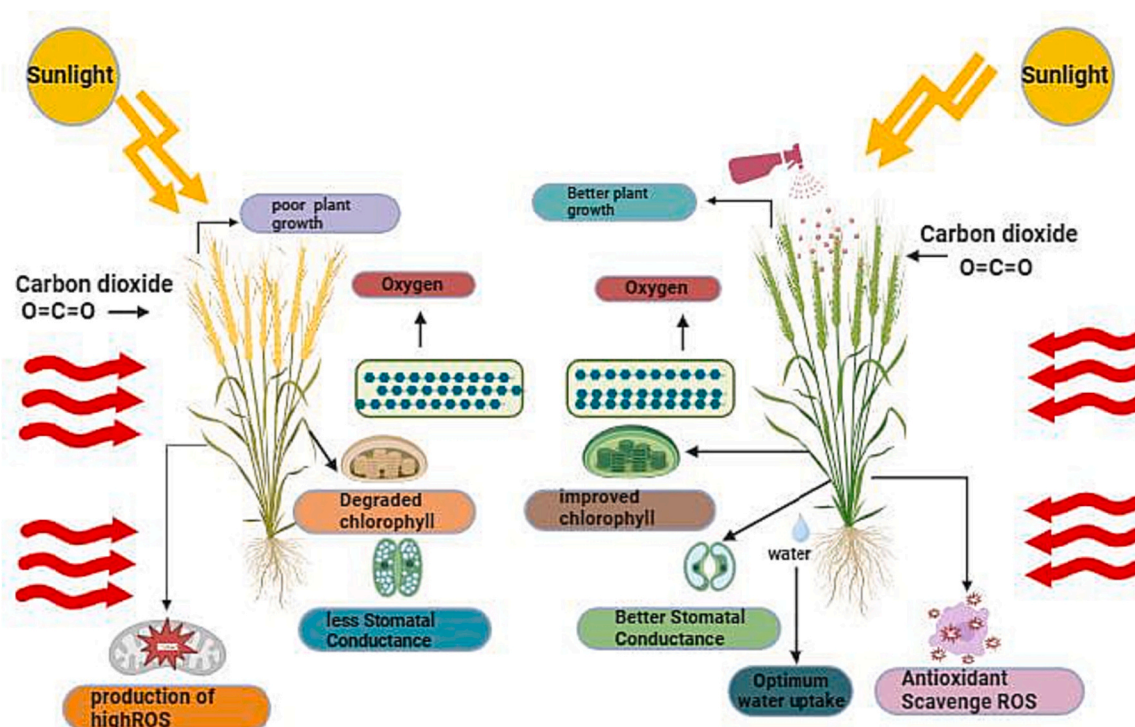


Fig. 1. Physiological and molecular aspects of wheat under heat stress (HS).

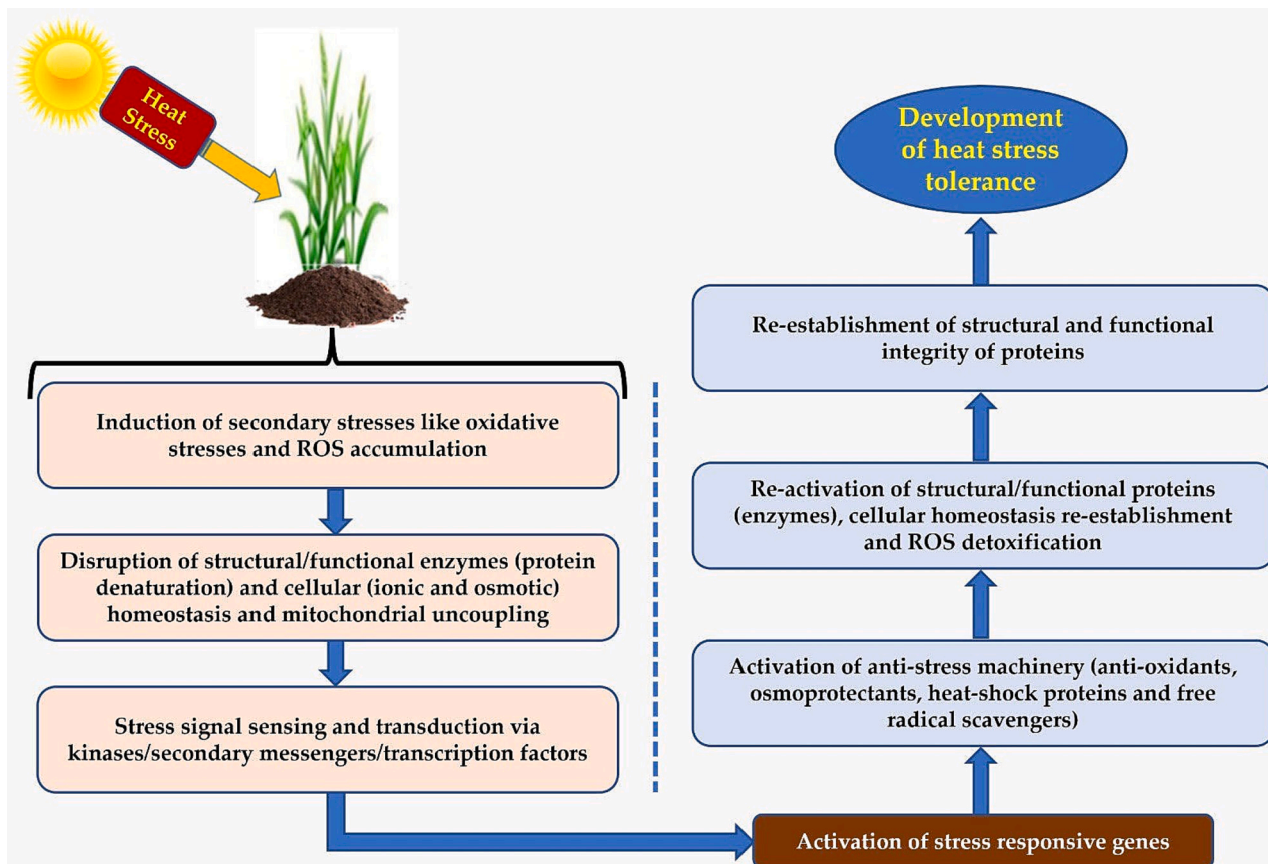


Fig. 2. Mechanism of ROS and activation of genes during heat stress (HS).

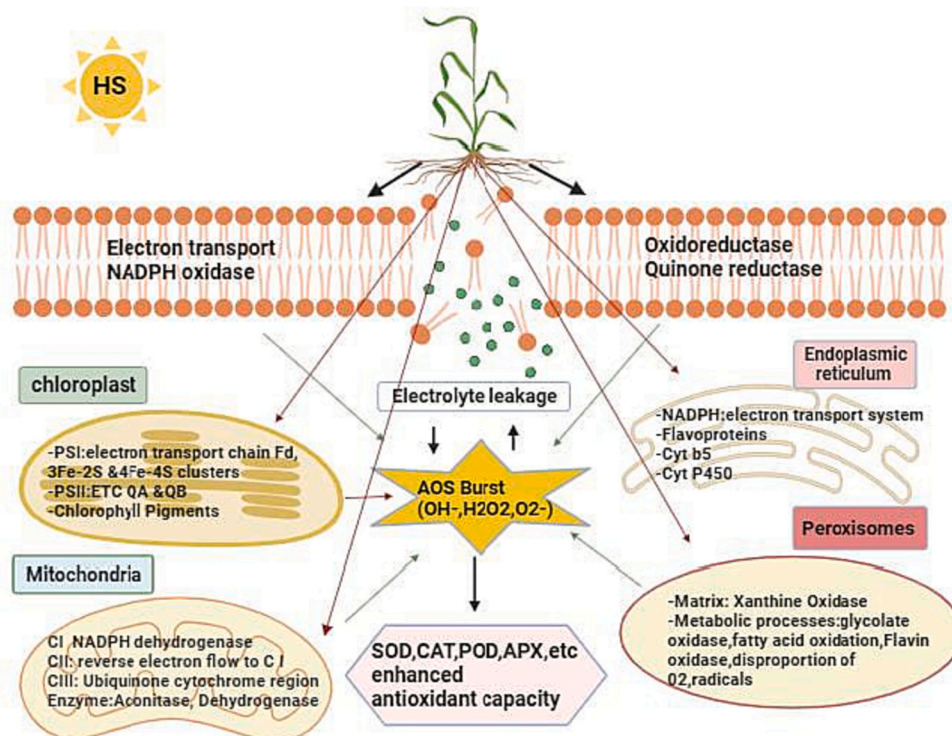


Fig. 3. Mechanism of antioxidant during heat stress.

they are necessary for several metabolic activities [8]. High stress (HS) induces an increase in ROS production, which is harmful for membranes, Deoxyribonucleic acid, proteins, and chlorophyll [70]. Accumulated ROS require detoxification to preserve plant integrity and growth. Ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), polyphenol oxidase (PO), peroxidase, and superoxide dismutase (SOD) are only a few of the enzymes and non-enzyme antioxidant defense mechanisms found in plants [65]. By controlling oxidative damage, these antioxidants defend cells when they detect HS shown in Fig. 3. The amelioration of plant growth by modulating various antioxidants against oxidative stress was revealed by [71–73]. These findings indicate that antioxidants reduce the ROS during the oxidative stage and improve wheat growth.

3.6. Plant growth regulators (PGR's)

Plant development controllers (PGRs) are substances that impact physiological cycles inside plants like development, advancement, and stress reactions [74]. They can improve wheat tolerance to heat by modifying hormone levels, encouraging stress adaption, and increasing water intake, all of which can help reduce the harmful impact of HS on crop development and advancement [75]. Cytokinins, hormones produced by plants that influence cell division and growth, have been discovered may defend from high temperature [76]. They boost photosynthesis, decrease leaf aging, and promote the efficiency of water [77]. They also control heat shock proteins, which protects defense the plants from heat damage [78]. It was already established as ABA and its equivalents, which govern stomata closure and water intake, improve water consumption effectiveness and drought tolerance [79]. Another plant hormone, ethylene, stimulates crop development by boosting heat stress sensitivity gene expression and influencing fruit ripening is an example of a physiological process and stress reaction [80,81]. It was experimentally demonstrated that PGRs like gibberellins can enhance crop development under high temperature, but their effectiveness depends on the crop species and heat stress severity [82]. Studies show that PGRs like proline and salicylic acid can reduce heat stress effects [83,84]. Proline treatment increases heat tolerance and reduces oxidative damage, while salicylic acid increases heat tolerance and decreases oxidative harm by expanding cell reinforcement chemical movement [85,86].

3.7. Chloroplast heat stress cross-talk

Plant photosynthetic systems serve as essential loci for cellular causing disruption, recognition, and adaptation to environmental stress [87]. Plant chloroplasts are sensitive to environmental stress, with the TOC-TIC complex transcribing and transferring nearly 95 % of proteins in the cytoplasm to the chloroplast membrane [88]. The TOC-TIC protein implication system is required for chloroplast homeostasis and protein import regulation. This apparatus's activity is selectively down-regulated in stressful situations, reducing plant photosynthesis [89,90]. The TOC and Spasm qualities, which encode chloroplast protein import hardware parts, are activated by blue light [88]. The TOC-TIC framework is a protein import system that monitors protein import flux during pressure, minimizing photo-oxidative damage caused by photosynthetic protein import while enhancing non-photosynthetic protein import connected to ROS scavenging and stress tolerance [91]. Temperature correction is performed by circadian clock genes such as CCA1, LHY, GI, PRR7 and 9, and EC components [92]. Heat stress response is linked to chloroplast genes, with plants responding better during daylight [92]. A plant protein termed photochromic interacting factor 4 (PIF4) activates heat stress genes in plants, but only during the day [93]. Heat stress harms chlorophyll production by producing chlorophyll breakdown, diminished leaf area expansion, and impaired photosynthetic machinery [94]. This causes premature leaf senescence, reduced wheat production, and substantial diurnal temperature change. Photosystems I and II,

photosynthetic pigments, and carbon dioxide reduction routes are all involved in photosynthesis, and the electron transport chain. Zeaxanthin reduces thylakoid membrane leakage and cyclic electron transport susceptibility to high temperatures [95,96]. Heat stress also produce irreversible alterations in Rubisco and Rubisco activase, result in a reduce in photosynthesis process [97]. Oxidative stress deactivates chloroplast enzymes and soluble proteins, lowering photosynthetic rate even further [98].

3.8. Hormonal response

In plants, stress resilience is intervened by a mind boggling organization of physiological, biochemical, sub-atomic, and hormonal frameworks [99]. Phytohormones like abscisic acid (ABA) govern stress responses and can be altered flexibly in response to environmental challenges [57]. Due to a lack of water and salt stress circumstances, ABA is essential for stomata closure, preventing excessive water loss [100]. It also activates signaling pathways and regulatory genes to allow the body to adapt to abiotic challenges such as drought and heat stress [101]. The protein 9-cis epoxy carotenoid dioxygenase (NCED) is up-regulated in response to drought or heat stress, but initially accumulates and then diminishes in response to combined stress. Auxin and cytokinins regulate source photosynthate/nutrient remobilization, which is essential for cereal grain filling and development [102–104]. Auxin upregulation improves sink capacity and nutrient assimilation. Abiotic stress-responsive genes in plants are identified using molecular approaches such as microarray and transcriptome analysis [105]. Cytokines, plant bioregulators, aid in the reduction of unsaturated fatty acid oxidation, the protection of membranes, and the rise of harvest index [76]. They enhance membrane stability and neutralize free radicals, preventing lipid peroxidation and membrane damage [106]. More research is needed to understand the role of plant hormones in heat stress and thermo-tolerance.

3.9. Starch biosynthesis

Heat stress considerably lowers starch production while increasing protein and total soluble sugar in wheat grain, which constitutes 60–75 % of its dry weight [107]. Heat shock above 30 °C, on the other hand, improves grain starch and insufficient dry matter growth [25]. Temperatures above 40 °C reduce starch synthase activity, which inhibits grain development and starch buildup. High seedling temperatures also diminish soluble sugar buildup and biomass output [34].

3.10. Leave senescence delayed

Staying green is an essential feature for genetic advancement and helps plants tolerate abiotic stress. The rate of chlorophyll degradation, which hinders photosynthesis and lowers yields, determines the rate of senescence [12]. Functional features, which postpone the start of senescence, and non-functional/cosmetic traits, which maintain leaf color but decrease photosynthetic activity, are the two different forms of stay-green traits [108]. Wheat and sorghum crops are the only ones where breeding attempts for this characteristic have been successful. [109] stated that wheat cultivars among a TaNAM RNAi line that has poor nutrient remobilization from leaves are more prone to delayed senescence. Furthermore, [110] revealed that in wheat genotypes exhibiting delayed senescence/stay green features, a significant clear connection in those qualities and yield-enhancing attributes was found. The creation of thermos-tolerant wheat cultivars having delayed senescence/stay greens properties. Features holds promise for maintaining wheat productivity under abiotic stress [58].

3.11. Canopy temperature depression

Canopy Temperature Depression has an effect on wheat plant

transpiration and canopies (CTD), what is the degree difference that exists between the canopy's surface and the air [111]. It is influenced by both biological and environmental elements, including the moisture content of the soil, wind, evapotranspiration, shadiness, conduction frameworks, plant digestion, air temperature, relative moistness, and persistent radiation [112]. Due to high vapor pressure deficit circumstances, CTD is best measured in situations of high relative humidity and high air temperature [113]. Additionally, [114] illustrated the fact that in Northwest Mexico, CIMMYT started monitoring CTD in irrigated studies in 1980. Using mass selection during the initial generations such as F3, CTD has been used as a criteria for selection in wheat breeding for droughts and high-temperature stress tolerance [115]. A crucial physiological component for high-temperature stress resistance is a cool canopy during grain loading. Moreover, [116] reported that on bright, sunny days, CTD was seen at 12 h, 14 h, and 16 h at 7-day intervals. As indicated, a correlation study found a high association between yield characteristics such as the amount of grain produced, grain production, biomass, and temperature by [117,118].

3.12. Acquired temperature sensing and signaling and thermo-tolerance

After a brief exposure to a sub-lethal temperature, a plant can become tolerant to extreme heat stress (HS) under the condition of acquired thermo-tolerance [49]. plant cells, the plasma membrane acts as the primary sensor, enabling early detection of small temperature changes and stimulating the momentary opening and depolarization of certain heat-sensitive Ca²⁺ channels [120]. The main heat-sensing organelles in plants are called cyclic nucleotide-gated channels (CNGCs). Plants gradually experience an increase in temperature from sub-lethal to fatal over time, with molecular and physiological changes assisting in the acquisition of HS [121]. The heat shock response (HSR) is a natural mechanism through which plant tissues respond to HS by momentary gene expression reprogramming patterns [122]. Two essential components, the timely perception of stress and the signal transduction cascade, are necessary for a plant to respond well to a stress tolerance mechanism and survive [123]. Numerous signaling pathways and their constituent parts have been found using two-way genomic analysis and gene expression research [124]. The cell redox system plays a significant role in stress signaling, and genome reprogramming triggers biological signaling pathways that include ROS, Ca²⁺, and hormones produced by plants [125]. Temperature change causes a physical state transition in the membrane, which is crucial for detecting and controlling gene expression. The expression patterns of numerous enzymes are eventually impacted by the multiple changes that at the membrane level, HS causes, including thylakoid membrane rigidification and a change in the ratio of saturated to unsaturated fats [126,127]. Under extreme temperatures, the Ca²⁺ ion is essential for temperature sensing and signaling.

4. Molecular mechanism

Molecular mechanisms besides physico-chemical and hormonal techniques, are also equally helpful in understanding the concept of heat stress in crops.

4.1. Heat-shock proteins (HSPs)

Protein synthesis, as well as folding, are crucial for cell function, but misfolded proteins significantly impact cell function [128]. Heat stress alters these processes, producing stressors that disrupt critical metabolic processes such as replication of DNA, transcription, protein transport, and translation. HSPs, produced as a defense mechanism, are divided into families based on molecular weight, amino acid sequence similarities, and functional properties [129,130]. HSPs have various functions related to heat stress, including acting as transcriptional activators and regulating gene expression through mechanisms like temperature

sensing, signal transfer, and binding to DNA [131]. HSPs act as molecular chaperones to prevent protein denaturation and aggregation at the time HS [22]. HSPs have various functions related to oxidative stress, including acts as transcriptional activators i.e. signal transduction and sensing MAPK, CDPK and gene expression during heat stress shown in Fig. 4.

Heat shock genes (HSGs) are water-soluble proteins that provide plants with the ability to withstand heat shock [130]. The HSP20, HSP60, HSP70, HSP90, and HSP100 families of HSPs are five that have distinct characteristics [132]. While HSP60 and HSP70 are essential conserved proteins for battling HS, HSP20 is in charge of destroying improperly folded proteins [133]. At their promoter region, HSGs contain a heat shock element (HSE), which causes HSG transcription [130]. When a plant experiences heat shock, HSFs form trimers and are mostly expressed under normal circumstances. HSP90, sometimes referred to as ClpB, is involved in the trafficking and activity of signaling proteins during HS. HSP100 aids in correct protein folding and disaggregation [134]. Overall, HSPs control the function of several signal transduction proteins during HS by maturing protein complexes and degrading peptides that are broken or misfolded [135]. This study addressed the HSP play a significant influence in transcriptional activators and regulating gene expression through mechanisms like temperature sensing, and signal transfer during the stress condition.

5. Recent approaches to improve stress tolerance in wheat

Heat-tolerant genotypes and tried-and-true agronomic techniques are necessary to maintain productivity of wheat under scenarios of changing in the climate [144]. Following is an explanation of how improvements in nanotechnology, breeding and biotechnological, and other agronomic techniques increase heat tolerance and enhance wheat yields in high-stress environments [145].

5.1. Nanotechnology as a new emerging science

Nanotechnology is one of the essential agricultural applications among many other applicable techniques, and it has been used for this purpose for many years. Nanomaterials are thought to increase productivity by reducing nutrient loss during fertilization and optimizing nutrients. Nanotechnology has been utilized to synthesize a variety of tools and technologies, including viral capsids, nanoparticles, and nanofertilizers [146]. Nanosensors, nanofertilizers, and nano-based insecticides are only a few examples of innovations and products that use modified nanomaterials in farming techniques to improve the efficiency of agricultural practices. Then again, fast-emerging engineered nanomaterials; silver nanoparticles is present in a variety of consumer products. Due to their environmentally favorable uses in the agriculture industry, many metal-based nanomaterials, particularly silver nanoparticles, have recently attracted significant attention. However, in the agronomic division, a more environmentally friendly technology for silver nanoparticles has been widely adopted as a [56,147].

Resources can be influenced and controlled by using implements with nanoscale dimensions (typically >100 nm) [148]. However, in the case of crop expansion and resilience to stress, when crops are exposed to heat-stress conditions, nanotechnology can increase crop growth and production. Nanoparticles have shown promise in lowering temperatures in wheat crops, increasing plant yield and resistance to heat stress [149]. Under heat stress, They can be used to boost nutrient uptake and utilization in order to stimulate crop development [150]. Nanoparticles made of silicon and zinc oxide, in particular, can increase the absorption of nutrients by crops by reducing the severe impacts of heat stress on plants [151,152]. Furthermore, they promote plants' resistance to heat stress. Nanoparticles like silver or copper, for example, The activation of heat shock proteins may protect plants from extreme heat [149]. Some nanoparticles, such as nanotubes of carbon and titanium dioxide, may reduce oxidative stress in plants under heat stress while neutralizing free

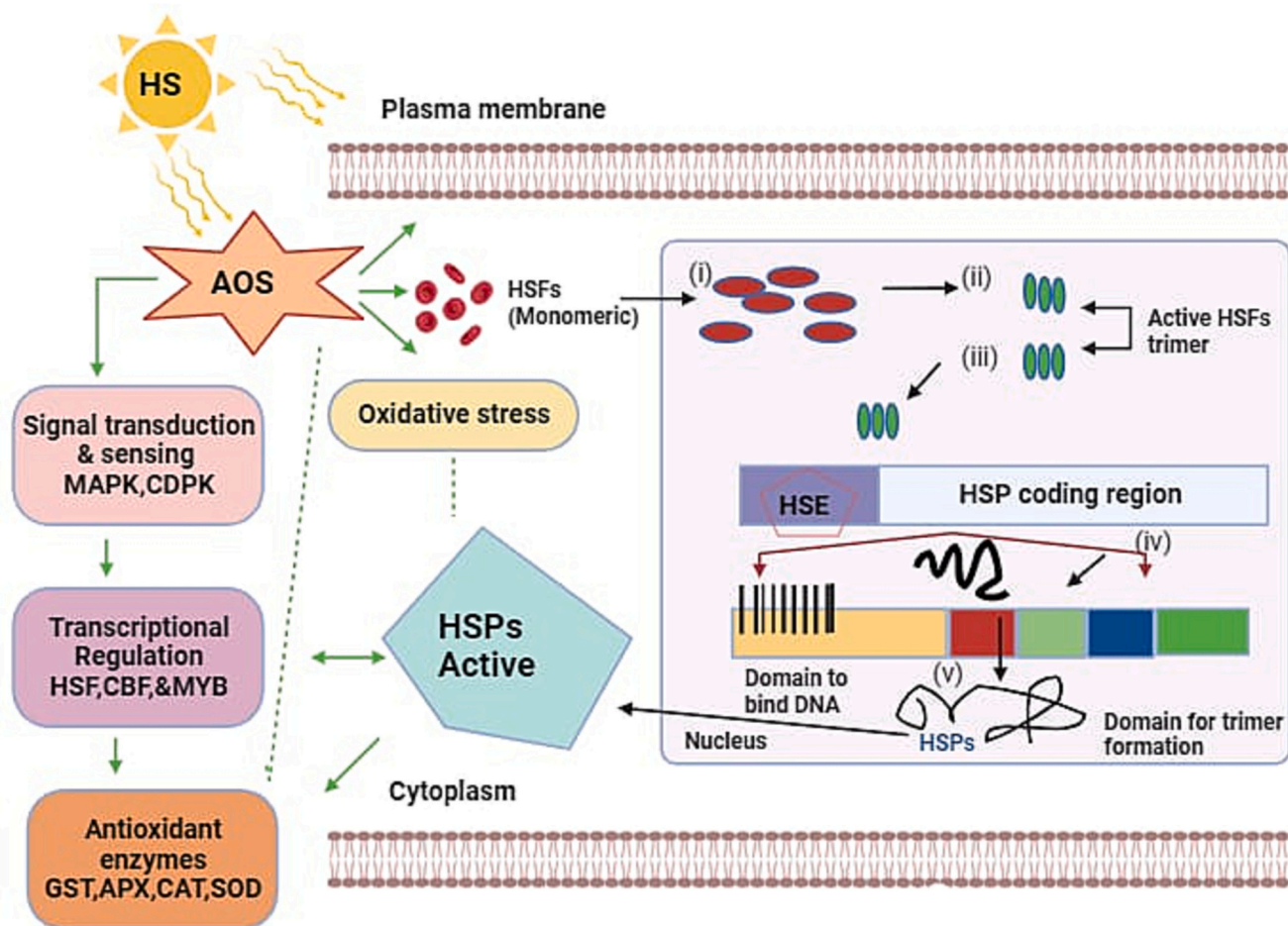


Fig. 4. Mechanistic overview of HSP response during oxidative stress.

radicals [153]. Crop development and adaptability almost stress can be evaluated as well as modified by employing nanosensors and nanoscale imaging techniques, in addition to nanoparticles [154]. For example, nanoscale imaging can detect plant stress zones and plant-microbe interactions [146].

Additionally, soil moisture content and availability of nutrients may be screened using nanosensors [155]. Different nanoparticles have been accounted for to increment plant resistance against heat pressure conditions. Gold nanoparticles (AuNPs) have been demonstrated to increment cell reinforcement action against oxidative pressure, prompting

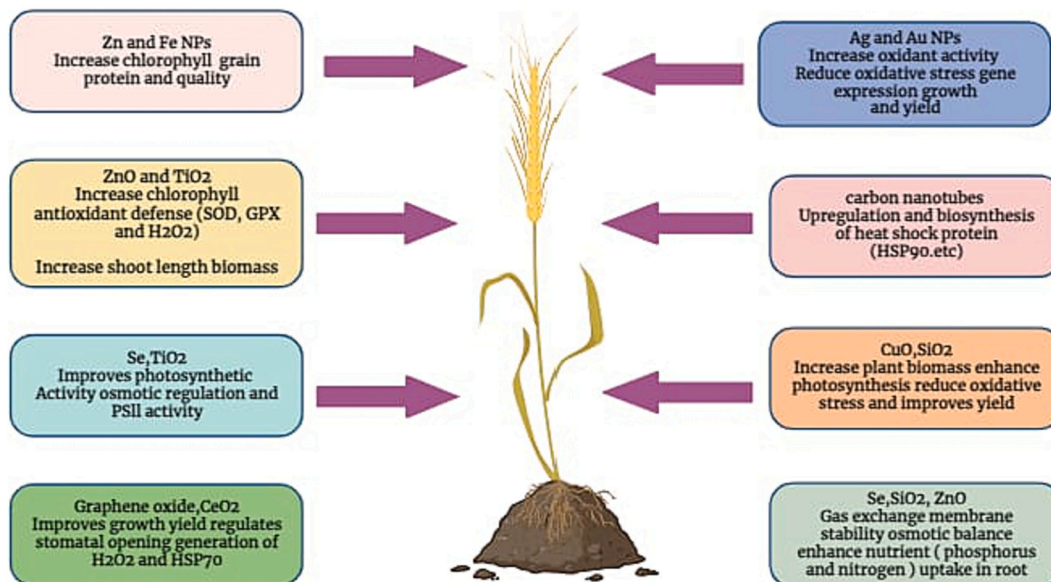


Fig. 5. A proposed model diagram representing the role of different Nanoparticles (NPs) in wheat against heat stress.

Wheat production and improvement under heat stress [156]. According to research reported by [71] silver nanoparticles (AgNPs) potentially relieve the harmful effects of stress from heat on wheat by boosting various biochemical activities. Additionally, numerous nanoparticles including (SiNPs, ZnNPs, and TiNPs) have been shown to reduce oxidative stress by enhancing antioxidant activity and encouraging plant development and agricultural productivity [152,157] Fig. 5.

Nanomaterials trigger the transcription factor and express the genes to activate antioxidants for example, SOD, CAT, POD, and GPx during wheat under conditions of high temperatures [158]. As a whole, we directed to emphasize recent data on factual information showing that nanoparticles or nanocomposites provide an effective solution to enhance and develop agro-based innovative ideas in food security, particularly in wheat against heat stress.

5.2. The promising future of CRISPR/Cas9

The DNA editing technology CRISPR/Cas9 has transformed plant breeding and genetics by adapting the genome of important crops to a variety of abiotic challenges, including heat, drought, and salt [159]. It may modify target genes by insertion, deletion, and knock-in/knock-out alterations, enhancing agricultural plants' capacity to scavenge reactive oxygen species (ROS). Various plant species, such as, including rice, wheat, and wheat, have benefited from using the technique to increase their tolerance to heat [160]. OsNTL3 in rice is in charge of heat tolerance, whereas TaMBF1c in wheat is increased during heat stress and controls translation.

5.3. Molecular breeding modifications

Because they need a lot of time, traditional breeding methods have limits. By evaluating variety and identifying QTLs, molecular techniques like as simple sequence repeats (SSRs) can aid in breeding for climate resilience [161]. SSRs are the best markers for these uses because of their abundance, homogeneous distribution, co-dominance with the natural world, and great polymorphism. These findings indicate that using advanced molecular breeding, QTL mapping plays an important role in climate resilience varieties.

5.4. QTL analysis

Using molecular markers, QTL analysis is a technique for locating genetic areas controlling considerable variance in a given characteristic [162]. It requires the use of a mapping population created from parental lines that contrast for features related to HS tolerance. The identification of significant and minor genetic areas that confer HS tolerance has advanced quickly because of QTL analysis [58]. Using Langdon chromosomal substitution sequences, QTL mapping was started in wheat in 1991, which led to the discovery of on chromosomal 3A and 3B, there are HS-tolerant genes. In wheat, several QTLs for HS-related characteristics have been identified, but the direct transfer is challenging since the majority of these QTLs have small effects and wide genomic spacing. Nevertheless, a small number of significant QTLs have been found, which are easily transferable and targetable for candidate gene discovery by precise mapping.

An SNP-based investigation was carried out to map characteristics related to HS tolerance, including wheat chlorophyll content, thylakoid, and plasma membrane damage [163]. With a phenotypic variance of approximately 30 %, the study identified two significant SPAD chlorophyll concentration and QTLs for thylakoid membrane degradation. Indicators of HS resistance include chlorophyll fluorescence kinetics (CFKs), and mapping experiments a substantial QTL for maximum fluorescence was discovered in a population of double haploids [58]. For the maximal quantum efficiency of photosystem II (FV/FM ratio), three significant QTLs accounting for >20 % of phenotypic variation were

found using a non-destructive method. Significant QTLs for the yield of grains per plant, 1000 kernel weight, and cereal yield were identified in wheat HS tolerance breeding projects can be targeted for introgression [162]. By verifying found candidate genes or QTLs, it is crucial to identify and minimize linkage drag effects connected to yield reductions or other unfavorable results [164].

6. Genetic modifications

An effective and practical strategy to counter rising temperatures in the ecology of wheat production is creation of heat-tolerant wheat varieties [165]. The first stage comprises screening under testing settings and selecting cultivars that are relatively HS-tolerant. The goal now is to create wheat genotypes that can withstand high temperatures, and molecular breeding is quickly becoming a viable method for creating genotypes that are climate-smart [166]. Additionally, promising for sustainable wheat production are transgenic wheat varieties [167]. Using a combination of traditional and genomics-assisted breeding methods and cutting-edge high-throughput phenotyping platforms can be a successful strategy for creating wheat cultivars that are HS-tolerant [58].

6.1. Traditional breeding modifications

A key component of conventional breeding is the thorough phenotypic characterization of germplasm under certain stress settings [168]. An essential requirement for HS breeding is genetic diversity for heat stress resistance. However, because of the usage of constrained germplasm for the development of new cultivars, previous research in wheat has argued that HS resistance requires an amount of genetic variation. In comparison to contemporary cultivars, wild progenitors had a huge genetic diversity of characteristics related to HS tolerance [169]. Because of their increased conductance and larger leaf chlorophyll levels, landraces are HS tolerant. Wheat breeders have recently changed their attention to using landraces to create cultivars resistant to heat stress [170]. Pre-breeding involves using wild forebears to change the genetic makeup of current germplasm for a variety of attributes. Highly heritable traits associated with the highest grain yields under HS can be chosen for success [171]. Direct selection is challenging due to its polygenic nature and poor heritability of yield-contributing characteristics. Indicator qualities (proxy traits) that have a greater link with wheat grain production under HS can be applied in these circumstances. Spike photosynthesis, photosynthetic rate, leaf amount of chlorophyll, canopy temperature depression (CTD), membrane thermostability, flag leaf stomatal conductance, stay-green length, stems reserves, stem carbohydrates remobilization, pollen viability, and antioxidant capacity are all variables to consider are among the physiological characteristics linked to HS resistance [172,173]. To deal with terminal heat stress, early-heading wheat types are used since they mature at the right temperature. Another important selection factor is the greatest grain yield under HS (grain filling). Root design for HS tolerance has the most compact and uniform growth, with maximum lateral root extension from the stem base and the capacity to create longer roots in deeper soil layers [174]. To reduce the effects of HS, deeper roots enable better soil moisture extraction, which results in transpiration cooling and canopy temperature depression. Selection indices can be used to choose genotypes that function equally well in both stressful and ideal conditions.

6.2. Marker-assisted selection (MAS)

Marker-Assisted Selection (MAS) is an efficient method to boost crop yield that, independent of the target environment, uses indirect selection at a very first stage of the yield to find QTLs (Quantitative trait loci) in lines, varieties, and populations for breeding [161]. Marker-helped backcrossing (MABC), marker-helped intermittent choice (MARS), broad affiliation studies (GWAS), and genomic determination (GS) are

all examples of MAS-based methods [175]. The two main molecular breeding techniques that have been effective in creating cultivars of maize that are climate-resilient are MABC and MARS [176]. Elite cultivars of wheat, HD 2733 and GW 322 were chosen for the introgression of revealed QTLs for high temperature tolerance traits, including decreased canopy temperature, chlorophyll concentration, thousand kernel weight, and grain yield. >90 % of the elite parents recovered in progenies resulting from two back-crosses, according to background selection [177]. In various site experiments, the lines' HS tolerance has to be better characterized. Molecular breeding for the discovery and functional validation of candidate genes will be accelerated by the availability of less expensive sequencing technologies and developments in omics methods [178]. Next-generation sequencing technology, which is quickly developing, has also contributed by offering very dense markers that enable high-resolution mapping of QTLs in GWAS and GS research. Positional cloning or a chromosomal walking method of significant To identify potential genes for HS tolerance, QTLs and transcriptome profiling of HS tolerant and susceptible genotype types can be employed. Consensus Additionally, QTLs It is possible to discover by doing QTL mapping tests under both ideal and stressful conditions [179]. Since QTL meta-analysis bases itself on a meta-analysis of multiple independent studies on the subject characteristics, it is a more statistically effective method of identifying genomic regions. Eight significant meta-QTLs for phenotypes related to drought tolerance and HS were found by QTL meta-analysis on eight distinct chromosomes. Further assisting in the thorough characterization of discovered clusters is fine mapping of these areas. With 37 relevant SNPs found under HS, SNP-based GWAS investigations have demonstrated considerable heterogeneity in spike ethylene production in wheat germplasm [180]. By lowering phenotyping frequency and cycle duration, the GS method, which is based on genome-wide SNP marker information, boosts yearly genetic gains via selection. In contrast to other important crops, wheat has used GS less frequently since the bulk of crossings were abandoned at an early stage. Major QTLs for HS resistance have been found using SNP-based investigations for mapping characteristics related to HS tolerance, including thylakoid and plasma membrane damage, chlorophyll content, and Hanxuan10 [58]. These findings indicate that using advanced molecular breeding, MAS and SNP markers play an important role in climate resilience varieties.

6.3. Epigenetics technique

To survive abiotic stressors, epigenetics involves modifying gene expression, histone changes, and non-protein coding RNAs [181]. The usage of this in heat stress resilience breeding suggests that it may contribute to the transmission of heat stress tolerance. Studies have demonstrated that heat stress tolerance may be conferred through histone hyperacetylation when the GCN5 gene is overexpressed in Arabidopsis. Another genome-wide expression-based investigation on wheat, however, produced conflicting findings with only minor impacts on DNA methylation patterns under heat stress. This underscores the need for more wheat studies to comprehend how DNA methylation and histone acetylation interact to control The emergence of genes that respond through high temperature [182]. HS-responsive genes in wheat are tightly regulated by non-protein coding RNAs like miRNAs.

6.4. Functional genes and genetic engineering

An additional method for creating wheat cultivars that are HS-tolerant is genetic engineering, commonly referred to as transgenic breeding [58]. This approach creates variation for a desired attribute that is not present in a given species and solves the linkage drag issue. The plant health of Heat stress accede to breeding, however, has been hampered by the complicated genetic pattern in wheat [183]. HS increases elongation factor (EF-Tu), a component of protein synthesis, in wheat chloroplasts. The maize EF-Tu1 quality is overexpressed in

transgenic wheat, and this gives HS resilience since the transgenic wheat has worked on photosynthetic limit, stable thylakoid layers, and safeguards against leaf protein denaturation and disease blockage [81].

Maize phospho-enol-pyruvate carboxylase (ZmPEPC) overexpression in wheat improves high temperature tolerance by boosting the activity of photochemical as well as enzymes that act as antioxidants, preserving chlorophyll content for longer periods, modifying proline accumulation, and upregulating genes that regulate the photosynthetic machinery [184]. In rice or Arabidopsis, functional genes that react effectively under wheat's HS conditions have previously been characterized. These functional wheat genes, which are overexpressed under HS and provide thermo-tolerance, include TaHSFA6f, TaFER-5B, and TaPEPKR2. However, more research has to be done on how these genes are affected by genetic background. The practical portrayal of HS-responsive qualities will continue all the more rapidly on account of late advancements in change innovation and the accessibility of freak libraries of wheat [185]. These findings indicate that using advanced genetic engineering tools can identify novel TaHSFA6f, TaFER-5B, and TaPEPKR2 that promising to tackle thermo-resistance during stress shown in Fig. 6.

7. The role of omics approaches in heat stress adaptation

Omics is critical for identifying the transcription factors and proteins which are differentially expressed when exposed to heat stress in different crops. Investigating important genes, enzymes, and metabolites governing heat stress response pathways using omics methods including transcriptomics, proteomics, and metabolomics helps with understanding the adaption process [186]. Phenomics is a likely technique for exact high-throughput phenotyping of elements connected to heat stress, and it is progressively being utilized in broad affiliation studies and genomic determination in many yields. Various HSP family genes are regulated in different ways in plants as a result of heat stress [137]. Using a coordinated omics-based strategy incorporating Genomic, transcriptomic, proteomic, and metabolomic techniques can improve the revelation of critical contender characteristics responsible for overseeing photosynthesis, osmoprotectants, and cell reinforcement compounds. This approach likewise adds to a more significant cognizance of the mechanisms hidden heat stress resilience across various wheat cultivars. [58,168,187]. A reasonable structure is presented by online omics-situated in-silico devices and data sets including the TIGR Genome Data set, Reap Wheat, Exhibit Express, and PLEXdb for an exhaustive examination of plant HS related to wheat genome designing using the CRISPR/Cas Framework.

8. Genomics analysis

An organism's genetic composition is represented by its genome, and genomics gives extensive information on the shapes, roles, linked networks, and metabolic and biochemical activities of individual genes. The discipline has developed over the years with structural genomics discovering regulatory sequences and gene structures and functional genomics facilitating molecular gene function and the sort of tolerance offered [188]. Genome-wide network knowledge about genes and how they interact with intricate stress-resilient characteristics is made possible by genomics. Genomic studies addressed that CRISPR/Cas9 technology and more online genomics Techniques are offered to genetically modify wheat cultivars to be more resistant to HS.

9. Transcriptomics analysis

The study of transcripts, which are expressed portions of a genome, is known as transcriptomics, and it makes use of cutting-edge technologies including RT qPCR, microarrays, and next-generation arrangement [189]. It aids in understanding the physiological & molecular procedures that plants use to respond to abiotic stimuli, particularly heat stress. For rice, wheat, and wheat under heat stress, transcriptome profiling has

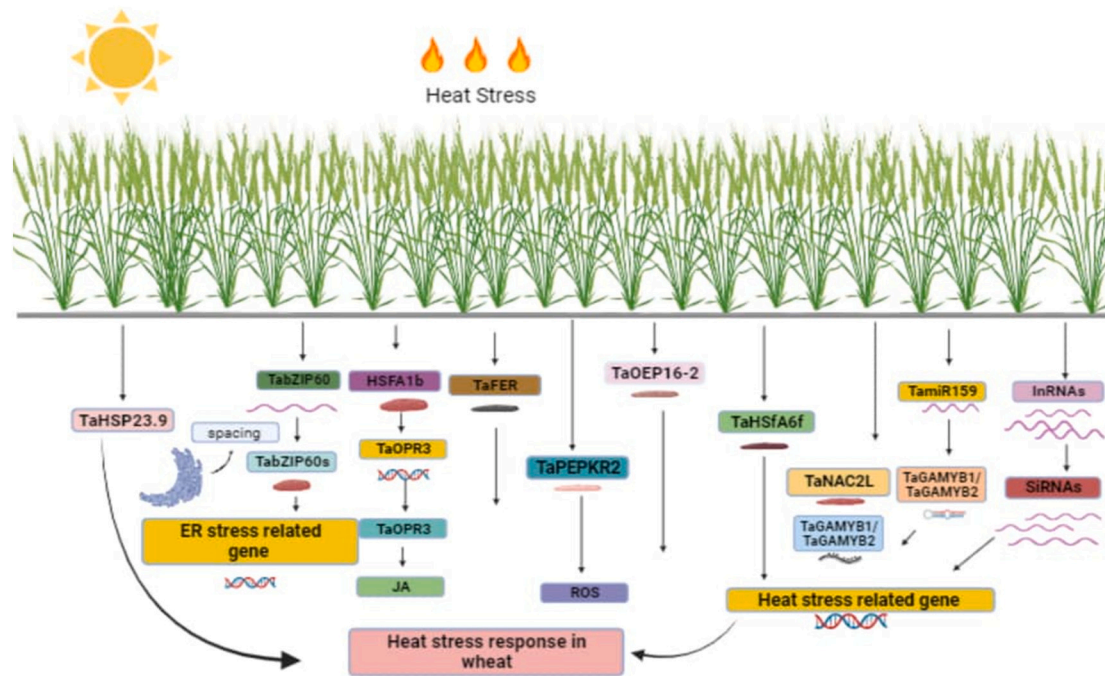


Fig. 6. Stress-related genes expression in wheat during stress condition.

been investigated, revealing several differentially expressed gene (DEG) clusters important in the transmission of signals and photosynthesis. In wheat, 50 DEGs that target the cellular division, stress, amino acids synthesis, Secondary metabolite synthesis, carbohydrate and sucrose metabolism, Other catabolic mechanisms include photosynthetic transport were shown to be active under heat stress [190]. 37 up-regulated DEGs, mostly involved in Mg + 2 binding, "C" fixation, and ribulose biphosphate carboxylase activity were discovered in wheat. However, limited study has been done on how wheat reacts to heat stress at various growth and development phases.

10. Proteomics analysis

Using techniques like MALDI-TOF/MS, 2D PAGE, SDS PAGE, and HPLC, proteomics investigates proteins expressed in a genome to comprehend their response in abiotic stress [191]. Important Heat stress has an effect on proteins involved in cellular metabolism, the process of photosynthesis replication, transcription, and translation [190]. On grains like wheat, rice, barley, tobacco, mustard, proteomic analysis has been done. Signaling molecules, HSPs, and cell reinforcement compounds are significant proteins engaged with the tolerance to high temperature. There are still unknowns, however, about how certain proteins help various wheat cultivars tolerate heat stress and how sensitive and resistant cultivars react to it [192,193]. Understanding proteome examination in wheat under HS resistance requires more review.

11. Metabolomics analysis

The concept of word "metabolomics" refers to a grouping of metabolites that help plants respond to Specific anxieties affect protein synthesis, post-translational modifications, as well as the expression of genes [194,195]. Various metabolic cycles, for example, glycolysis, the citrus extract cycle, the electron transport framework, and the development of cancer prevention agent proteins are affected by heat pressure. The wheat plant produces a variety of metabolites that change in light of stress conditions, making it an effective tool for choosing cultivars that can withstand heat. X-beam crystallography, GC-MS, and TOF-MS are utilized in metabolic examinations to look at how plants answer

heat stress [196,197]. The grain of wheat seeds, Arabidopsis leaves, young rice seeds, and leaves of *Populus tomentosa* all display resistance to heat stress, according to studies [58,198]. Wheat metabolism under various types of heat stress, including chronic and heat shock, is not well understood. Wheat plant growth is considerably enhanced influenced by environmental factors that affect their overall development, which also govern metabolite production. Establishing the source-sink connection for several wheat cultivars under heat stress might offer important insights into enhancing protein content [60]. Innovative methods to improve wheat crop quality in an HS environment can be developed by combining genetic and breeding techniques with contemporary biotechnological capabilities [199].

These studies addressed the study of the metabolites, transcriptomics and transgenic approaches required for expression genes in wheat is significantly influenced by environmental variables, which also govern metabolite production and defense during heat stress Fig. 7.

12. Others strategies

12.1. Agronomic methods

12.1.1. Management of efficient nutrients

Effective nutrition management is crucial for reducing the impacts of heat stress (HS) and maintaining crop productivity. By improving stomatal conductance, chlorophyll content, and photosynthetic rate at high temperatures, nitrogen supply optimization can raise wheat production [200]. Nitric oxide (NO) shields the plant from oxidative Scavenging reactive oxygen species (ROS) causes harm [201]. By increasing membrane integrity and antioxidant thyme, thyme seed treatment and foliar spray application increase heat stress tolerance. Potassium orthophosphate (KH₂PO₄) applied topically activates metabolic and physiological activities such as photosynthesis, respiration, and nutrition balance while also raising tissue water potentiality. Foliar silicon treatment at the heading stage reduces terminal heat stress by enhancing antioxidant and osmo-protective mechanisms [202]. The addition of calcium to CaCl₂ and CaNO₃ increases photosynthesis and activates antioxidant enzymes to boost heat tolerance. Wheat that lacks magnesium and sulfur is more susceptible to HS, thus fertilization is essential to maintaining an

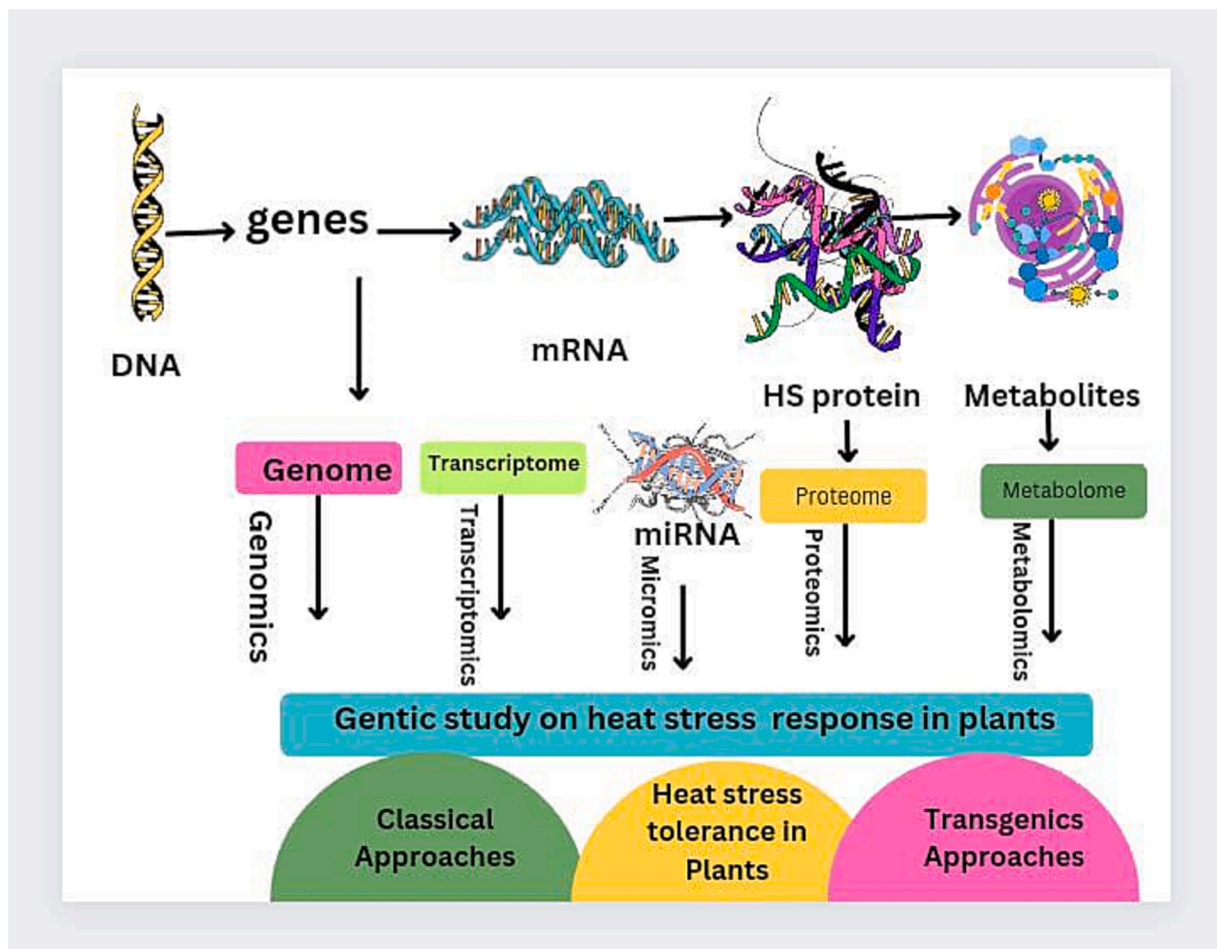


Fig. 7. Overview of genomics, transcriptome, proteome, and metabolomics approaches.

adequate supply. By preserving the integrity of the membrane and the SOD enzymes' function, optimal Zn supply by foliar fertilization gives HS resistance. By boosting antioxidant activities and reducing accumulated ROS, foliar treatment of boron (B) at the blooming stage also increases HS tolerance [202,203].

12.2. Utilization of plant growth regulators

Under high-stress conditions, wheat's photosynthetic rate and physiological capability can be improved by exogenous osmoprotectants such as inorganic salts, stress signaling molecules, nitrogenous substances, and natural and synthetic plant growth regulators [204,205]. For example, selenium in sorghum increases chlorophyll content, antioxidant activity, and osmotic adjustment capacity, lowering oxidative destructive and electrolyte leakage [206]. Plant development regulators were found to affect plant physiology and biochemistry under stress conditions [207,208]. The biomass and tolerance of wheat are increased by progesterone and salicylic acid foliar treatments [209]. Nitrate reductase activity and RLWC are improved by CaCl₂. By enhancing grain number and weight at high temperatures, silver nanoparticles and plant growth regulators including ABA, IAA, and GA have been shown to boost wheat grain output [210].

12.3. Utilization of cultivated soil microbes

Whenever presented to refined microorganisms from the dirt so as arbuscular mycorrhizal parasite (AMF) or plant development empowering rhizobacteria (PGPR), plants might be better ready to endure heat

pressure [211].

These microbial inoculants can be utilized as an environmentally friendly seed treatment or seed priming [212]. By lowering oxidative damage and stopping ROS formation under high temperatures, seedlings with PGPR strains such as *Bacillus amyloliquefaciens* as well as *Azospirillum brasilense*, for instance, increased high temperature tolerance in wheat seedlings [213]. Additionally, *Pseudomonas putida* strain AKMP7 increased root and shoot length, cellular metabolites, and antioxidant enzyme activity, enhancing wheat survival and development under heat stress. The AMF symbiosis in wheat encourages growth and development by decreasing the potassium-to-calcium ratio, increasing the amount of accessible photosynthates, and increasing grain production [214]. The potential benefits of PGPRs and AMF to their hosts should be confirmed through further studies on their resilience systems.

12.4. Modification to planting timing and technique

The negative consequences of heat stress on wheat can be relieved by changing the timing and strategy of planting. Reduced grain test weight occurs in wheat planted sometime in the future since it is more inclined to have terminal HS during post-blossoming or the stage of grain growth in which grains are filled [58,215]. Conservation measures are being implemented agriculture (CA)-based management practices can advance sowing by 15–20 days in India's northwest area. Previous study has been reported to conserve soil moisture under stress conditions [216]. Early planting is necessary to avoid terminal HS. Depending on the crop type and genotypes utilized for biomass production capacity, The canopy temperature can be lowered by 1.5–3.0 °C using CA-based

management practices like as no cultivation, perennial bed growing, including elevated bed systems with furrow irrigation [217]. For the maximum yield in HS-prone areas, using CA methods to assure early or timely planting, notably in South Asia's rice-wheat farming scheme, may be a suitable strategy. [58].

12.5. Accurate irrigation and conservation of soil moisture

In regions with precipitation wheat-growing habitats, in particular, water management is essential to preventing high salinity (HS) from negatively affecting crops [58]. Sprinklers and drip irrigation are two watering methods that can lessen the impact of drought stress and (HS). While drip irrigation retains moisture and lowers canopy temperature, sprinkler systems lower soil and canopy temperatures [218]. Mulching enhances soil moisture, aeration, seedling and root development, and soil aeration. Furthermore, soil moisture can prevent HS and reduce canopy temperature by transpiration cooling. Different scientists [219,220] in their examinations showed the useful impacts of mulching in keeping up with soil dampness.

13. Conclusion and future prospective

Changes in global temperature, wheat has trouble with the effect of heat stress. In no <20 years, the typical world temperature is supposed to increment by 1.5 degrees Celsius, which would affect the turn of events and development of wheat. It is alluring to comprehend the physiological, biochemical, and hereditary administrative components that execute different seed shaping occasions under pressure conditions to further develop crop creation and quality. Under pressure, plants incorporate various metabolites, like cell reinforcements and HSPs. Molecular research on such metabolites is critical to understanding the mechanism behind stress tolerance. As a result, research into molecular response and nanotechnology comprehension and acceptance processes for harvest sustainable grain yields is required. Very little is realized about the drawn out effect of environment changeability on wheat yield; thusly, there is a need to foster variation systems to lessen its adverse consequence. A functional genomics approach and use of nanofertilizers can help wheat respond to heat stress. Over-articulation of record elements, carriers, and qualities associated with phytohormone biosynthesis, miRNAs, and other pressure responsive qualities have been accounted for to be promising methodologies for battling various abiotic stresses. Likewise, by consolidating and controlling stress-related qualities in crop plants, the 'omics' strategy might support the improvement of transgenic plants. To accomplish powerful intensity resistance, the transgenic approach should be joined with marker-helped rearing projects for heat pressure related qualities and QTLs.

These findings indicate molecular approaches and nanomaterials associated with yield contributing traits at anthesis stage or heat stress are key findings for heat resilient varieties. Moreover, identified genes, their expression and nanomaterials that enhance the antioxidant can be linked with eco-physiology, antioxidants profile to see the potential of identified genes in crops. These strategies can further be utilized in other crop species for alleviating stress.

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CRedit authorship contribution statement

All authors of this review article have significantly contributed to writing the research paper and critically revised the review article. All

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CRedit authorship contribution statement

Fozia Abasi: Writing – review & editing, Visualization, Validation, Resources, Investigation, Conceptualization. **Naveed Iqbal Raja:** Supervision, Resources, Formal analysis. **Zia-ur-Rehman Mashwani:** Supervision, Resources, Data curation, Conceptualization. **Maria Ehsan:** Writing – review & editing, Validation, Data curation. **Habib Ali:** Writing – review & editing, Methodology, Data curation. **Muhammad Shahbaz:** Validation, Resources, Data curation.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

All the obtained data are presented in this article.

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