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REVIEW ARTICLE

Effects, Responses and Management of Heat Stress in Wheat, An Overview

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ABSTRACT

Wheat is a major cereal crop that fulfills the world's food and fiber demand. Currently, an increase in the temperature causes a drastic effect on wheat yield. The nutritional composition of the wheat grains somewhat depends on soil and climate conditions. High temperatures cause a decrease in wheat yield as heat stress severely damages the plant's physiological, morphological, and biochemical processes. Wheat production decreased by up to 6% with each 1-degree rise in temperature. Heat stress significantly affects both the vegetative and reproductive stages of plants. High temperature inhibits seed germination, loss of pollen viability, less seed setting and grain number, and also affects grain quality, which causes a reduction in yield. High temperatures trigger different mechanisms in wheat against stress, including the production of heat shock proteins, the oxidative defense mechanism, and the delay in senescence (loss of chlorophyll). This review focuses on management practices and genetic engineering techniques against heat stress in wheat plants.

Key words: *Triticum aestivum*-Wheat-Heat stress- Heat shock proteins- Genome editing

INTRODUCTION

Triticum aestivum, is a cereal crop that belongs to the Poaceae family. It is a significant cereal grass cultivated globally and serves as the primary crop in Pakistan (Abid, 2018). Wheat is an annual plant with shallow fibrous roots, 3-12 stems called tillers, and a single head known as a spike (Tripathi et al., 2003).

The wheat plant, which expresses different phenotypes based on the genotypic constitution, is characterized by having long and hollow stems, leaf shape, area of flag leaf, and phenotype of spikes (awn and awnless) (Takumi et al., 2009). In different genotypes, the number of tiny blooms packed inside the inflorescence varies from 20 to 100. The flowers are in cluster form with two to six atop structures known as spikelets (Woo et al., 1999). These spikelets consist of up to 12 florets but only two or three grains are formed due to flower fertility inhibitor genes (Konopatskaia et al., 2016). Wheat can be cultivated in most of the soils and climates but it is best acclimatized in temperate regions where annual rainfall is 30-90 centimeters (Ouda et al., 2015).

Wheat is rich in nutrients such as protein and carbohydrates. The nutrition quality usually varies by both climate and genotypes that are being used in a particular area. Although thiamin, riboflavin, and niacin are present as well as trace levels of vitamin A, the majority of these elements, along with the bran and germ, are removed during the milling process (Onipe et al., 2015).

Wheat kernel composition

Parameter	Amount
Carbohydrates	70%
Water	12%
Protein	12%
Crude Fiber	2.22%
Fat	2%
Minerals	1.18%

Wheat is mostly used for making pasta, biscuits, muffins, crackers, and other baked products. However, the highest wheat grain is used for making bread to fulfill the daily meal requirements in most countries (Igrejas & Branlard, 2020). Wheat grown in high-temperature regions has a low protein level (11–15%)

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and strong gluten, which is an elastic protein and makes it perfect for making bread. The presence of the gluten protein component, which gives the dough its viscoelastic characteristics and enables it to be formed into bread, pasta, noodles, and other food products, is another essential component that contributes to its success (Onipe et al., 2015). Wheat grown in high-humidity regions tends to have a lower level of gluten and low protein concentration around 8-10 percent (Nuttall et al., 2017).

Wheat is a cheap and good source of energy for both humans and animals as food and feed respectively. Wheat is an excellent complement to the human diet because of the beneficial phytochemicals, essential amino acids, minerals, and vitamins, in addition to the dietary fiber that it provides (Shewry, 2018). However, on the other hand, these products include allergic and intolerant diseases (especially celiac), which can affect both the respiratory and digestive systems and may produce a variety of adverse effects in some people (Ricci et al., 2019). Another primary concern is developing wheat lines with higher quality for specific end-consumer purposes, in particular for the production of biofuels and human sustenance (Pereira et al., 2019). There is a need to focus on improving wheat yield up to 60 percent by 2050 to meet the rising demand of the constantly growing world population (Guarin et al., 2022).

Extreme temperatures in tropical, subtropical, arid, and semi-arid locations globally impact wheat productivity. Wheat encounters difficulties in the tropical region during germination and early growth because to high temperatures, whereas in the Mediterranean region, the reproductive stage is especially affected by climatic conditions (Ouda et al., 2015). Wheat yield in Asia is reduced by 10–50% when the optimal temperature for grain filling is exceeded by temperatures of 3–4 degrees Celsius (Zampieri et al., 2017). Depending on the wheat variety, grain yield drops by 0.07% per degree Celsius when the temperature is high. Every degree that the temperature rises during the grain-filling period results in a 6% decrease in wheat output worldwide and anywhere from 3% to 17% in South Asia, which includes India and Pakistan (Mondal et al., 2016). It is directly or indirectly responsible for the disruption in a variety of cellular, physiological, and metabolic pathways related to the grain-filling stages and ultimately yield (Zafar et al., 2022; Zafar et al., 2023; Zafar et al., 2024).

However, several environmental challenges, including excessive temperature stress, are currently limiting wheat production. The seeds can germinate between 3.5 to 35°C, however the optimal temperature range for wheat seed germination is 20-25°C (Reed et al., 2022). Climate change and increasing temperatures had harmful impacts on plant growth and development, resulting in a significant decrease in wheat productivity (Zafar et al., 2021).

The elevated levels of greenhouse gases like carbon dioxide (CO2), nitrous oxide, and methane (CH4) are the primary reason for the ongoing climate emergency. These gases have the potential to absorb the sun's rays, which can exacerbate the severity of adverse conditions that can affect plant growth (Riaz et al., 2021). The concentration of CO2 in the atmosphere has increased by 2.3 ± 0.6 ppm/year during the past decade, compared to 0.6 ± 0.1 ppm/year in the early 1960s. In the meantime, the amount of CH4 gas has increased by a rate of 12 parts per billion every year since the Industrial Revolution until the 1980s (Hmiel et al., 2020). This increase occurred after the Industrial Revolution. Nevertheless, during the course of the previous three decades, it was rising at a rate of two to five parts per billion every year. The concentration of nitrogen oxide was increased by 18% higher than it had been in the 1970s, and it climbed by 0.8 parts per billion per year (Mikhaylov et al., 2020).

One of the most significant physical elements impacting a plant's health is high temperature. Due to global warming, which has had a significant rise in air temperature over the previous two decades and will continue to do so annually, our environment is being negatively impacted on a big scale (Zandalinas et al., 2018). High-temperature stress will rank among the most prevalent abiotic stresses for plants in the upcoming years. The total temperature will continue to rise by 1.0 to 1.7 C, which along with other abiotic factors reduces crop production by up to 50% (Riaz et al., 2021). Oxidative and osmotic stresses are brought on by high temperatures singly or in combination, which inhibits plant growth and development. Different types of environmental stress can cause plants to produce ROS. That temperature ranges from low to high. When ROS are produced in the mitochondria and chloroplast, they damage the chloroplast membrane and reduce photosynthesis, which increases cell death (Akter & Rafiqul Islam, 2017; Zafar et al., 2024).

Effects of Heat Stress on Wheat

Heat stress impacts the various growth and development stages of wheat and ends up in high yield loss. However, heat stress on plants depends upon the fundamental measure of the warmth or plant heat exposure.

Effects on Wheat Morphology

Heat stress in wheat mainly hinders seed germination and results in weakened crop structures. Embryonic cells are impacted when the temperature reaches or surpasses 45°C, causing a delay in seed germination and emergence (Riaz et al., 2021). Elevated temperatures harm embryonic cells, disrupt germination, and impact the viability of the productive tiller, resulting in reduced production. Heat stress in wheat results in a reduction of tillers by a maximum of 15.38% and ultimately, grain production by up to 53.57% (Akter & Rafiqul Islam, 2017). HS has a significant impact on the procreative process. The seeds can germinate between 3.5 to 35°C, however the optimal temperature range for wheat seed germination is 20-25°C (Reed et al., 2022). Early developmental stages are damaged when exposed to heat stress during meiosis (Riaz et al., 2021).

HS causes significant affects such as decreased germination percentage, plant emergence, aberrant seedlings, low phanerogam vigor, reduced body shape, and down feather growth in germinated seedlings. Under high temperature conditions (30/25°C, day/night), wheat suffered a significant decrease in leaf area and productive tillers/plants. Elevated temperatures of 1–2 °C over the ideal range result in reduced grain filling durations and have a detrimental impact on wheat yield components (Ashry et al., 2018).

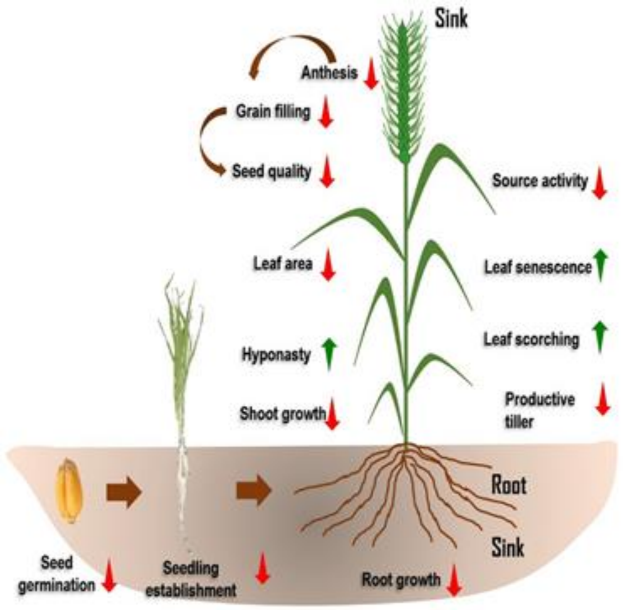

Fig. 1.1: Shows that an increase in temperature can modify plant morphology and inflorescence which leads to less grain filling and seed quality.

Effects on Wheat Physiology

Photosynthesis is a sensitive process and is utterly disturbed or inhibited by any quiet heat stress because an increase in temperature produces a chemical change which can lead to inhibition of the photosystem (Gao et al., 2021). Heat stress caused different changes in chloroplasts, such as alterations in the structural arrangement of thylakoids, disruption of grana stacking, and enlargement of grana. Photosystem II (PSII) activity is significantly decreased or halted during heat stress, and heat shock decreases the amount of chemical reaction pigments (Zafar et al., 2023).

Disruptions within the structure and performance of chloroplasts, reduction in pigment content, and inactivation of plastid enzymes are the major reasons for slow or stopping in the photosynthesis process (Hu et al., 2020). The cut down of Chemical action activity at the grain filling stage led to less grain filling and finally less yield. Along with this, respiration is also affected by heat stress, therefore, once each chemical change activity and respiration is cut down, plant production is hampered.

Effect on Wheat Biochemical Characters

Enzyme Function

The temperature dependency of the main photosynthetic enzyme, Rubisco, is directly related to the effects of photosynthesis response, and its activation is reduced at high temperatures. Additionally, in high-temperature stress, CO2 solubility is reduced more than O2, favoring the oxygenation activity of rubisco which results in more photorespiration and less photosynthesis. A little essential subunit of rubisco is called starch synthase (SS) (Riaz et al., 2021). It is an enzyme that causes wheat grains to fill out. The SS activity, however, diminished as the temperature rose over 25C. Therefore, SS would not function due to heat stress, which would lead to decreased grain filling and a consequent decrease in yield (Abdelrahman et al., 2020). Additionally, high temperature controls the transcriptional level of the SS gene expression. So basically, heat stress is what makes the rubisco enzyme inactive.

Membrane Stability

Cell membrane stability has been used to study drought and heat stress. Drought and heat stress had an identical impact on the plant cell, causing damage to the plasma membrane's selective permeability. Wheat yield in hot environments is closely connected with membrane thermo-stability (Zininga et al., 2018). The cell and cell membrane might be affected by too high or too low temperature. Increased heat exposure can harm the cells. A single temperature change can denature or damage proteins, which are a little more complex. When a protein denatures, its original structure is lost (Gall et al., 2015).

High-temperature Effects on different Growth Stages in Wheat

High temperatures shorten all wheat growth phases' durations, resulting in significantly fewer developmental stages from emergence to anthesis. Heat stress negatively affects seedlings, however, the anthesis stage is more susceptible to high temperatures (Maulana et al., 2018). Wheat tends to be more susceptible to high temperatures during flowering time and if it occurs during or immediately after anthesis can cause severe harm to the plant physiology, which results in low seed setting. This is mostly caused by factors like the production of nonviable pollen, barriers to the expansion of the pollen tube, poor pollen performance, and reduced fertilization rate (Hlaváčová et al., 2017). Wheat production is badly damaged by high temperatures during reproductive development. Because grain filling and grain number production take place during the reproductive stages the heat stress at this stage may affect the formation of the grains and result in a damaged and low number of grains (Rehman et al., 2021). Thus, heat stress at the reproductive stage causes a low seed setting rate and ultimately low yield.

Yield Factors Affected by Heat Stress

The basic unit of yield in wheat is grain number. An increase in temperature hastens the spike generation but decreases the number of grains and spikelets per spike. A constant rise in temperature reduces the production of several grains per spike due to an increase in pollen grain sterility which results in poor seed setting (Bhusal et al., 2017). In addition, it reduces the size of endosperm which leads to decreased starch deposition and grain weight.

In response to heat stress plants tend towards their reproductive growth which reduces grain filling time and rate as well as the weight of each grain. Wheat grain yield is reduced as a result of losses in the number of fertile pollens per floret, number of fertile florets per spikelet, number of spikelets per spike, number of spikes per plant, and the weight of the grains (Fábián et al., 2019). Moreover, wheat grain quality is also negatively regulated with high-temperature stress during post-heading because it affects grain protein content and inhibits starch deposition. High temperatures alter the characteristics of wheat dough by enhancing the grain's gliadin-to-glutenin ratio, which results in a weak dough (Barutcular et al., 2016).

Response Mechanism of Wheat against Heat Stress

Plants are sensitive to heat stress and other problems. Heat stress tolerance allows plants to survive, thrive, and profit. Heat stress is mitigated by various plant systems. Wheat uses antioxidant defense, HSP generation, stay green, and canopy temperature depression to tolerate heat.

Antioxidants Defense System

In numerous enzymatic and non-enzymatic reactions, ascorbic acid provides an electron donation. Glutathione removes singlet oxygen, hydrogen peroxide, and hydroxyl radicals (Caverzan et al., 2016). Tocopherol is an important antioxidant that acts as an H_2O_2 scavenger; involved in the upregulation of APX and GR. While Carotenoids prevent the production of singlet oxygen atoms (Hasheminasab et al., 2012).

Electrons from the electron transport chain inevitably leak out through the mitochondria, chloroplasts, and plasma membrane. The production of ROS is restricted to specific cellular areas and results from the acceptance of an electron leak by O_2 or as a byproduct of many metabolic processes. ROS production is associated to oxidative stress, but it can also signify abiotic stress resistance (Mickky & Aldesuquy, 2017). Thus, ROS should be preserved to prevent oxidative damage.

Enzyme	Function
O_2	Disputed by SOD into H_2O_2 and O_2 via catalysis.
APX	Oxidizing ascorbate to scavenge H_2O_2
PO	Catalyzes the oxidation of monophenols and diphenols which react with the oxygen and proteins and form ROS
CAT	Without using any reducing power, convert H_2O_2 into water and oxygen. Catalyze the elimination of H_2O_2 with GPX.

The Heat Shock Proteins ((HSPs)

Inside the body of the plant, under HS, several physiological and metabolic processes take place, and regular protein synthesis is blocked. To maintain the physiological equilibrium inside the cells, several new proteins are rapidly generated at the same time (Kumar et al., 2018). The heat shock proteins are the most crucial of these novel proteins. They are a class of conserved proteins that help to denature proteins to avoid irreversible aggregation as well as retain or restore their biological functions in response to environmental challenges. They are coupled with the polypeptides being produced and aid in their proper folding (Khan & Shahwar, 2020). Molecular weight divides HSPs into five categories: HSP100, HSP90, HSP70, HSP60, and small heat shock proteins. Wheat contains 753 HSP genes (Cheng et al., 2016). As they protect the heat-sensitive photosynthetic system 2 protein complex, maintain electron transport chain and ATP synthesis, and allow plants to grow normally, chloroplast and mitochondrial HSPs are thought to be more important than others in plants' heat tolerance. Heat stress transcription factors, which regulate HSP gene transcription, are inactive in the cytoplasm (Li et al., 2017).

Functions of different Heat Shock Proteins

Protein aggregation is destroyed by HSP100 and this process depends on ATP. HSP90 mediates the signal transduction associated with HS. By inhibiting aggregation formation, HSP70 promotes correct protein folding and stabilizes freshly produced proteins (Banerjee & Roychoudhury, 2018). HSP60 assists in protein folding and inhibits the accumulation of denatured proteins. HSP40 Once the fully refolded protein is created, HSP40, HSP70, and HSP100 release tiny HSPs that participate in the refolding process (Banerjee & Roychoudhury, 2018). Small heat shock proteins assist in the refolding of denatured proteins, preventing heat-induced aggregation. Antioxidative defense systems and reactive oxygen species (ROS).

Hydrogen sulfide damages the plant by producing hazardous reactive oxygen species (ROS) like singlet oxygen, superoxide, and hydroxyl radical. Redox homeostasis refers to the equilibrium between reactive oxygen species (ROS) production and removal in normal cells. Activating the related Enzymes that scavenge free radicals triggers the anti-oxidative defense mechanism in response to the increase in ROS signals associated with HS (Fragkostefanakis et al., 2015). Plants possess enzymatic and non-enzymatic elements that form their antioxidant defense system. Plants have substantial levels of superoxide dismutase, catalase, and peroxidase. Ascorbic acid, beta-carotene, tocopherols, and glutathione are non-enzymatic antioxidants. Antioxidants remove reactive oxygen species (ROS) and protect cells from oxidative damage in the absence of stress. Under stressful circumstances, the quantity of ROS in the cell rises and the overall antioxidant status drops or antioxidants lower their action (Akter & Rafiqul Islam, 2017).

Stay Green

High temperatures during the grain-filling stage pose a substantial challenge to successful wheat cultivation in various places worldwide. Research has explored the effectiveness of many morphological and physiological traits in breeding for heat tolerance. Plants' ability to keep their leaves active for photosynthesis in high temperatures is called "stay green." The term "stay green" (SG) refers to a variant where the process of senescence, which involves the loss of chlorophyll, is delayed compared to a standard genotype (Kamal et al., 2019). Premature aging in plants affects their ability to absorb nutrients and develop grains. The pace of senescence determines the preservation of chlorophyll and, therefore, the process of photosynthesis for sink production. Certain crops are being assessed for their stay-green traits, with notable achievements limited to cereals such as wheat and sorghum. The ASG QTL (44 loci) in the "Seri/Babax" wheat mapping population grown under high salinity (HS) conditions shown a significant positive correlation with HS tolerance, grain yield, and grain filling rates (Pinto et al., 2016).

Hence, it is believed that agricultural plants will yield more due to any defense mechanism that postpones the onset of senescence and sustains green leaves. Stomatal conductance (SG) preserves the space for photosynthesis and enhances the transfer of nitrogen to the mature grains, playing a crucial role in heat stress tolerance in wheat (Christopher et al., 2016). Semantic generalization is not consistently beneficial and can manifest in two forms.

Functional SG

The onset of senescence is either postponed or progresses slowly in the case of a functioning SG mutant. Therefore, agronomic interest is in the functional SG trait (Thomas & Ougham, 2014).

Non-functional SG

Senescence occurs normally in non-functional SG mutants, and while photosynthetic capacity is reduced, leaf color is preserved as a result of abnormalities in the chlorophyll degradation pathway (Wang et al., 2020).

CTD (Canopy Temperature Depression)

Canopy Temperature Depression is the term used to describe the variance between canopy temperature and air temperature. Under well-irrigated circumstances, transpiration rises, leading to cooler canopies (Ayeneh et al., 2002). CTD is influenced by a range of biological and environmental variables. Vapor pressure significantly influences CTD more than air temperature and wind speed (Karimizadeh & Mohammadi, 2011). CIMMYT has conducted various tests to evaluate CTD, revealing favorable phenotypic associations between CTD and grain yield (Yadav et al., 2022). CTD has been utilized as a criterion for selecting wheat varieties with high salinity tolerance. The reduced temperature of the upper layer of foliage while grains are developing is crucial for heat stress tolerance in wheat (Thapa et al., 2018).

Acquisition of Thermotolerance and Temperature Sensing and Signaling

Acquired thermotolerance refers to a plant's ability to withstand heat stress after being exposed to slightly lower temperatures for a brief period. Developing thermotolerance is a crucial approach to dealing with heat stress (El-Rawy, 2020). PGPR enhances thermo-tolerance in wheat by decreasing reactive oxygen species (ROS) generation, minimizing membrane damage, and preserving chloroplast function and structure. Various organelles in plants function as sensors to detect little temperature elevations. The plasma membrane is the main sensor in plant cells for detecting stimuli early on, which then triggers the activation of heat-sensitive channels. Proteins coded by CNGCs are identified as heat sensors in plants (Yadav et al., 2022).

Modern Techniques for the Development of Heat Tolerance in Wheat

Heat tolerance has a quantitative character and is also regulated by several genes and QTLs mapping (quantitative trait loci). The genetic underpinnings of heat tolerance have been attempted to clarify throughout the past three decades. Several QTLs that significantly impact heat tolerance were identified by using different traits as markers of tolerance (Acuña-Galindo et al. (2015). Wheat's genetic susceptibility to heat has been studied using genome-wide association studies (GWAS). Significant SNPs for SET and SDW were found by GWAS in both field and glasshouse settings (Bhusal et al., 2017). A path was opened up for the development of wheat cultivars with diminished ethylene effects on yield under heat stress by the phenotypic and genetic explanation of SET.

Transgenesis, another method for enhancing wheat's heat tolerance, is the introduction of superior genes into potential wheat genotypes. Utilizing genes that are inaccessible in hybridization-based breeding or co-transferring undesirable nearby gene segments is avoided by this method. Wheat terminal heat tolerance could be successfully improved by genetic engineering that boosts osmolyte levels, boosts the production of heat-shock proteins, modifies membrane fluidity, or modifies different cell detoxification enzymes (Guo et al., 2015).

Research on genetic modification has been hindered by the intricate wheat genome compared to other plant species. Wheat with overexpressed ZmPEPC (a maize phosphoenolpyruvate carboxylase) genes showed improvements in heat tolerance, including an upregulation of genes involved in photosynthesis, an increase in antioxidant and photochemical activities, changes to the composition of proline and other metabolites, and a delay in the degradation of chlorophyll (Yadav et al., 2022).

Wheat chloroplast-resident protein synthesis elongation factor (EF-Tu) enhanced heat tolerance and protected the plant from heat stress. According to Wang et al. (2018), transgenic wheat that has EF-Tu constitutively expressed shows improved photosynthetic performance, less thylakoid membrane breakage, and protection of leaf proteins from thermal degradation. Transgenic wheat with enhanced heat tolerance was shown to be a result of overexpressing the maize EFTu1 gene (Ullah et al., 2022). Finally, genetic engineering has the potential to increase wheat's tolerance to terminal heat.

Heat stress rapidly alters the expression patterns of genes that are connected to heat. More and more, researchers are turning to functional genomics tools like metabolomics, transcriptomics, and proteomics to identify and understand the molecular components of heat stress tolerance and the pathways that contribute to it (Sharma et al., 2017).

Chromatin remodeling regulates the expression of several genes in plants that are subjected to heat stress. Hypermethylation of histone H3 lysine 4 (H3K4) acts as a thermos-memory, allowing cells to endure repeated episodes of heat stress (Shekhawat et al., 2021). It has been proposed that HSFA2 recruit's histone methyl transferases to thermos memory loci, given that it binds to this histone alteration (Guo et al., 2020). Keeping memory-gene expression going even after heat stress has gone away requires FORGETTER3/HEAT SHOCK TRANSCRIPTOR A3 (FGT3/HSFA3), according to a recent study (Friedrich et al., 2021).

Plants can't adapt to different environments without phytohormones. According to Lämke et al. (2016), phytohormones are essential for plants to adapt to different environments since they control growth, development, nutrient distribution, and source/sink transitions. An increasing amount of evidence points to abscisic acid (ABA) as a key plant hormone that regulates wheat's heat tolerance. Iqbal et al. (2022) found that a wheat genetic variant that was insensitive to ABA had significant improvements in kernel weight and yield when compared to its mother line.

It has been proposed that HSPs, which prevent cellular proteins from being damaged, may play a pivotal role in thermos tolerance. Although the other three methods for achieving thermotolerance in transgenic studies function in their unique ways, they may also indirectly contribute to the development of a more reductive and energetic cellular environment and reduce the buildup of damaged proteins.

The primary objective of genetically modifying crops to withstand high-temperature stress seems to involve intervening in protein metabolism to decrease the buildup of damaged proteins (Ni et al., 2018). By adding certain genes into the candidate genotype, transgenic techniques and genetic modification can enhance terminal heat tolerance in wheat.

Plants have been genetically modified to tolerate high temperatures primarily by over-expressing the genes for heat shock proteins or inadvertently by changing the amounts of heat shock transcription factor proteins (Qin et al., 2015). In addition to heat shock proteins, osmolyte levels have increased, cell detoxification enzyme levels have increased, and membrane fluidity has changed, affecting thermotolerance.

Recent breakthroughs such as transformation technologies and the development of durum wheat and bread wheat libraries are expected to accelerate the discovery of heat-responsive genes in wheat (Aberkane et al., 2021). Transcriptional variables related to abiotic stress tolerance have been discovered and altered in several types of cereal, such as wheat.

Conclusion

Ultimately, heat stress significantly endangers wheat production by impacting its growth, development, and yield. The increasing global temperatures caused by climate change are leading to more noticeable negative impacts of heat stress on wheat crops. Heat stress affects wheat in various ways, including its morphology, physiology, and biochemistry. This review has outlined how high temperatures negatively impact seed germination, photosynthesis, enzyme development, and cellular structures, resulting in decreased grain production and quality.

To address these challenges and ensure food security in the face of rising global temperatures, it is crucial to adopt effective strategies for mitigating the impact of heat stress on wheat. This review has discussed several mechanisms and responses that wheat employs to counteract the effects of heat stress. These include the production of heat shock proteins (HSPs), antioxidant defense systems, the "stay green" trait, and canopy temperature depression (CTD).

Furthermore, modern techniques for enhancing heat tolerance in wheat, such as genetic engineering and transgenesis, hold promise for developing wheat varieties that can thrive in high-temperature environments. These techniques provide the means to introduce genes that improve osmolyte levels, enhance the production of HSPs, modify membrane fluidity, and enhance various cellular detoxification enzymes. The ability to delay senescence and maintain chlorophyll levels, known as "stay green," can significantly contribute to heat tolerance in wheat.

It is essential to comprehend the molecular and genetic foundations of heat tolerance in order to design wheat types that are hardier. Functional genomics, transcriptomics, proteomics, and metabolomics advances have shed light on the molecular mechanisms and components underlying wheat's ability to withstand heat stress.

As we face the ongoing challenges of a changing climate, the development of heat-tolerant wheat cultivars is essential to ensure global food security. The collective efforts of researchers, breeders, and biotechnologists are integral to the ongoing development of wheat varieties that can withstand the rigors of heat stress, contributing to a sustainable and secure food supply for the growing world population. Ultimately, the pursuit of heat stress tolerance in wheat is a critical step toward achieving the goal of zero hunger.

Future Perspectives

Research on wheat's resilience to heat stress has a bright future ahead of it. The creation of wheat varieties that can withstand high temperatures is probably going to be greatly aided by developments in genomics, genetics, and marker-assisted breeding. Breeders will have significant tools for targeted selection thanks to the continuous investigation of the wheat genome and the identification of important genes and quantitative trait loci linked to heat tolerance. Breeding tactics will become more informed as omics technologies, like as transcriptomics, proteomics, and metabolomics, continue to untangle the complex biological responses to heat stress.

Additionally, biotechnological approaches such as genetic engineering and genome editing offer opportunities for precise gene manipulation to enhance heat tolerance. The development of high-throughput phenotyping platforms, a deeper understanding of environmental interactions, and global collaboration are expected to further accelerate progress in the quest for heat-resistant wheat varieties. Effective communication, policy support, and a focus on sustainable agriculture will be crucial in translating research into real-world solutions for global food security.

In summary, the prospects in the study of heat stress in wheat are marked by ongoing innovation, collaboration, and the pursuit of sustainable, climate-resilient agriculture. These endeavors are essential not only for addressing the immediate challenges of heat stress but also for building a more food-secure and resilient future in the face of climate change and a growing world population.

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