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Heat stress in wheat: a global challenge to feed billions in the current era of the changing climate

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Crop failure is largely caused by various climate hazards, and among them, heat stress is the primary factor hindering crop production. The significant global loss of crop yield is primarily due to heat-related damage during the reproductive phase. Terminal heat stress has been well documented in wheat, causing morphophysiological alterations, biochemical disruptions, and reduction of genetic potential. The formation of shoots and roots, the effect on the double ridge stage, and early biomass in the vegetative stage are also impacted by heat stress. The final negative outcomes of heat stress include reduced grain number and weight, slower grain filling rate, reduced grain quality, and shorter grain filling duration. Plants have developed mechanisms to adapt to heat stress through modifications in their morphological or growth responses, physiological and biochemical pathways, and changes in enzyme reactions. Numerous heat tolerance genes have been identified in wheat, but the more extensive study is needed to increase heat tolerance in crops to satisfy the food demands of the world's growing population. The global food policy needs to prioritize and promote additional joint research and the development of heat-tolerant wheat breeding to ensure the world's food security.

KEYWORDS

wheat, heat stress, changing climate, food security, current era

1. Introduction

The rate at which the world's population is expanding is 1.1% every year (The World Bank, 2019) which is faster than the experts' predictions a few years ago (Yale University, 2020); hence the food consumption rate is also increasing. Agricultural research is being achieved quantum leaps in terms of commodity and non-commodity outputs to serve global food production. However, this achievement is always under pressure and becomes unstable due to several reasons. Climate change imposes significant uncertainty on crop production due to biotic agents or abiotic stresses. The significant climatic hazards are heats, droughts, salinity, floods,

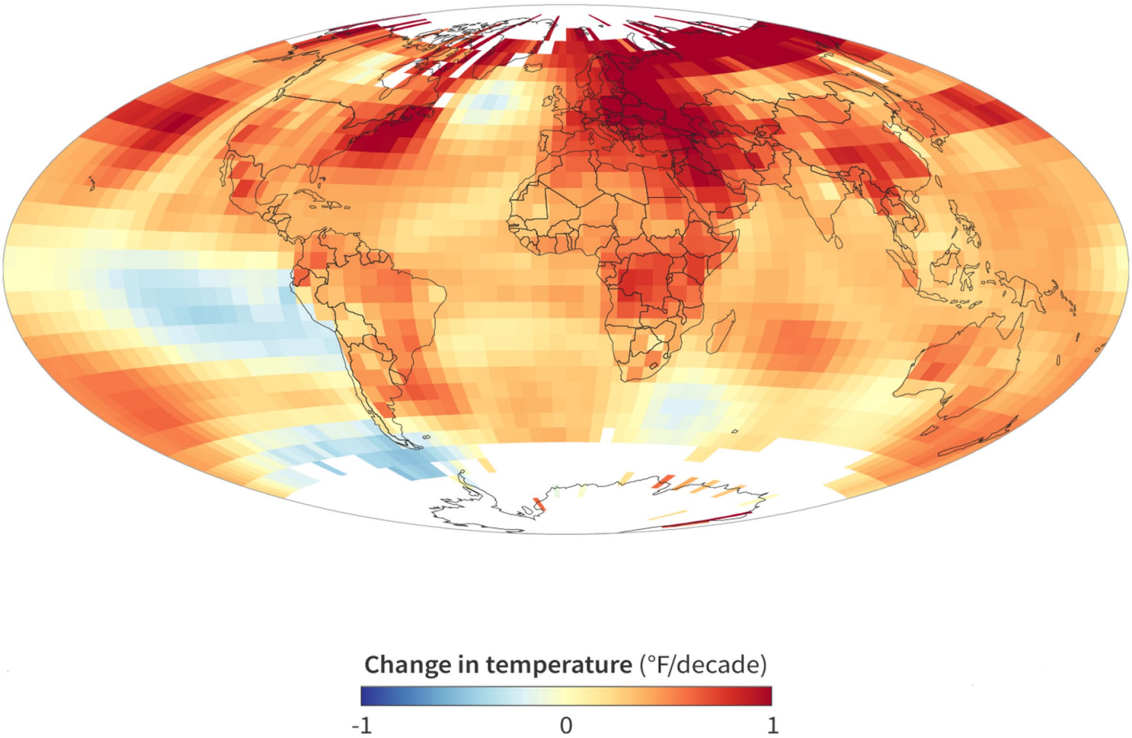

FIGURE 1
According to the map provided by NOAA Climate.gov, there is a discernible trend of rising global temperatures between the years 1993 and 2022, except for certain regions within the Southern Hemisphere oceans. https://www.climate.gov, Accessed on 28 April 2023.

unexpected high or low rainfall, humidity, increasing windstorms and decreasing groundwater table and resources. These climate hazards hinder crop production, particularly in developing countries having fewer resources.

Heat is a crucial influence impacting agricultural output, making it one of the most important abiotic stresses. The term "heat stress" refers to temperatures that are higher than the critical threshold. Extreme heat stress is defined by the magnitude, duration, and pace of temperature increase. Threshold temperature varies from crop type, growing season, and crop growth stages. Heat tolerance is the capability of living beings to develop naturally or to produce economic yield at a temperature above the threshold. A significant cause of yield loss in agricultural production globally is heat-related reproductive tissue damage in various crops (Suzuki et al., 2012). A strong negative association between high seasonal temperature and crop yields, which is largely correlated with heat stresses, has been consistently reported by Akter and Rafiqul Islam (2017), Gammans et al. (2017), and Cui (2020). It's possible that the floodplain regions of Asian countries like China, India, Bangladesh, Nepal, Iran, etc., may be hit the worst by global climate change (Braun et al., 2010). The data of The National Oceanic and Atmospheric Administration (2023) provided a global view of climate change over time, showing a growing portion of the Earth's surface becoming warmer.[1] It was revealed from Figure 1 that global warming is very prominent in all continents of the world. It was revealed that winter crops determine several yield contributing factors like the grain numbers, grain weight and grain size during this time (Poudel and Poudel, 2020).

Wheat is the prominent food grain globally which is grown in the winter season. The adverse effects of climate change on wheat production pose a danger to global food security, and sustained wheat output is anticipated to be increasingly negatively impacted by rising global temperatures (Tripathi et al., 2016). Heat stress has a negative impact on wheat output in various parts of the world. This is especially detrimental during the reproductive phase of the wheat plant (Mondal et al., 2013). It is essential that the implications of heat stress and potential means of enhancing heat tolerance for the profitability of wheat production in heat owing to global warming and alters in the extreme climate pattern be recognized. This is because heat stress and potential means of enhancing heat tolerance are directly related to the profitability of wheat production in heat. This is because these consequences must influence the performance of wheat production in heat.

Global wheat yield loss with the increase of each degree-Celsius temperature is 6.0 ± 2.9% (Zhao et al., 2017). The high seasonal climate in January and February affects the formation of the double ridge stage. The high temperature at the grain filling period is called terminal heat stress and the elevated temperature at sowing is called early heat stress. Wheat development as well as growth are facing a difficult constraint brought on by early and terminal heat shocks. A plant experiencing heat stress is the function of ambient temperature, agronomy and genetic factors that determine evaporative cooling potential (Braun et al., 2010). The majority of prior studies aimed to increase hexaploid wheat's tolerance to heat stress by drawing on the variety present in its wild ancestors (Elbashir et al., 2017; Liu H. et al., 2019; Ma'arup et al., 2020; Poudel and Poudel, 2020; Elhadi et al., 2021; Itam et al., 2021, 2022;

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[1] https://www.climate.gov, Accessed on 28 April 2023.

Ullah et al., 2021). Wild emmer wheat (*T. turgidum* ssp. dicoccoides) is considered a plausible resource due to its direct lineage to domesticated durum wheat (*T. durum*) and the A and B genomes of bread wheat (*T. aestivum*). The genetic introgression of wild emmer wheat for wheat improvement has been demonstrated to be feasible through the two lineages it possesses. Wild emmer wheat has been identified as a valuable resource for enhancing the resilience of wheat to environmental stressors (Peng J. et al., 2013; Tsujimoto et al., 2015; El Haddad et al., 2021) It is noteworthy that the inherent diversity of wild emmer wheat encompasses significant agronomic, physiological, and yield-related characteristics that are linked to the ability to withstand heat stress (Peng J. et al., 2013). The preservation of diversity in wild emmer wheat is essential for the enhancement and maintenance of wheat tolerance toward heat stress. Over the last decade, various omics methodologies have significantly transformed the manner in which biotechnologists and plant breeders explore the fundamental mechanisms of stress tolerance and cellular homeostasis (Yadav et al., 2022). In the upcoming sections, we will be discussing more on the specific heat stresses in wheat. When there is an increase in the average temperature throughout the winter, there is a major impact on wheat productivity and planting area. The effects of thermal stress on human well-being, especially food security, depend greatly on the combination of natural ecosystem stability and the approach taken by farmers and other stakeholders in the agricultural system. This review will also concentrate on basic heat stress in the development and growth of wheat, its morpho-physiological, biochemical, and molecular mechanisms, varietal improvement, or cultivation practices for heat stress management.

2. Impact of heat stress on wheat

Heat stress affects the whole development and growth system in plants, including phenological stages, morpho-physiological alteration, developmental process, biochemical reactions, and even genetic potentials to produce yield. Canopy humidity for evaporative cooling plays an important role in how plants respond to heat stress, and its intensity and duration may have a significant impact on how plants react (Braun et al., 2010). The temperature rise was directly related to a decrease in photosynthetic efficiency and ultimately a reduction in crop yield (Mathur et al., 2011). A computer modeling study on crop response revealed that global warming causes premature aging in wheat (Lobell et al., 2012). The high temperature of the day can damage the leaf photosynthesis components, reducing the rate of CO_2 assimilation during the vegetative process compared to the optimal temperature setting. Heat stress inhibits the development of plants both throughout the plant growth and reproduction phases. Heat stress had a detrimental effect on the length of roots during the seedling stage, with notable differences observed among various wheat genotypes. Seedlings exhibiting heat tolerance demonstrated a lower reduction in root length compared to those that were susceptible. The wheat cultivars that exhibited tolerance during the seedling stage demonstrated a greater yield during the adult stage following exposure to heat treatment. It was found that heat stress had a detrimental effect on the length of roots during the seedling stage, with notable differences observed among various wheat genotypes. Wheat plants are susceptible to heat stress, which impedes growth, causes morpho-physiological changes in the plant, and eventually results in a large loss of yield and the heat stress can be caused by prolonged exposure to high temperatures (McClung and Davis, 2010; Grant et al., 2011). The response of plants to heat stress varies considerably with the degree and length of the temperature and the growth phases (Ruelland and Zachowski, 2010). The effects of high-temperature stress on growth and development may be seen in practically every developmental stage of the crop growth cycle (Cossani and Reynolds, 2012). Diagrammatic representation of the impact of heat stress on different major traits of wheat (Figure 2) and also discussed in different sub-headings below:

2.1. Heat stress in the vegetative stage

The wheat plants' periodic life cycle events are highly responsive to heat shock. Poor stand establishment results from high soil temperatures, which inhibit healthy wheat germination. High temperature affects vegetative growth and accumulation of shooting biomass. High-temperature harm photosynthetic machinery which shortens the vegetative period increases oxidative stress, reduces tillering, and advances flowering. High temperatures have a direct influence on the photosynthetic apparatus of wheat and other cereal crops, decreasing photosynthesis, photoassimilate generation, and shoot biomass production throughout the vegetative process (Wahid et al., 2007). The extent of damage will be determined by the developmental phase at which wheat plants are subjected to temperature extremes. After 7 days post germination, it has been demonstrated that heat treatment at 45°C for 2 hours may diminish the length of the shoots and roots, as well as the dry mass, chlorophyll content, and the membrane stability index (Gupta et al., 2013). For 24 h, heat treatment at 42°C prevented the growth of roots and the first leaves; it also caused a rise in reactive oxygen species and lipid peroxidation products in the development of coleoptile and seedling stage organs (Savicka and Škute, 2010). After the double ridge stage, heat stress had a more harmful influence on spikelet production than it had before (Frank and Bauer, 1997).

2.2. Heat stress in reproductive stages

Because of its direct effect, heat stress during the process of reproduction is more detrimental to a number of grains and dry matter production than heat stress during any other phase (Wollenweber et al., 2003). Several more studies have demonstrated that wheat is also likely to experience an increase in 'terminal' or end-of-season heat stress (Mitra and Bhatia, 2008; Semenov, 2009). The reproductive phases and growth of crops are considered the most vulnerable stages in cereals to high-temperature stress, which alters spikelet production and grain development due to insufficient assimilated supply, resulting in fewer spikelet/grains and reduced sink size (Barnabás et al., 2008; Shi et al., 2022). The effect of heat stress that eventually induces floret abortion at anthesis results in pollen sterility attributable to tissue dehydration, decreased CO_2 assimilation and enhanced photorespiration (Wardlaw and Wrigley, 1994). For three consecutive days, when pollen mother cells divide, if wheat plants are exposed to 30°C, it significantly decreases grain set and grain yield (Saini and Aspinall, 1982). On the other hand, stigma and ovule development is accelerated by high temperatures reducing the duration of pollen and pollen tube development (Hedhly et al., 2009). For grain development, the optimal temperature varies between 12°C and 22°C (Farooq et al., 2011) and ample sterility is

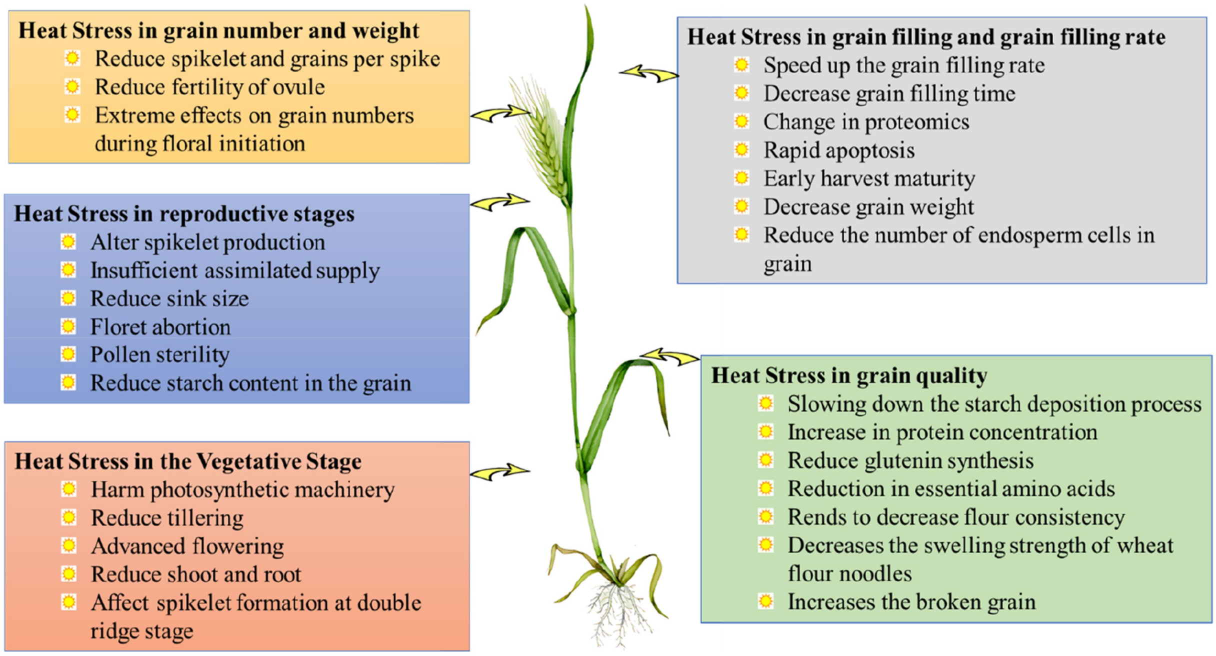

FIGURE 2
Diagrammatic representation of the impact of heat stress on different major traits of wheat.

caused by temperatures above 30°C during floret formation (Saini et al., 1983). Photosynthesis boosts the supply's rising temperature. Still, it may not fully compensate for starch deposition by the shortened duration, which leads to smaller grains and restricts yield (Andrew, 1987). Therefore, when temperatures escalate between anthesis and grain maturity, due to the reduced time to collect resources, grain yield is reduced. Day and night temperature variations between 28 and 37°C for about 10 to 20 days have been linked to having adverse effects. The filling and maturation times of grains are shortened, and their fresh weight, dry mass, protein, and starch content, and their size are all diminished, among other unfavorable outcomes. Ultimately, this leads to a reduction in yield (Hurkman et al., 2009).

2.3. Heat stress in grain number and weight

The number of grains is a major component of wheat yields. Temperature increases have been shown to hasten spike development while decreasing the number of spikelets and seeds formed per spike (Evans, 1978). In many places, heat stress is a substantial threat to wheat productivity when temperatures rise, particularly during the reproductive and grain-filling stages. Dry matter build-up and grain production are both negatively impacted by heat stress because of the negative effects on photosynthesis caused by metabolic constraints and oxidative damage to chloroplasts. When the temperature rises above 31°C just before anthesis, it leads to pollen sterility, which means that the pollen is unable to fertilize the ovules and produce viable seeds causing several pre-anthesis disruptions and subsequently affecting yield and yield components (Roychowdhury et al., 2023). This leads to a reduction in the total amount of grains produced since there are now fewer seeds being created. Following this, a lower total grain yield is achieved as a result of the decreased grain number (Fokar et al., 1998a). Elevated temperatures may have a substantial influence on wheat grain production, making it important for breeders to develop heat-tolerant varieties that can withstand such conditions. By reducing the sensitivity of the pollen to high temperatures, breeders can improve the grain yield of wheat and help ensure a stable food supply for the growing global population. Heat stress has extreme effects on grain numbers during floral initiation. For example, in the 30 days before anthesis, the number of grains per spike decreased by 4% for every 1°C (from 15 to 22°C) rise (Wheeler et al., 1996). At mid-anthesis, an increase in temperature of about 10°C induced a 40% decrease in grain number per spike. After being exposed to high temperatures of 30°C during the day and 20°C at night for 3 days, or 30°C for a single day, the number of grains produced by wheat plants was shown to decline. This decreased grain set was attributed to the high temperatures that were experienced (Saini and Aspinall, 1982).

2.4. Heat stress and grain development efficiency

Typically, extreme heat accelerates the grain-filling rate and shortens the grain-filling duration (Dias and Lidon, 2009). Increased temperature may accelerate phenological development, decrease grain filling time, change in proteomics, more rapid apoptosis, and achieve earlier harvest maturity and thus produce shriveled grain (Altenbach et al., 2003; Majoul-Haddad et al., 2013).

A study found that stress during the early phases of grain filling reduced the number of endosperm cells in the grain, leading to a decrease in grain weight (Nicolas et al., 1985). Endosperm cells play a critical role in grain filling as they provide the nutrients and energy necessary for the grain to grow and mature. When heat stress occurs during the early phases of grain filling, it can disrupt the normal development of the endosperm cells, leading to a decrease in their number. This reduction in the number of endosperm cells results in a reduction in grain weight as there are fewer cells available to contribute to grain growth. The research findings suggest that heat stress during the early phases of grain filling can have a significant impact on the weight and overall yield of wheat grains. This emphasizes the need of reducing heat stress to safeguard wheat quality and output. Starch synthesis, especially in the latter phases of grain filling, might be inhibited by insufficient grain assimilation resources (Blum, 1998). Compared to the daytime temperature, the night time temperature increase is more sensitive, has a negative effect on grain production by reducing filling time and crop yields. Temperatures between 20 and 23°C at night have delayed the grain filling period by 3 to 7 days (Prasad et al., 2008). Another study discovered a significant slowing of wheat grain filling when day/night temperature changes ranged from 32 to 22°C, as compared to 25 to 15°C (Song et al., 2015). During the grain-filling season, estimated grain yield losses in South Asia range from 6 to 10% per °C increase in temperature (Mondal et al., 2013). In the grain-filling stage, a day-night temperature swing of 34/26°C for 16 days raises leaf temperature, lowers leaf chlorophyll and photosystem-II maximum quantum production, and decreases the total grain output and the weight of individual grains (Pradhan and Prasad, 2015). High-temperature tension during post-anthesis causes leaf senescence. Research findings showed that during the grain-filling stage, a daily mean temperature of up to 30°C had a positive effect on the strength of the dough. However, when the temperature exceeded 30°C, the strength of the dough began to decline. In other words, there was a relationship between the daily mean temperature and the strength of the dough, with an optimal temperature range for maintaining strong dough (Irmak et al., 2008). Adapting some techniques, such as advancing the sowing date, adding additional nitrogen dose and irrigating at the grain filling point, help minimize the effect of heat stress by 7.5, 6.4, and 9%, respectively, in current heat-stressed scenarios in 2020 and 2050 (Dubey et al., 2020). In high temperatures, grain filling happens more quickly but for a shorter period of time. Research findings suggest that while elevated temperatures can cause a reduction in the grain growth rate, the number of grains is less affected. When the temperature exceeded 30°C, the grain filling rate did not increase enough to compensate for the shorter grain filling time, resulting in a decrease in total grain weight. This highlights the complex effects of elevated temperatures on grain filling and the limitations of this compensation mechanism in mitigating the negative impact of heat stress on wheat grain production (Sofield et al., 1977). According to the findings of other investigations, quick grain filling rates have not been able to compensate for the length of time grains take to fill when subjected to heat stress (Stone and Nicolas, 1995). Besides, length and grain growth rate are decreased by heat stress in genotypes (Viswanathan and Khanna-Chopra, 2001). Under ideal temperature circumstances, the decrease in grain filling time is counterbalanced by an increase in the grain filling rate. However, under high-temperature stress, compensatory correction does not take place, leading to a significant drop in grain weight. The essential explanations for reduced grain filling at high-temperatures are reduced leaf and spike photosynthesis and declined stem reserves remobilization One effective strategy for improving heat tolerance is to increase the rate at which grains fill and mature under high-temperature stress (Dias and Lidon, 2009). An improved grain filling rate can be achieved by optimizing the photosynthetic activity of the plant, which provides the energy required for grain growth and development. In addition, an improved grain filling rate can be achieved by optimizing the water relations in the grain, which is crucial for maintaining grain size and weight. Growing wheat with a higher grain filling rate is an important step toward making the crop more resilient to rising temperatures and assuring a steady supply of food in the face of a changing environment. It is conceivable to increase food security for millions of people throughout the world by employing this function to maximize grain filling in wheat types that are more resistant to high temperatures and yield more grain.

2.5. Heat stress in grain quality

The percentage of protein found in the grain and the average size of individual grains are the two most essential factors that determine the quality of wheat grain (Coles et al., 1997). Since it slows down the process of starch deposition, heat stress during grain filling can have a detrimental influence on the quality of the grain's protein (Gooding et al., 2003). This statement highlights the adverse effect of high temperatures on the grain-filling stage and its impact on grain protein. The heat stress affects the grain's ability to properly deposit starch, thereby altering the quality of the grain protein. Heat stress disrupts the balance of nitrogen and starch in wheat grains, leading to an increase in protein concentration. As the heat stress causes the grain to allocate more nitrogen toward the formation of protein, the resulting grains have a higher concentration of protein compared to those grown under normal temperature conditions (Stone and Nicolas, 1995). Heat stress applied during the initial stages of grain filling has been shown to result in a substantial increase in the protein content of wheat grains (Castro et al., 2007). Exposure to heat stress, however, reduces glutenin synthesis, while gliadin synthesis remains stable or increases (Majoul-Haddad et al., 2013). Heat stress can lead to a shift in the grain's composition, causing an increase in protein levels but a reduction in essential amino acids. This change can also impact the sedimentation index, a measure of the grain's protein quality (Dias et al., 2008). By reducing gluten strength-related parameters of lactic acid retention ability and mixograph peak time, heat tends to decrease flour consistency (Li Y. F. et al., 2013). During grain filling, high temperatures (>35°C) adversely affect the dough properties of wheat (Blumenthal et al., 1993). High-temperature stress also decreases the swelling strength of wheat flour noodles and increases the broken grain (Stone and Nicolas, 1996). A drop in starch content, which accounts for more than 65% of the dry weight of cereals, contributes to significant losses in yield (Rakszegi et al., 2006; Barnabás et al., 2008). Protein composition changes in a situation with a daily maximum temperature of more than 32°C, resulting in shriveled grains involving a higher proportion of bran and reducing the quality of wheat (Naeem et al., 2012).

3. Heat stress response and adaptation in wheat

Excessive heat can lead to cellular damage and cell death in plants, ultimately resulting in the breakdown of the plant's structure and organization. Under intense heat stress, the cells of the plant become damaged and may die, leading to disruptions in the plant's normal functioning. This can result in a loss of stability and order, causing the plant's organization to deteriorate. The ultimate impact of this cellular damage and cell death is a reduction in the plant's overall health and ability to produce a healthy crop. From the seedling stage to the maturing of the grain, heat stress can have an impact on production. However, it is most likely to reduce yields during the reproductive and maturing phases. Wheat can cope with heat stress either by escape, avoidance, or tolerance mechanism. In the escape process, the plant attempts to stop heat stress by completing its life cycle before stress pressure arrives. The avoidance mechanism is responsible for controlling the plant's water status and limiting the amount of water lost through stomatal closure, stem and leaf waxiness, leaf rolling, changes in leaf orientation, leaf hairs, and the senescence of older leaves. The tolerance mechanism includes canopy cooling survival under low water potential, better photosynthesis to preserve the supply of assimilates, better efficiency of radiation usage, and extended time of grain filling at higher temperatures. Wheat responses are manifested at morphological, physiological, and biochemical levels and its adaptation to heat stress depends on how efficiently it responds (Akter and Rafiqul Islam, 2017). These responses are brought by a series of signaling cascades involving various transcription factors and signaling molecules which ultimately affect the transcriptome, proteome, and metabolome of the cell.

3.1. Morphological/growth responses

The number of seeds that germinate and the strength of the seedlings are both reduced when plants are subjected to heat stress (Hossain and Teixeira da Silva, 2012). The decreased efficiency of the endosperm is to blame for the lower rates of germination that occur when temperatures are extremely high. This is because a larger amount of carbon is used for respiration (Blum and Sinmena, 1994). Early maturing wheat genotypes avoid the severe effects of terminal heat stress. These genotypes exhibit rapid ground cover and accelerated grain-filling responses to minimize the impact of heat stress (Sharma et al., 2019). Wax deposition on the stem and leaf surface reduces plant dehydration by limiting the absorption of solar radiation. Leaf rolling provides heat tolerance as a beneficial trait by preserving the operation of photosystems I and II and efficient stomatal transpiration control (Sarieva et al., 2010). The number of productive tillers per plant and green leaf area substantially reduces due to heat stress (day/night temperature 30/25°C; Rahman et al., 2009). Plants accumulate lesser biomass under warm environments compared to optimum or cooler environments. There is a strong relationship between agronomic characteristics and yield under conditions of heat stress. These characteristics include but are not limited to, grains per spike, spikelet fertility, early ground cover, canopy temperature, thousand-grain weight, days until heading, days until maturity, and grain filling duration.

3.2. Physiological responses

Heat stress occurs when temperatures rise beyond the tolerance level of the plant, causing disruptions in its physiological processes and reducing the quality and quantity of grain produced (Hasanuzzaman et al., 2013). The physiological responses of plants to heat stress are complex and involve various physiological and biochemical pathways. Understanding these responses is critical for developing heat-tolerant wheat varieties and improving crop yields in regions prone to elevated temperatures. The following section will provide an overview of the physiological responses of heat stress in wheat and the mechanisms that plants use to cope with heat stress.

3.2.1. Photosynthesis in wheat or C_4 crops

Plants rely on photosynthesis to flourish, however, this process can be inhibited by high temperatures. Heat stress during the vegetative and reproductive stages of wheat causes a sharp decline in the photosynthetic rate. Heat stress poses a risk to the thylakoids, contributing to chlorophyll degradation (Ristic et al., 2009). The electron transport activity of chloroplasts is substantially reduced during heat stress, followed by increased lipid peroxidation in thylakoids (Mishra and Singhal, 1992). Chlorophyll content can therefore be used as an index for assessing the heat tolerance of wheat. Stroma and thylakoid lamellae of the chloroplast are the sites where a heat-induced injury occurs affecting the carbon metabolism and photochemical reactions. When elevated temperatures suppress the current process of photosynthesis, transferring energy stored in the stem from previous photosynthesis to grain production can greatly improve grain filling (Blum, 1988). This stem reserve mobilization helps to keep the grain-filling process going even when current photosynthesis is hindered by heat stress. In simpler terms, utilizing the energy stored in the stem before flowering helps to maintain grain growth even when heat stress is reducing the plant's ability to produce energy through photosynthesis. Elevated temperatures can take a toll on the chloroplast enzymes, rendering them ineffective and causing a drop in leaf photosynthesis. The cause of this inactivation is due to oxidative stress, which arises when temperatures rise and disrupt the delicate balance of the chloroplast system. This oxidative stress damages the chloroplast enzymes, making it difficult for them to function properly. As a result, the process of photosynthesis in the leaves slows down, leading to a decrease in overall photosynthesis. This reduction in photosynthesis can have a significant impact on the health and growth of the plant, ultimately reducing its yield and quality. The activity of Rubisco, the most abundant enzyme in the plant system and a key enzyme involved in photosynthesis, is reduced at high temperatures. In cool-season crops such as wheat, Photosystem-II is more susceptible to heat stress, while photosystem-I is relatively stable (Marutani et al., 2012; Mathur et al., 2014). At temperatures >40°C chlorophyll 'a/b' proteins of the 'light-harvesting complex-II' get dissociated from the photosystem-II (Iwai et al., 2006). The thylakoid membrane damage at high temperatures leads to the termination of photophosphorylation (Dias and Lidon, 2010). Wheat production under heat stress can be improved by selecting plants with a high normalized difference vegetation index (NDVI), an indirect indicator of chlorophyll content and biomass build-up (Liu C. et al., 2019). Leaf senescence is a distinctive heat injury symptom that occurs due to chlorophyll biosynthesis inhibition accompanied by vascular breakdown, membrane integrity loss and cellular homeostasis disturbance (Khanna-Chopra, 2012).

3.2.2. Respiration effect on heat stress

The effect on respiration of heat stress is not well known. As temperatures rise, the cost of respiration in plants also increases, eventually reaching a point where the rate of photosynthesis is unable to keep up with the energy demand (Levitt, 1980). At this point, the respiratory losses become too high, and the plant is unable to compensate, leading to a reduction in growth and overall health. In simpler terms, as temperatures increase, plants have to work harder to maintain their functions, and if this cost becomes too high, it will negatively affect their growth. This can be compared to a person who has to work harder to maintain their health in hot weather, and if this becomes too demanding, they will eventually tire and become exhausted. High-temperature stress induces mitochondrial production of oxygen radicals, and these organelles respond to stress tolerance by producing separate anti-stress proteins (Davidson and Schiestl, 2001). The combined effect of drought and high temperatures changed the mitochondrial ultrastructure of susceptible wheat cultivars in the leaves (Grigorova et al., 2012). In conditions of heat stress (daytime temperatures of 35°C and night-time temperatures of 25°C), the respiration rate in the flag leaf of wheat is much higher in susceptible varieties than it is in resistant types (Almeselmani et al., 2009).

3.2.3. Water status

When plants are subjected to high temperatures, the heat causes the tissues of the plants to lose moisture, which ultimately results in the plants being dehydrated. Because of this, the plant's growth and development may be stunted, which will prevent it from realizing its full potential. Just like how we need to stay hydrated to perform our best, plants also rely on having enough water to thrive. When the heat causes the plant's tissues to become dehydrated, it negatively impacts the plant's overall health and growth. To retain maximum water potential during flowering, an upper limit of 31°C is required (Atkinson and Urwin, 2012). Water capacity and relative water content in leaves decrease with increasing leaf temperatures due to heat stress, which ultimately decreases photosynthetic ability (Farooq et al., 2011). Transpiration rate decreases during heat stress thus affecting plant growth. At high temperatures, there is an increase in the aquaporin activity, membrane fluidity, and membrane permeability, as well as a reduction in the water's viscosity. This leads to an increase in the cell membrane's hydraulic conductivity (Cochard et al., 2007; Martínez-Ballesta et al., 2009).

3.2.4. Stomatal conductance

When the temperature difference between the interior and exterior of a plant is higher, the plant is better able to control its temperature by allowing water to evaporate via its stomata. Evaporative cooling is the process that helps to reduce the temperature within the plant's canopy, which in turn serves to protect the plant from the negative effects of heat stress. When the temperature is high everywhere around it, the plant cools itself down by exhaling water vapor via its stomata. This effectively lowers the temperature inside the plant's canopy. The phenomenon is known as "Canopy Temperature Depression (CTD)" describes this drop in temperature. By utilizing evaporative cooling through stomatal conductance, plants are better equipped to cope with high temperatures and maintain optimal growing conditions. A strong association exists between CTD and wheat stomatal conductance in hot environments (Amani et al., 1996; Reynolds et al., 1998). Vapor pressure deficit between the canopy and the atmosphere as well as chemical signals generated in dehydrating roots regulate stomatal opening/closure, thus maintaining the water potential of the plant (Pirasteh-Anosheh et al., 2016). As a useful selection criterion for wheat yield under heat stress, stomatal conductance has been proposed and has a high heritability (Rebetzke et al., 2003; Condon et al., 2004).

3.3. Biochemical responses

Elevated temperatures can disrupt the normal functioning of biochemical processes, leading to significant reductions in crop yield. To cope with heat stress, plants have evolved complex mechanisms to regulate their biochemical responses and maintain metabolic homeostasis. Understanding these biochemical responses is crucial for the development of heat-tolerant crops and sustainable agriculture. In this context, it is important to examine the changes in the biochemical processes of wheat in response to heat stress, as well as the mechanisms involved in the regulation of these processes. When exposed to elevated temperatures, the normal metabolic activities of the plant can be disrupted, leading to a range of physiological responses. Some of the key biochemical responses of heat stress in wheat plants include:

3.3.1. Enzyme activities

The major photosynthetic enzyme Rubisco is heat sensitive and its activity declines sharply under high-temperature stress. Rubisco-activase which drives the activity of Rubisco also gets diminished under heat stress and this leads to a drop in carbon fixation. Additionally, at higher temperatures, the solubility of CO_2 is substantially reduced in comparison to that of O_2, which favors the oxygenation activity of Rubisco, ultimately leading to an increase in photorespiration and a reduction in the rate of photosynthesis (Lea and Leegood, 1999). Under conditions of extreme temperature stress, the endogenous levels of the enzyme rubisco-activase can be a determining factor in wheat yield (Ristic et al., 2009). When a conserved sequence that provides thermal stability to the enzyme in a heat-adapted species was mutated in wheat, the thermostability of wheat rubisco-activase was enhanced (Scafaro et al., 2019). Starch synthase is an important enzyme that plays a role in both the manufacture of endosperm starch and the filling of grains (SS). The activity of SS decreases at temperatures above 25°C which leads to impairment of starch accumulation eventually affecting grain filling (Keeling et al., 1993). SS is regulated at the transcriptional level during heat stress, where the level of transcripts for the enzyme decreases rapidly relative to other enzymes for starch biosynthesis (Hawker and Jenner, 1993). Temperatures that are higher than this range have a detrimental impact on the activity of soluble starch synthase (SSS), which ultimately leads to less starch being accumulated. The optimal temperature range for SSS is 20–25°C (Prakash et al., 2004). This impact can be reversed when the heat stress lasts for just a short amount of time; however, when the heat stress lasts for a longer period of time, there is a suppression of the enzyme activity that is almost impossible to reverse (Sumesh et al., 2008).

3.3.2. Membrane stability

The thermostability of the membrane is a valuable feature for selecting genotypes of heat-tolerant wheat (Blum et al., 2001). The genetic variability and heritability for membrane stability in wheat are high. (Shanahan et al., 1990; Fokar et al., 1998b). Heat stress affects the plasma membrane and leads to the leakage of solutes. The level of heat damage is dependent on the degree of unsaturation of the lipids in the membrane. Plants that can preserve their high-temperature membrane functionality can better withstand heat stress (Blum, 1988). A set of diverse wheat lines for cell membrane stability (CTS) was evaluated at heat stress conditions and concluded that CTS can efficiently discriminate heat-tolerant and susceptible lines and displayed a significant correlation with yield (Islam et al., 2017). Increased membrane stability index at elevated temperatures was observed in genotypes of heat-tolerant wheat due to an increase in antioxidant enzyme activity (Sairam et al., 1997).

3.3.3. Reactive oxygen species

Plants exposed to high-temperature stress secrete substantial amounts of reactive oxygen (ROS) species including superoxide radical ($^1O_{2-}$), hydrogen peroxide (H_2O_2), hydroxyl ion (OH-) and singlet oxygen ($^1O2$) triggering oxidative stress. The major organelles that generate ROS during stress include chloroplast, mitochondria, and peroxisomes. Heat injury damages the cell membrane and protein which causes the liberation of ROS (Farooq et al., 2011). Increased ROS production results in the depolarization of cell membrane, lipid peroxidation, inactivation of many enzymes and programmed cell death (Blokhina, 2000; Mittler et al., 2011). Long-term (24 h) temperature that is really high (42°C) wheat seedlings exposed to stress showed elevated levels of superoxide ion and malondialdehyde content in their leaf tissue (Savicka and Škute, 2010).

3.3.4. Antioxidants

The antioxidant defense mechanism is accountable for maintaining the balance of reactive oxygen species (ROS) production and detoxification in plants. When exposed to stressors from the environment, these antioxidants scavenge excess ROS and guard against cellular damage. The antioxidant system in plants comprises enzymatic and non-enzymatic components (Caverzan et al., 2016). Enzyme components include superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), guaiacol peroxidase (POX), peroxiredoxin (Prxs), ascorbate-glutathione (AsAGSH) cycle enzymes such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (DHAR) (GR). Ascorbate (AsA), glutathione (GSH), tocopherol, carotenoids, and phenolic substances are nonenzymatic components that play a crucial role in cellular redox buffering. The conversion of ROS to O_2 and water is responsible for superoxide dismutase, catalase and peroxidase systems. Superoxide dismutase is involved in the superoxide anion scavenging process (O_2-). The scavenging of hydrogen peroxide (H_2O_2) is carried out by catalase and peroxidase. Antioxidant enzyme levels (catalase, guaiacol peroxidase and superoxide dismutase) increased significantly when wheat seedlings were exposed to short-term heat stress (45°C for 2 h) and were highly correlated with other heat tolerance traits (Gupta et al., 2013). Ascorbic acid is an antioxidant molecule that is water-soluble and plays a role in H_2O_2 enzymatic detoxification. Pre-anthesis treatment of the 400 mM ascorbic acid wheat cultivar increased heat resistance by controlling the activity of the APX and CATT antioxidant enzymes (Kumar et al., 2014).

3.3.5. Heat shock proteins

Heat shock proteins (HSPs) are a distinct class of proteins that are produced during high-temperature stress by plants. There are two types of HSPs: HSPs with high molecular weight (MW: 68 to 110kD) and HSPs with low molecular weight (MW) (MW: 15 to 27 kD). In all species, high molecular weight HSPs are contained, whereas low molecular weight HSPs are distributed abundantly in higher plants. Five big plant HSP families exist in the system *viz.*, HSP100, HSP90, HSP70, HSP60, and minor HSPs (Gupta et al., 2010). The majority of plant-made HSPs are caused by heat stress and are referred to as molecular chaperones. By binding to them these proteins stabilize partially unfolded or denatured proteins and protect them from thermal aggregation (Vierling, 1991; Feder and Hofmann, 1999). After the stress is relieved, these proteins assist in re-folding of the folded proteins to recover them from stress. Some HSPs also participate in degrading harmful proteins generated from misfolding, denaturation or aggregation and aid in regulating cellular homeostasis (Wang et al., 2004). heat-tolerant wheat cultivars had high levels of HSP100 in the developing grains compared to heat susceptible cultivars under heat stress treatment (Sumesh et al., 2008).

Transgenic wheat encoding the elongation factor (Ef-Tu) of maize plastidial protein synthesis improved heat tolerance in wheat by decreasing thermal aggregation of leaf proteins, reducing heat damage to thylakoid membranes and raising the rate of CO_2 fixation (Fu et al., 2008). Heat shock transcription factor TaHsfA6f over-expression in wheat up-regulated multiple HSPs and other heat stress defence proteins such as Golgi anti-apoptotic protein (GAAP) and the broad Rubisco-activase isoform (Xue et al., 2015). Under high-temperature conditions (37°C and 42°C), the TaHsp90 gene was expressed 7.6 times higher in the heat and drought-tolerant Indian wheat cultivar C^{-306} using subtractive hybridization suppression (SSH; Vishwakarma et al., 2018). HSP70 gene expression level varies temporally and spatially in heat-tolerant and heat-prone wheat cultivars at various stages of growth under heat stress (Kumar et al., 2016). The expression of *HSP70* was found to be always higher in the tolerant cultivar compared to the susceptible cultivar at all the observed stages. *HSP70* expression was also positively correlated with total antioxidant capacity and negatively correlated with cell membrane stability. In wheat genotypes, an SNP heat shock protein (HSP16.9) was found to contribute a 29.89% phenotypic difference in grain weight per spike between a heat-resistant and heat-susceptible protein (Garg et al., 2012). There are now 753 HSP genes known to exist in the wheat genome (Figure 3), including 169 TaSHSP, 273 TaHSP40, 95 TaHSP60, 114 TaHSP70, 18 TaHSP90, and 84 TaHSP100 (Kumar et al., 2020).

3.4. Heat stress on wheat disease

The future of world wheat production is threatened by a number of biotic constraints, one of the most important being disease. One research found that plant diseases were responsible for around 20% of the world's total yield loss in major crops (Thind, 2012). The estimated actual yield losses of wheat caused by fungi and bacteria is about 10% and with viruses is 2% (Oerke, 2006). The major biotrophs are *Blumeria graminis* causing powdery mildew, *Puccinia graminis* causing stem rust, *Puccinia treticina* causing leaf rust, and *Puccinia striiformis* causing stripe rust to wheat production. Necrotrophic pathogens like *Pyrenophora tritici-repentis* causing tan spot, *Mycosphaerella graminicola* causing Septoria tritici leaf blotch, *Phaeosphaeria nodorum* causing *Septoria nodorum* blotch, *Cochliobolus sativus* causing spot blotch, and *Fusarium graminearum* and other *Fusarium* species causing Fusarium head or ear blight diseases of wheat. Many more fungal pathogens are causing soil-borne root rots of wheat (Duveiller et al., 2007). Common bunt caused by *Tilletia caries* and Karnal bunt caused by *Tilletia indica* can be of great importance in some regions to wheat production (Oerke, 2006; Bockus et al., 2010) summarized wheat pathogens including fungi, viruses, and bacteria as obstacles to wheat production.

Heat stress, especially high temperatures, makes the crop more susceptible to pathogen attack and difficult to combat. The development of plant and plant-pathogen interaction is highly influenced by both the rising temperature and the duration of its exposure. In a region relocation of warming climatic conditions due to changing climatic conditions causes several changes including synchronization of pathogen life-cycle stages, over-wintering, changes in polycyclic pathogens in wheat diseases generation number, and geographic distribution with increased risk of pathogen invasion (Chakraborty et al., 2000; Ghini et al., 2012; West et al., 2012) Global warming weakens a plant's natural defense system because, at above-normal temperatures, decreases the production of a defense hormone called salicylic acid. Crop physiology and canopy architecture are both affected by varying weather conditions (Pangga et al., 2013), as well as disease levels and disease spread. Like above-ground leaf Pathogens, the growth, and prevalence of economically important soil-borne plant pathogens e.g., *Alternaria*, *Fusarium*, and Phoma species are also subjected to favor by warming (Delgado-Baquerizo et al., 2020). In addition, insects that feed on plants (Miedaner, 2018) make it easy to get an entry into mycotoxin-producing Fusarium species.

Temperature-sensitive genes in wheat *L210* and *L217* due to the temperature effect become susceptible to wheat leaf rust (Das et al., 2016). In European wheat stripe rust isolates higher aggressiveness against higher temperatures was reported by Mboup et al. (2012). It was reported by Walter et al. (2016) two isolates of yellow rust *PstS1* and *PstS2* in Western Australia and the South-Eastern USA were 3 days earlier and produced 370% more spores (area/day) at high temperatures (28/12°C) than the old races. Wheat cultivars having the gene Sr6 are resistant to stem rust growing at 18°C but at 27°C these cultivars become susceptible (Moerschbacher et al., 1989). Fusarium head blight incidence is estimated to increase at anthesis 10–16% by the 2050s and might be the risk of higher grain losses with mycotoxin contamination of grain because of the forecasted increase of temperatures in the United Kingdom, especially in southern England (Madgwick et al., 2011). *Blumeria graminis* f. sp. *tritici*, were found more resistant at the booting stage at 25°C until prior to inoculation (Desaint et al., 2021). Severe wheat yield loss in susceptible cultivars ranges up to 100% due to wheat blast disease as the result of the coincidence of growth stage with the warm temperature and wet years (Cruz and Valent, 2017; Singh et al., 2021). In Bangladesh, optimum planted wheat which faces minimum temperature at the heading stage had less blast severity but it was increased with the later sowing dates during the 2017–18 cropping season (BWMRI, 2018).

Resistance breeding to diseases of wheat under global climate change has several challenges. There is an increasing risk of diseases like leaf rust and fusarium head blight, re-emergence of the old pathogen as an example of stem rust including the emergence of a new or still unknown pathogen, and high adaptation of pathogens like *P. striiformis*, In the future, it is inevitable to adjustments into resistance breeding strategies with stability and durability of disease resistance under heat in long-term disease occurrence. Continuous delivery of appropriate and adapted wheat varieties to farmers to manage climate change-driven changes is unavoidable. A study found that breeding cultivars with better disease resistance are included in trials in nations with warmer temperatures that nevertheless reflect projected conditions in cooler places (Butterworth et al., 2010). Future research should reflect on multi-disease resistance genes (MDRs), i.e., genes or QTLs that confer resistance to multiple diseases. Manipulating the sowing date or alternations of heading and flowering dates have consequences on disease patterns in wheat, particularly for flower-infecting fungi such as *Fusarium* species (West et al., 2012).

4. Genetics of heat stress

Heat tolerance is a quantitative trait that is governed by the number of QTLs. Genetics under heat stress is being studied for the past three decades. Using Langdon CSLs (chromosome substitution lines), the first mapping investigation for heat tolerance was carried out in 1991. The genes responsible for heat tolerance were located on chromosomes 3A, 3B, 4A, 4B, and 6A, respectively, (Sun and Quick, 1991). Chromosomes 3A, 3B, and 3D were found to be correlated with heat tolerance in a wheat cultivar name Hope (Ruqiang et al., 1996). Increased heat tolerance was achieved in cultivar Hope by using CSLs between Chinese Spring and Hope (Ni et al., 2018). Chromosomes 3A and 3B harbored important genes regulating heat tolerance. To obtain comprehensive information on QTLs associated with heat tolerance in wheat, a thorough search was conducted using online databases, Google Scholar[2] and PubMed.[3] In addition, we utilized information available in WheatQTLdb.[4] The identified QTLs were compiled and listed in Table 1.

Many QTLs regulating heat tolerance have consistently been located on chromosome 3B (Mason et al., 2010). A drought and heat-tolerant QTL, *qDHY.3BL* was mapped on Chr 3B in a ~ 1 Mbp interval which harbored 22 genes. Developments in quantitative genetics and molecular markers offered potential tools to identify QTLs influencing heat tolerance in wheat (Thomelin et al., 2016). Eight major QTL regions showing association with drought and heat tolerance located on 1B, 2B, 2D, 4A, 4B, 4D, 5A, and 7A chromosomes were recorded in a meta-QTL study, suggesting that fine-mapping would help locate the genes in these regions (Acuña-Galindo et al., 2015). With the availability of the published sequencing data progress in map-based cloning for heat-tolerance can be achieved for cloning major QTLs (Clavijo et al., 2017).

A heat-tolerant major QTL *thermo-tolerance 1* (*TT1*) was located and cloned in *Oryza glaberrima* (African rice) which degrades the ubiquitinated proteins. The allele from heat-tolerant accession *OgTT1* increases heat tolerance by eliminating the cytotoxic and degraded proteins contrary to heat sensitive-cultivar with *OsTT1* allele. Overexpression of *OgTT1* showed increased heat tolerance in *oryza*, *Arabidopsis* and *Festuca elata* (Li et al., 2015). Over-expression of *OsMYB55* in maize increased heat and drought tolerance under stress conditions as indicated by high biomass and lesser leaf damage in the tolerant lines. Transcriptome analysis from RNA sequencing showed a constitutive upregulation of the genes involved in heat stress among the wild-type plants in *OsMYB55* transgenic maize. In one of the three

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[2] https://scholar.google.com, Accessed on 27 May 2023.

[3] https://pubmed.ncbi.nlm.nih.gov, Accessed on 27 May 2023.

[4] http://www.wheatqtldb.net, Accessed on 27 May 2023.

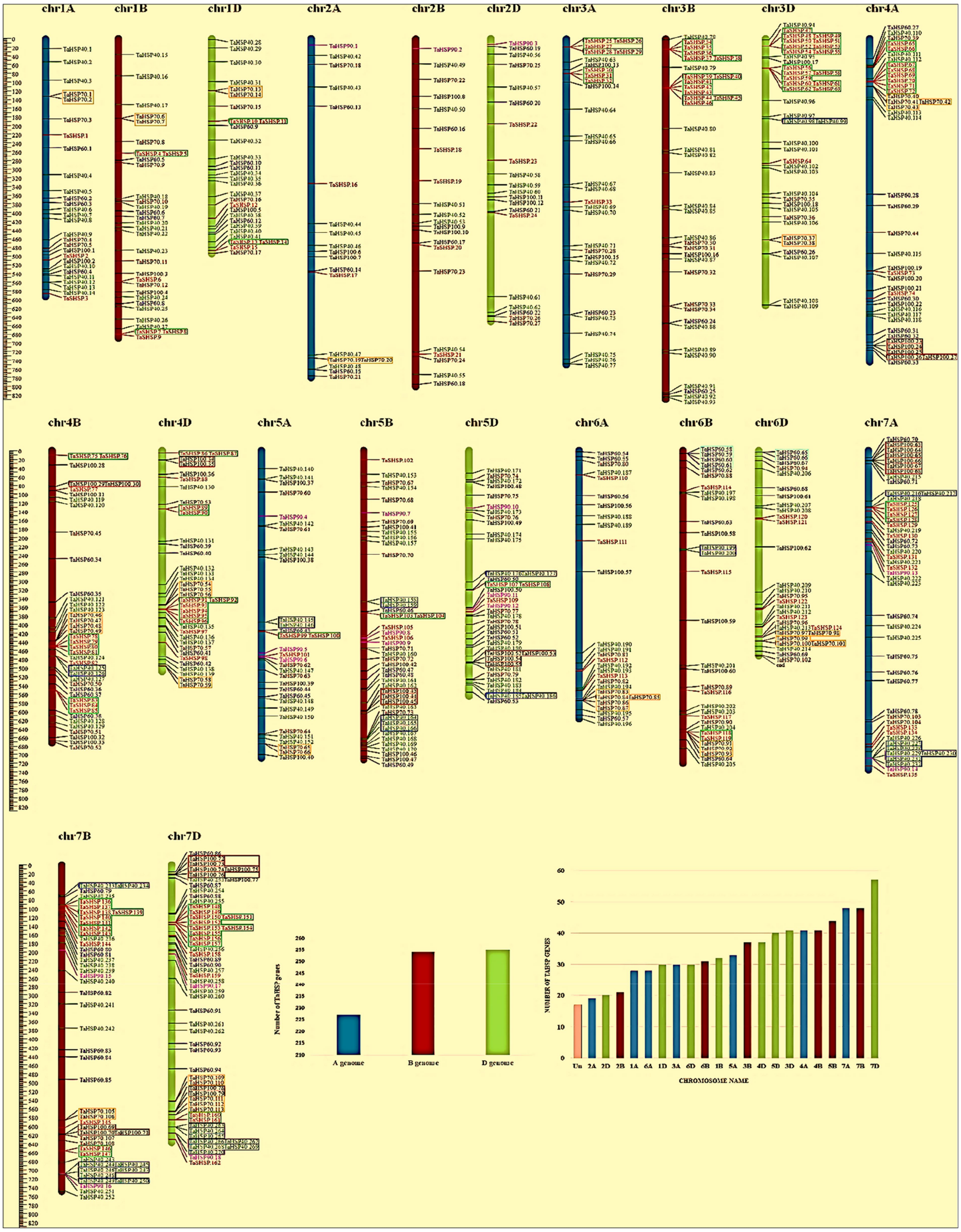

FIGURE 3
Wheat's 21 chromosomes and three subgenomes HSP gene distribution. Boxed genes are tandem duplications. **(A)** Physical map of chromosomal distribution with gene names on the right and location on the left. HSP gene distribution on 21 chromosomes. **(C)** HSP gene distribution in three sub-genomes. Retrieved and modified from Kumar et al. (2020) with permission.

QTL regions, the candidate gene encoding HSc70 shows higher yields among the diploid potato population in a hybrid called *Phureja-Tuberosumum* (Casaretto et al., 2016; Trapero-Mozos et al., 2018). *HSc70* expression was greater than others under moderate heat stress conditions, as seen with a greater tolerance to heat stress with enhanced yields among plants grown from stem cuttings.

TABLE 1 A list of identified QTLs so far associated with heat tolerance in wheat.

Sl No	Trait	QTL	Marker or flanking marker	Chromosomes	References
1	HSI of Grain weight/ main spike	Qgws.iiwbr-2A	GWM448	2A	Bhusal et al. (2017)
2	HSI of Thousand Grain Weight	Qtgw.iiwbr-2A	Gwm122	2A	
3	HSI of grain filling duration	QhtHSI ofgfd.iiwbr-2B	Gwm257	2B	
4	HSI of Thousand grain weight	QHSI oftgw.cau-1A	RAC875_c54380_249	1A	Guan et al. (2018)
5	HSI of thousand grain weight	QHSI oftgw.cau-2D	Kukri_c19540_425	2D	
6	HSI of thousand grain weight	QHSI oftgw.cau-4B.1	Excalibur_c51845_186	4B	
7	HSI of thousand grain weight	QHSI oftgw.cau-4B.2	WMC652	4B	
8	HSI of thousand grain weight	QHSI oftgw.cau-4B.2	gpw7390	4B	
9	HSI of thousand grain weight	QHSI oftgw.cau-5B	barc59	5B	
10	HSI of Thousand grain weight	QHSI oftgw.cau-6A	BS00068092_51	6A	
11	HSI of thousand grain weight	QHSI oftgw.cau-6B	BS00009825_51	6B	
12	HSI OF thousand Grain weight	QHSI oftgw.cau-6D	IACX10982	6D	
13	Grain yield	QGY-2B	aag/ctc-13-acc/ctc-9	2B	Hassan et al. (2018)
14	Grain yield	QGY-2D	wPt-6,657-gdm035	2D	
15	Water soluble carbohydrates	QWSC-4A	act/cag-3-agg/cta-12	4A	
16	Cytoplasmic membrane stability	QCMS-4B	wPt-1708-wmc048a	4B	
17	Proline content	QPro-5B	acc/ctc-3-gwm133	5B	
18	Maximum efficiency of photosystem II (Fv/Fm)	QFv/Fm-6A	wmc0256-acc/ctg-6	6A	
19	SSI of Grain yeild	QTL.ICD.Heat.03	AX-94538070	2A	El Hassouni et al. (2019)
20	SSI of Grain yeild	QTL.ICD.Heat.08§	AX-94631521	5A	
21	SSI of grain yield	QTL.ICD.Heat.09§	AX-95182463	5B	
22	SSI of grain yield	QTL.ICD.Heat.10§	AX-94408589	6B	
23	Grain number per main spike	QGNP-HS-R1	AX-95652063-AX-95660318	1A	Li et al. (2019)
24	Grain yield per plant	QGYP-HS-R1	AX-111105973-AX-94402739	1A	
25	Thousand kernel weight	QTKW-HS-R1	AX-94745844-AX-110935476	1D	
26	Grain number per main spike	QGNP-HS-R2	AX-109501025-AX-108731558	2B	
27	Grain yield per plant	QGYP-HS-R2	AX-94940181-AX-108730045	2B	
28	Grain number per main spike	QGNP-HS-R3	AX-94684189-AX-110122723	3A	
29	Grain number per main spike	QGNP-HS-R4	AX-111656976-AX-110051593	3A	
30	Grain yield per plant	QGYP-HS-R3	AX-111659209-AX-94667190	3A	
31	Grain yield per plant	QGYP-HS-R4	Xwmc532-AX-109285546	3A	
32	Thousand kernel weight	QTKW-HS-R2	AX-111475478-AX-89654830	4D	
33	Grain yield per plant	QGYP-HS-R5	AX-95630862-AX-95630256	5A	
34	Thousand kernel weight	QTKW-HS-R3	AX-111764369-AX-95659703	5A	
35	Grain number per main spike	QGNP-HS-R5	AX-95658487-AX-109829036	5B	
36	Thousand Kernel weight	QTKW-HS-R4	AX-108805055-AX-109308225	5D	
37	Grain number per main spike	QGNP-HS-R6	AX-95177681-AX-94427873	6B	
38	Thousand Kernel weight	QTKW-HS-R5	AX-110986080-AX-109476271	6B	
39	HSI of Kernel number of main-spike	QHknm.tam-1A	cfa2129	1A	Mason et al. (2010)
40	HSI of Kernel weight of main-spike	QHkwm.tam-1B	gwm268	1B	
41	HSI of Single kernel weight of main-spike	QHskm.tam-2A	gwm294	2A	
42	HSI of Single kernel weight of main-spike	QHskm.tam-2A c	gwm356	2A	

(Continued)

TABLE 1 (Continued)

Sl No	Trait	QTL	Marker or flanking marker	Chromosomes	References
43	HSI of Kernel number of main-spike	QHknm.tam-2B	gwm111.2	2B	
44	HSI of Kernel number of main-spike	QHknm.tam-2B	barc200.2	2B	
45	HSI of Kernel number of main-spike	QHknm.tam-3B c	barc147	3B	
46	HSI of Kernel weight of main-spike	QHkwm.tam-3B	wmc326	3B	
47	HSI of Kernel weight of main-spike	QHkwm.tam-3B	wmc527	3B	
48	HIS Single kernel weight of main-spike	QHskm.tam-4A	barc170	4A	
49	HSI of Kernel number of main-spike	QHknm.tam-4A	wmc89	4A	
50	HIS Single kernel weight of main-spike	QHskm.tam-5A	barc151	5A	
51	HSI of Kernel number of main-spike	QHknm.tam-5A.1	barc197	5A	
52	HSI of Kernel number of main-spike	QHknm.tam-5A.2	gwm126	5A	
53	HSI of Kernel weight of main-spike	QHkwm.tam-5A	gwm291	5A	
54	HSI of Kernel number of main-spike	QHknm.tam-5B	gwm213	5B	
55	HIS single kernel weight of main-spike	QHskm.tam-7A	gwm282	7A	
56	HSI of Kernel weight of main-spike	QHkwm.tam-1B	gwm153	1B	
57	HSI of Single kernel weight of main-spike	QHskm.tam-2D.1	gwm261	2D	
58	HSI of single kernel weight of main-spike	QHskm.tam-2D.2	cfd56	2D	
59	HSI of Single kernel weight of main-spike	QHskm.tam-3B	barc229	3B	
60	HSI of Single kernel weight of main-spike	QHskm.tam-4A.1	wmc707	4A	
61	HSI of Single kernel weight of main-spike	QHskm.tam-4A.2	wmc313	4A	
62	HSI of Kernel weight of main-spike	QHkwm.tam-5A.1	gwm179	5A	
63	HSI of Kernel weight of main-spike	QHkwm.tam-5A.2	gwm291	5A	
64	HSI of Single kernel weight of main-spike	QHskm.tam-5A	gwm443	5A	
65	HSI of Kernel number of main-spike	QHknm.tam-5B	gwm408	5B	
66	HSI of single kernel weight of main-spike	QHskm.tam-5B	wmc73	5B	
67	HSI of single kernel weight of main-spike	QHskm.tam-6D	cfd49	6D	
68	HSI of Single kernel weight of main-spike	QHskm.tam-7A	wmc603	7A	
69	HSI of Single kernel weight of main-spike	QHskm.tam-7B	wmc182	7B	
70	Number of leaves per seedling	QLNHR.nri-2A.2	IWB61157	2A	Maulana et al. (2018)
71	Leaf chlorophyll content	QLCCHR.nri-2B	IWB55435	2B	
72	Leaf chlorophyll content	QLCCHR.nri-2D.1	IWB18745	2D	
73	Leaf chlorophyll content	QLCCHR.nri-2D.2	IWB66401-IWB36817	2D	
74	Number of leaves per seedling	QLNHR.nri-3A	IWB50704	3A	
75	Shoot length	QSLHR.nri-3B.1	IWB1428	3B	
76	Shoot length	QSLHR.nri-3B.2	IWB26717	3B	
77	Leaf chlorophyll content	QLCCHR.nri-4A	IWB37183	4A	
78	Leaf chlorophyll content	QLCCHR.nri-4B.1	IWB48055	4B	
79	Leaf chlorophyll content	QLCCHR.nri-4B.2	IWB42264-IWB35851	4B	
80	Number of leaves per seedling	QLNHR.nri-4B	IWB64397-IWB10366	4B	
81	Leaf chlorophyll content	QLCCHR.nri-5B	IWB64287-IWA4329	5B	
82	Number of leaves per seedling	QLNHR.nri-5B.1	IWB71913-IWB43528	5B	
83	Number of leaves per seedling	QLNHR.nri-5B.2	IWB58120	5B	
84	Number of leaves per seedling	QLNHR.nri-7B	IWB34893	7B	
85	Shoot length	QSLHR.nri-7D	IWB12476, IWB12582	7D	

(Continued)

TABLE 1 (Continued)

Sl No	Trait	QTL	Marker or flanking marker	Chromosomes	References
86	SSI of Kernel weight	–	gwm190	1B	Mohammadi et al. (2008)
87	SSI of Kernel weight	–	gwm133A	5B	
88	SSI of Kernel weight	–	gwm63B	7B	
89	HSI of thousand grain weight	QHtHSI oftgw.bhu—2B	Xgwm935 – Xgwm1273	2B	Paliwal et al. (2012)
90	HSI of thousand grain weight	QHtHSI oftgw.bhu—7B	Xgwm1025 – Xgwm745	7D	
91	HSI of thousand grain weight	QHtHSI oftgw.bhu—7D	Xgwm1025 – Xgwm745	7D	
92	Days to heading	Qdh.ccshau-2A	xgwm512-xgwm448	2A	Sangwan et al. (2019)
93	iWUE	Qiwu.ccshau-2.1A	xgwm497-xgwm512	2A	
94	iWUE	Qiwu.ccshau-2.2A	xgwm512-xgwm448	2A	
95	iWUE	Qiwu.ccshau-2.3A	xgwm512-xgwm448	2A	
96	Plant heigh	Qph.ccshau-2A	xgwm512-xgwm448	2A	
97	Days to heading	Qdh.ccshau-2D	barc124-xgwm102	2D	
98	Days to maturity	Qdm.ccshau-2.1D	barc124-xgwm102	2D	
99	Days to maturity	Qdm.ccshau-2.2D	gwm249-gwm382	2D	
100	Photosynthetic rate (Pn)	Qpn.ccshau-2.1D	barc124-xgwm102	2D	
101	Photosynthetic rate (Pn)	Qpn.ccshau-2.2D	barc124-xgwm102	2D	
102	iWUE	Qiwu.ccshau-4A	xgwm165-xcfd71	4A	
103	Plant height	Qph.ccshau-4A	xgwm165-xcfd71	4A	
104	Transpiration rate (E)	Qe.ccshau-4A	xgwm165-xcfd71	4A	
105	NDVI	Qndvi.ccshau-5A	barc186-barc141	5A	
106	HSI of single grain weight	QHsgw.aww-3B	wsnp_BE497169B_Ta_2_1	3B	Shirdelmoghanloo et al. (2016)
107	HSI of single grain weight	QHsgw.aww-3B	wsnp_Ex_c12875_20407926	3B	
108	HSI of single grain weight	QHsgw.aww-6B	wsnp_Ex_c11573_18650189	6B	
109	SPAD chlorophyll content	QHtscc.ksu-1B	gwm18, Bin1130	1B	Talukder et al. (2014)
110	Thylakoid membrane damage	QHttmd.ksu-1D	Bin747, Bin1596	1D	
111	Plasma membrane damage	QHtpmd.ksu-2B	Bin178, Bin81	2B	
112	Thylakoid membrane damage	QHttmd.ksu-6A	Xbarc113, AGCTCG347	6A	
113	SPAD chlorophyll content	QHtscc.ksu-7A	Bin754, Bin45	7A	
114	Thylakoid membrane damage	QHttmd.ksu-7A	Xbarc121, barc49	7A	
115	Spikelet number per spike	QSpn.agt-SG.1D	–	1D	Telfer et al. (2021)
116	Grain yield per spike	QGwe.agt-RG.2A	–	2A	
117	Spikelet number per spike	QSpn.agt-RG.3A.1	–	3A	
118	Spikelet number per spike	QSpn.agt-RG.4B	–	4B	
119	Spikelet number per spike	QSpn.agt-RG.4D	–	4D	
120	Spikelet number per spike	QSpn.agt-RG.5A.3	–	5A	
121	Spikelet number per spike	QSpn.agt-RG.6A.1	–	6A	
122	Spikelet number per spike	QSpn.agt-RG.6A.2	–	6A	
123	Spikelet number per spike	QSpn.agt-RG.6B	–	6B	
124	SSI of thousand-grain weight	QSsi.cau.4B_33	wsnp_Ex_c18318_27140346-wsnp_Ra_c9755_16200944	4B	Wang et al. (2021)
125	SSI of thousand-grain weight	QSsi.cau.5A_91	IAAV3365-Kukri_c33022_198	5A	
126	SSI of Thousand-grain weight	QSsi.cau.5D_138	RFL_Contig1091_1538	5D	
127	Grain-filling duration	–	Xgwm11	1B	Yang et al. (2002)
128	Grain-filling duration	–	Xgwm293	5A	

(Continued)

TABLE 1 (Continued)

Sl No	Trait	QTL	Marker or flanking marker	Chromosomes	References
129	Chlorophyll fluorescence (Fv/Fm)	TaHST1	Xhau-1	4A	Zhai et al. (2021)
130	Chlorophyll fluorescence (Fv/Fm)	TaHST1	Xhau-2	4A	
131	Chlorophyll fluorescence (Fv/Fm)	TaHST1	Xhau-3	4A	
132	Chlorophyll fluorescence (Fv/Fm)	TaHST1	Xhau-4	4A	
133	Chlorophyll fluorescence (Fv/Fm)	TaHST1	Xhau-5	4A	

Heat tolerance results from a combination of different genes that regulate adaptive characteristics such as enhanced photosynthetic activity, cool canopy, stomatal conductivity and improved pubescence, as most of these characteristics have been correlated with grain yield under heat stress conditions (Cossani and Reynolds, 2012). Leaf wax lowers heat uptake and reduces the leaf temperature (Ishag, 1994). Under conditions of limited water availability leaf waxiness showed an association with a cooler canopy (Richards et al., 1986) however, beneath the heat stress situation the influence of leaf wax in lowering the canopy temperature is not known. QTLs for flag leaf wax content were located on 1B, 3D and 5A chromosomes of which 1B and 5A harbored stable loci. Two QTLs for flag leaf waxes (*QWax.tam09-1B* and *QWax.tam09-5A*) showed a phenotypic variation of 9 and 12%, respectively, from 121 RIL populations generated from a cross between tolerant genotype 'Halberd' and susceptible genotype 'Karl92' were found to be located for heat tolerance (Mondal et al., 2015).

Plant survival, growth and reproduction are severely affected by heat, salinity, and other abiotic stress to which the plants respond by expressing stress-responsive genes that are regulated by heat stress transcription factors (*HSFs*) which in turn regulate the heat shock proteins (*Hsps*). *HSF* are *TFs* that bind to *HSE cis* components in the gene-promoting region and play a key role in plant tolerance against heat stress. Heat stress transcription factors have highly conserved regions however their notable diversity across plants shows their multiple functions and their incorporation into several stress-signaling and response networks. In Arabidopsis, ectopic expression of *oryza HSFA2e* and *lily HSFA2* results in enhanced heat tolerance. Overexpression of soybean *GmHSFA1* improved heat tolerance in soybean due to the activation of *GmHsp70*, *GmHsp22* and *GmHsps* downstream genes (Zhu et al., 2006). *Tomato HSFA1a* is a unique and key regulator for acquired heat tolerance and is not replaced by other *HSFs*. *HSFA1* subfamily is considered a key regulator of heat-stress response. However, the role of *HSF* genes is to be better understood to reduce the negative impact in transgenic plants. In tobacco, over-expression of *VpHSF1* increased acquired heat tolerance but decreased basal heat tolerance and osmotic stress tolerance (Peng S. et al., 2013). *SlHSFA3* led to an improvement in heat tolerance in Arabidopsis over tomato expression and showed a negative effect on seed germination under salinity stress (Li Z. et al., 2013). Since *HSFs* and molecular chaperones play a key role in cellular homeostasis, *HSF* modification can impede homeostasis, leading to pleiotropic and unwanted effects (Cabello et al., 2014). Much progress has been attained in characterizing the *HSFAs* class however, the biological function needs to be understood for *HSFB* and *HSFC*. The regulation factors of *HSFS* are to be clearly studied. Hence the regulatory mechanisms of these *HSF* genes are to be understood properly. They can be further integrated with several crop improvement projects through biotechnological methods.

Under conditions of stress, abscisic acid induces stomatal closure and activates stress-responsive genes. Improvements in molecular technologies, such as microarray and transcriptome analysis, led to the discovery of several stress-responsive genes. These genes not only produce enzymes and proteins for cellular defense, but also control signal transduction pathways and gene expression. In the leaves of heat-sensitive and heat-tolerant genotypes, i.e., Chinese Spring and TAM107 respectively, microarray analysis was used to match up gene expression assessment. After short and continued heat treatment, distinct gene expression patterns were established between the genotypes. The genes found included several significant factors responsible for different biological pathways that promoted the need for different wheat genotypes to decipher the genetics behind heat tolerance (Qin et al., 2008).

Genome-wide association study (GWAS) is a potential and proven approach to determine which genes are responsible for responding to heat stress because the process of heat tolerance is so complicated. GWAS has been used in wheat to dissect the complex genetic locus of heat tolerance (Tian et al., 2011). One hundred forty-eight MTAs with a phenotypic variation from 0.25 to 0.36 were identified in a study (El Hassouni et al., 2019). Grain number per spike reported the highest number of MTAs located over 10 loci, and harvest index over six loci. Under heat stress conditions a common region for grain yield, grain number per spike, harvest index and biomass were located on 6BS. A study on a double haploid population in bread wheat found a major QTL on 1A chromosome affecting grain number, grain weight per spike and spike per meter square (Heidari et al., 2011).

5. Strategies to be taken to combat heat stress

The discrepancy in environmental change has an ongoing impact on agriculture and food safety globally. The increasing frequency and intensity of heat stress events pose a major threat to global food security and the sustainability of wheat production. To mitigate the impact of heat stress on wheat, a range of strategies and practices must be implemented. These can include breeding for heat tolerance, proper irrigation and water management, soil management, mulching and shading, crop management practices, agronomic practices, the use of heat-tolerant cultivars, climate-smart agriculture, and research and development. By adopting these strategies, the resilience of wheat to heat stress can be improved, ensuring sustainable food production and food security for a growing global population. The following tactics can be taken as vital for crop adaptation in a heat-stress environment.

5.1. Agronomic and cultural management for adaptation to heat stress

By altering certain agronomic management techniques such as (i) conservation farming to minimize soil moisture loss (ii) using a balanced dose of fertilizers (iii) changing the sowing period and methods and (iv) using exogenous protectants to mitigate the impact of extreme heat, wheat can be better prepared to grow in warmer environments (Singh et al., 2011a). Mulching can be a good option for minimizing water loss owing to heat stress, especially in rainfed areas where water availability is a serious concern. Organic mulches help in maintaining soil moisture, improving plant growth and nitrogen use efficiency (Singh et al., 2011a). In the north-western plains zone of India, planting wheat in the presence of rice stubbles using zero tillage technique helps in conserving water, and soil nutrients, minimizing weed incidence, adapting to terminal heat stress and improves the overall health of the wheat crop (Erenstein and Laxmi, 2008). Delaying the wheat sowing beyond the recommended sowing time can expose the crop to heat stress during post-reproductive stages which ultimately affects the yield and grain quality. Therefore, late sowing of wheat varieties needs to be avoided at any cost. Planting cultivars having early maturity and long grain filling duration can avoid the effects of terminal heat stress (Al-Karaki, 2012).

For plants to thrive in the face of biotic and abiotic challenges, they must receive adequate and well-balanced amounts of fertilizers. A foliar spray of nutrients can help ameliorate the effects of heat stress. Potassium nitrate (KNO_3) foliar spray at booting and grain filling stages increased grain yield in wheat by delaying senescence and improving carbohydrate transport and starch synthesis in the sink organs (Singh et al., 2011b). Orthophosphate (KH_2PO_4) used as a post-anthesis foliar spray reduced heat-induced leaf senescence and increased grain production (Dias and Lidon, 2010). The application of calcium chloride ($CaCl_2$) enhanced the activities of antioxidant enzymes during heat stress in wheat. Calcium plays a role in stomatal regulation and guards chlorophyll against photo-oxidative damage which helps the plant in tackling heat stress (Dias et al., 2009). Supplementation with zinc during high-temperature conditions improves the plant's responses by maintaining cell membrane stability, stabilizing chlorophyll fluorescence, improving water uptake efficiency and improving evaporative cooling (Peck and McDonald, 2010). An exogenous spray of magnesium in the form of magnesium sulphate ($MgSO_4.7H_2O$) during high-temperature stress improved heat tolerance by minimizing oxidative damage (Mengutay et al., 2013).

Recently, there is a rising demand for the use of osmoprotectants, growth regulators and signaling molecules as an exogenous therapy to reduce different abiotic stresses (Upreti and Sharma, 2016; Ahmed et al., 2019). These molecules reduce the effect of heat stress by activating various antioxidants that are responsible for alleviating oxidative damage. In wheat, the role of various growth protectants like arginine, salicylic acid, putrescine, ascorbic acid and α-tocopherol (vitamin E) in improving heat tolerance has been well elucidated. Treatment with salicylic acid increased heat tolerance in wheat by improving proline metabolism, reducing the formation of ethylene and improving photosynthesis under heat stress (Khan et al., 2013). By decreasing lipid peroxidation (malondialdehyde content), increasing proline biosynthesis and upregulating enzymatic antioxidants, melatonin (N-acetyl-5-methoxy tryptamine), a pleiotropic signaling molecule, enhanced heat stress tolerance in wheat (Buttar et al., 2020). By increasing the operation of antioxidant enzymes and proline biosynthesis, the exogenous application of polyamines (spermidine and spermine) reduced the impact of heat stress at the grain-filling stage in the heat-responsive wheat variety (Jing et al., 2020). In addition, there was a reduction in the malondialdehyde, soluble sugar and putrescine content. Plant growth regulators which are successfully utilized in other crops can also be tested for their effectiveness in wheat. The dosage and mode of the application need to be standardized for these growth protectants for their successful commercialization (Ratnakumar et al., 2016). The environmental toxicity assessment of these new-generation molecules must be carried out rigorously to confirm their safety.

5.2. Marker-assisted selection

Genetic divergence is a vital technique of breeding for new cultivars based on genetic resources (Raza et al., 2019). Landraces are a significant resource for genomic studies which contain larger genomic variance and are treasured for stress tolerance as it contains adaptable genetic resources to various climatic stresses (Lobell et al., 2011; Kumar et al., 2023). The urgent need for the hour is a genetic variation of heat tolerance in the case of wheat breeding, research and the use of new variants (Kayastha et al., 2023). High throughput MAS breeding can fast-track plant breeding with high productivity (Zafar et al., 2018). Heat tolerance is a much complex trait, which is governed by genotype and genotype × environment interaction effects (Tayade et al., 2018). In Mexican wheat landraces (>1,200) gathered from places with varying heat-stressed management areas, a group of superior accessions was detected, and a strong connection was observed between the amount of leaf chlorophyll and the thousand-grain weight (Ma et al., 2009). There are already certain heat-tolerant cultivars and lines established in Asia, and these can be utilized to cultivate new heat-resistant cultivars. A testified inherent foundation of germplasms from *T. dicoccoides* and *T. monococcum* that can be used to improve heat tolerance in bread wheat along with *Aegilops speltoides*, *Ae. longissima* and *Ae. searsii* because of capricious notches of heat tolerance were detected from them (Yoshida et al., 2002). However, only a small proportion of the recorded genomic variation in heat tolerance has been exploited due to restrictions on traditional breeding. GWAS and other QTL mapping related to heat stress tolerance characteristics can help to develop wheat cultivars that are ideal for high-temperature climate conditions (Paliwal et al., 2012). In general, QTLs perceived in environments known as constitutive QTLs could be used to build heat-tolerant landraces. On the other hand, QTLs detected solitary in explicit environments called adaptive QTLs, could be utilized for specific heat-stressed areas (Vargas et al., 2006; Collins et al., 2008).

5.3. Genome selection for heat tolerance crop improvement

Genomic selection (GS) was initially presented by Lande and Thompson (1990), but it was Meuwissen et al. (2001) that brought it to the public's attention. Genomic selection is a modern approach to plant breeding that involves the use of DNA markers to predict the breeding values of individuals for different traits. Genomic selection are effective in promoting novel cultivars in many crops (Tayade et al., 2018). This technique has gained considerable attention in wheat breeding because of the complexity of the wheat genome and the need to develop improved varieties that can withstand various biotic and abiotic stresses. The development of high-density SNP arrays has facilitated the application of genomic selection in wheat breeding. The foremost gain of GS compared to MAS having minor effects alleles are also detected and utilized in the marker selection process (Cairns and Prasanna, 2018). GS is a helpful strategy for preparing novel breeding and advancing ground-breaking genomic evaluation marker-based models. Accessibility of high-throughput, lucrative genome-wide and scalable molecular markers suitable for a large population, in addition to or without the reference genome, is essential for the successful application of genomic selection in crops (Bhat et al., 2016). GS can be used as a pre-breeding device to aid in to detect of genomic resources with an advantageous variation for compound traits through predicting the breeding values of a specific population within the breeding population and offers new prospects to upsurge genetic gain of complex traits (Wang X. et al., 2018). GS has been applied in successful breeding programs in wheat (Song et al., 2017; Juliana et al., 2019a). The first use of genomic selection in wheat was reported in 2009 by the International Maize and Wheat Improvement Center (CIMMYT) in Mexico (Sun et al., 2020). Since then, it has been used by many researchers and breeders around the world to improve wheat varieties. They found that the accuracy of genomic selection increased with the size of the training population and the number of markers used. Since then, numerous studies have been conducted to evaluate the performance of genomic selection for different traits in wheat. In the past decade, numerous studies have investigated the potential of genomic selection in wheat, particularly for yield-related traits, disease resistance, and abiotic stress tolerance wheat (Song et al., 2017; Singh et al., 2019, 2022; Juliana et al., 2019a,b; Larkin et al., 2020; Dreisigacker et al., 2021; Mondal et al., 2021; Saini et al., 2022). These studies have shown promising results, indicating that genomic selection can enhance breeding efficiency and accelerate the development of improved wheat varieties. Their results showed that genomic selection could effectively predict wheat improvement. Utilization Genomic Selection for the breeding of wheat to adapt to heat-stressful environments is also employed in several breeding institutes, companies and universities (Mondal et al., 2021). Despite the promising results, several challenges still need to be addressed to fully realize the potential of genomic selection in wheat breeding. One of the major challenges is the lack of diversity in the training population, which can result in biased predictions. To overcome this challenge, efforts are being made to develop diverse training populations that capture the genetic variation in the target population. Another challenge is the high cost of genotyping, which can limit the adoption of genomic selection in small breeding programs. However, advances in genotyping technologies and the development of low-cost SNP arrays are expected to address this challenge in the near future.

5.4. Genome editing in wheat for heat tolerance

Wheat is a complex crop with a large genome, and many genes contribute to heat tolerance. As a reverse genetic tactic for targeting heat tolerance gene activity, genome-editing techniques such as transcription activator-like effector nucleases (TALENs), zinc finger nucleases (ZFNs), and clustered regularly interspaced short palindromic repeat (CRISPR) can also be used in addition to MAS. Compared to other genome-editing techniques, CRISPR-Cas9 has developed a powerful method for precise genome editing to study the pathways associated with heat stress and to increase thermotolerance in cropping systems (Nguyen et al., 2018; Biswal et al., 2019; Sun et al., 2022). The theory of CRISPR involves the design of a ~ 20 nucleotide RNA guide complementary to the gene of interest, while a Cas9 nuclease enzyme that cuts 3–4 bases next to the adjacent protospacer motif is repaired by homology-directed repair pathway or by non-homologous error-prone end-joining (Jiang and Doudna, 2017; Jaganathan et al., 2018). Using *in silico* and *in vivo* TILLING methods, four new small Hsp26 (sHsp26) alleles suitable for improving heat tolerance in durum wheat were identified (Comastri et al., 2018). Genome editing methods have unlocked new opportunities to instigate targeted editing of crop genomes involved in heat stress tolerance (Parmar et al., 2017; Haque et al., 2018). For example, stress-induced transcriptional factors from the AP2/ERF superfamily improved abiotic stress tolerance in crops based on CRISPR-Cas9 genome editing of ethylene response factors (ERFs; Debbarma et al., 2019).

Several reports describe the use of Agrobacterium-delivered CRISPR/Cas9 for wheat genome editing, despite the low transformation efficiency of this crop (Howells et al., 2018; Zhang et al., 2018; Okada et al., 2019; Zhang Z. et al., 2019). One of the primary targets for genome editing in wheat for heat tolerance is the Heat Shock Transcription Factor (HSTF) genes. HSTFs are a group of transcription factors that regulate the expression of heat shock proteins, which play a crucial role in protecting the plant from heat stress. By editing HSTF genes, scientists can increase the expression of heat shock proteins, which enhances the plant's ability to tolerate heat stress. Another target for genome editing in wheat for heat tolerance is the Rubisco activase (RCA) gene. Rubisco is the key enzyme responsible for carbon fixation during photosynthesis. Under heat stress, the activity of Rubisco is reduced, leading to a decline in photosynthetic efficiency. RCA is a chaperone protein that activates Rubisco, and editing RCA genes can increase the expression of RCA and, therefore, enhance Rubisco activity under heat stress. Furthermore, genome editing can also be used to improve the wheat plant's water use efficiency, which is closely linked to heat tolerance. By editing the genes that regulate stomatal opening and closing, researchers can control the plant's water loss through transpiration, leading to more efficient use of water under heat-stress conditions. Target genes used in genome editing with their function to improve stress tolerance are presented in Table 2.

6. Global policy in breeding for heat tolerance and future prospects

Global policies on breeding for heat tolerance in wheat have been developed to address the challenges posed by global climate change, which is causing increasingly frequent and severe heat stress events. The followings are some of the current policies and future prospects in breeding for heat tolerance in wheat:

6.1. National and international research programs

National and international research programs have been established to develop heat-tolerant wheat varieties through

TABLE 2 Genes used in genome editing with their function to improve stress tolerance.

Sl No	Target genes	Description of functions	Stress	References
1	TaDEP1, TaGW2	Through CRISPR-Cas mutagenesis was used to generate wheat mutants of TaDEP1 and TaGW2 genes to enhance herbicide resistance	Herbicide resistance	Mishra et al. (2020)
2	TaDREB2, TaERF3	Drought tolerance in wheat was enhanced by CRISPR-Cas editing for dehydration-responsive element binding protein 2 (TaDREB2) and ethylene-responsive factor 3 (TaERF3)	Drought stress	Kim et al. (2018)
3	TaFER-5B	Heat tolerance is increased by overexpression of the wheat ferritin gene TaFER-5B	Heat/Cold Stress	Zhang H. et al. (2017)
4	TaFt-D1	Flowering time gene	Increased number of spikelets	Chen et al. (2022)
5	TaGASR1	Wheat plants that overexpress TaGASR1 gene are more resistant to heat and oxidative stress	Heat/Cold stress	Zhang Z. et al. (2017) and Zhang H. et al. (2017)
6	TaGASR7	Control of grain length and weight	NS	Zhang et al. (2016), Lin et al. (2020), and Wang et al. (2020)
7	TaGW2	Regulate grain size by promoting cell division in the early stage of grain development	Enhanced grain weight	Shan et al. (2014), Zhang et al. (2016), Zhang R. et al. (2019), Liang et al. (2017), Wang W. et al. (2018), and Lin et al. (2020)
8	TaHsfA6f	Overexpressing of TaHsfA6f gene enhances thermotolerance in transgenic wheat	Heat/Cold stress	Xue et al. (2015)
9	TaHsfC2a	This gene functions as a transcriptional activator and promotes heat stress tolerance by modulating ABA signaling	Heat/Cold stress	Hu et al. (2018)
10	TaIPK1	Encodes inositol pentakisphosphate 2-kinase 1involved in the phytic acid biosynthesis pathway	Increased bioavailability of iron and zinc	Ibrahim et al. (2022)
11	TaPEPKR2	Its overexpression conferred heat stress tolerance both in wheat and Arabidopsis	Heat/Cold stress	Zhang et al. (2018)

breeding and genetic engineering. These programs aim to identify and characterize the genetic basis of heat tolerance and to develop and distribute heat-tolerant seed varieties to farmers. There is a growing trend toward international collaboration in wheat breeding, with countries working together to share their knowledge, expertise, and resources. This collaboration allows for the pooling of genetic diversity, which can be used to develop heat-tolerant wheat varieties.

6.2. Research and development

There is a significant emphasis on conducting research aimed at understanding the mechanisms underlying heat tolerance in wheat and developing new breeding strategies to improve the heat tolerance of wheat crops. Investment in biotechnology is being made to develop new technologies for the breeding and genetic engineering of heat-tolerant wheat. This includes the development of new tools for gene editing and the use of molecular markers to track the inheritance of heat-tolerant genes. The integration of new technologies, such as genomic selection, precision breeding, and phenotyping, is playing an increasingly important role in the development of heat-tolerant wheat varieties. These technologies allow for the rapid and efficient evaluation of large numbers of wheat varieties, making it possible to identify those with the highest levels of heat tolerance.

6.3. Adoption of sustainable farming practices

Global policies are promoting the adoption of sustainable farming practices, such as conservation tillage and cover cropping, which can help to mitigate the effects of heat stress on wheat crops. The adoption of sustainable farming practices can help to mitigate the effects of heat stress on crops and improve their resilience to high temperatures.

6.4. Partnerships between the public and private sector

Partnerships between the public and private sectors are being formed to facilitate the development and distribution of heat-tolerant wheat varieties. This collaboration helps to accelerate the pace of research and bring new varieties to market more quickly.

6.5. Funding to mitigate future challenges

There is an increasing amount of funding being allocated to studies aimed at making wheat more resilient to high temperatures. This funding is being provided by governments, non-profit organizations, and private companies, and in doing so, it is facilitating the spread of knowledge and the implementation of novel breeding procedures.

In the future, it is expected that these policies will continue to evolve and expand, as the need for heat-tolerant wheat varieties becomes more pressing. There may also be a greater focus on the development of new technologies and the integration of traditional and modern breeding techniques to achieve the goal of developing heat-tolerant wheat varieties. Additionally, there may be an increased emphasis on the deployment of these heat-tolerant varieties in regions that are most vulnerable to heat stress, such as developing countries in Africa and Asia. Wheat can strengthen food and nutrition security in many parts of the world, including places of the world where rising temperatures pose a threat, such as Sudan and Nigeria, as well as countries in South Asia. The lowest agricultural productivity in the world has been recorded in the African region. Most of the countries in this continent fullfil their rising food demand through overseas food imports. But these countries have the potential to increase their wheat production by improving policies to use their ready winter fellow land to produce wheat. According to research, new kinds of wheat that are both super-early and heat-tolerant have already been tested along the Senegal River basin, and these types are widely available through the CGIAR-WHEAT program (Sall et al., 2019).

An integrated effort is required for the development of climate-resilient agricultural output under extreme climatic circumstances and household farming systems. This includes the development of plant breeding and seed systems as well as production systems. This is achievable through the development of the commodity supply chain as well as the extension and training of farmers to implement heat-tolerant varieties. The use of heat-tolerant genotypes in a breeding program and developing commercial heat-tolerant varieties are being in priority for the last decade. South Asia, comprising Bangladesh, India, Nepal and Pakistan, is the largest region where nearly 40 million ha of wheat is grown by small farmers and it has been predicted that climate change has the highest impact on South Asian Agriculture. Nevertheless, there is no specific policy to work on heat stress tolerance wheat development. To address climate-smart agriculture, the Indian Council of Agricultural Research (ICAR) India initiated a fast-track variety release program and successfully release high yield potential verity namely DBW303 for the early sown condition of NWPZ. Similar tactics have been taken in several NARS-system in South Asia including Bangladesh Wheat and Maize Research Institute (BWMRI) in Bangladesh, Wheat Research Institute (WRI) in Pakistan, Nepal Agricultural Research Council (NARC) in Nepal are working on the heat-tolerant wheat development program. In the collaboration with International Maize and Wheat Improvement Center (CIMMYT) and other international research organizations, the NARS system of these countries is developing their skill and resources to do research combating heat stress.

The most recent directive issued by the government of Sudan about heat-tolerant wheat completely revamped food production in that country. The Technologies for African Agriculture Transformation (TAAT) program increased the use of technologies that have already been proven effective. These technologies included newly introduced varieties that are resistant to heat, drought, and disease; improved irrigation methods; the bed planting method of farming; control of rust (*Puccinia graminis*); highly automated growing and harvesting as well as compact milling systems. The National Agricultural Research System (NARS), in collaboration with the International Maize and Wheat Improvement Center (CIMMYT) and the International Center for Agricultural Research in Dry Areas (ICARDA), developed and released many high-yielding heat-tolerant wheat varieties to increase Sudan's overall wheat production. This results in a robust production record of approximately 0.85 million tons of wheat, which is sufficient to meet almost 45% of the country's demand for wheat. Between the years 2012 and 2016, Sudan only generated 24% of the country's national wheat requirement, which means that the country is extremely dependent on imports totalling more than 1.5 million tons annually. Recent heat-tolerant varieties, such as Imam, Goumria, Zakia, Elnielain, and Bohaine, have a yield potential ranging from 5 to 8 t/ha (Evergreennews.com, 2019). The fast-track release of variety through national programs and scale-up of recent production technologies like the improved seed of climate-resilient, disease resistant and high-yielding varieties, engineered irrigation, improved agronomy and farm mechanization are the potential area where policy may play a significant role. Global policies and future prospects in breeding for heat tolerance in wheat aim to address the challenges posed by global climate change and ensure that farmers have access to heat-tolerant seed varieties that can help to maintain stable and sustainable food supplies. Overall, the prospects for breeding for heat tolerance in wheat are promising, with a growing commitment from governments, organizations, and the scientific community to address the challenges posed by global climate change.

7. Conclusion

Higher temperatures toward the end of the season, at the time of planting as well as short periods of heat shock, are the constraints of wheat production. Globally temperature is likely to rise with climate change, while fluctuations of the temperature may vary among regions. To prepare for adaptation to climate change, it is essential to segregate the effects of a specific aspect for influences on yield because fluctuations in diverse factors typically need different adaptation tactics. Approaches should specifically focus on the appropriate exploration of germplasm and the exploitation of novel alleles from the wild gene pool, due to the increasing demands for global food supply associated with the scathing pressure of population growth and climate change pathways. In addition, through physiological trait breeding, adaptive as well as morpho-physiological characteristics may be integrated into the high-yielding genotype. Even if multiple genes in wheat have been effectively engineered to enhance heat stress tolerance, their role in different conditions of heat stress and genomic structure is still to be explored. New high throughput phenomics techniques increase hope for difficult-to-measure module characters associated with heat tolerances. Because of all breeding methods, success depends on outstanding phenotypic characterization. When used with system biology techniques, new Omics-based applications could enormously improve conservative breeding to alleviate the tasks of heat stress and modernize the future of sustainable agriculture.

Author contributions

MF, UK, VT, PB, NK, KM, and AH gestated the concept and write-up of the overview. MF compiled and wrote the original draft. MF, AH, VB, and MB revised and edited the original draft. VB and

MB received the financial support for the article. All authors carefully read and approved the article for submission to the journal.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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