

Heat stress responses and mitigation strategies in wheat: an updated and comprehensive review

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Abstract

The main consequence of climate change on temperature is global warming. Over the past century, worldwide temperature has increased, rising by about 0.14 degrees Fahrenheit every year. Rising temperature negatively affects morphology, physiology, and yield of crops. Over the last 5 years, agriculture production in Pakistan affected due to temperature increase. Pakistan is an agriculture based developing country. About 2.2% GDP of Pakistan depends on wheat crop which is 1st major cereal crop and ranked as staple food. Nutritionally it provides proteins, dietary fibers, carbohydrates, calcium, and other important compounds but because of the harmful effects of a high temperature, yield of wheat crop in Pakistan has reduced to lowest levels in the last few years. Heat stress affects wheat plants by reducing growth, raised reactive oxygen species (ROS) production, denature cell membranes, and enzymes activity, decreasing photosynthetic activity and disturbing respiration processes. Improving wheat crop productivity is urgently needed to feed the rapidly growing population. Several techniques like Quantitative Trait Locus mapping, omics techniques, and application of nutrients have been used in the past to mitigate high temperature effect on wheat and other different crop plants. This review critically analyzes the response of wheat towards heat stress and its impacts on wheat crop as well as provides critical information on advanced strategies and techniques for the mitigation of heat stress.

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Introduction

Global crop productivity is being negatively impacted from the detrimental effects of climate change (El Melki *et al.*, 2023; Al-Khayri *et al.*, 2023). With the significant increase in the global population there is a need for maximum production of food to avoid food insecurity. It is predicted that in 2050 about 9.8 billion population will increase and to feed this population, 198 million tonnes wheat will be required (Patil *et al.*, 2022). For this, there is great need of maximizing food production (Iqbal *et al.*, 2017). Economy of Pakistan depends upon agriculture sector that is facing different challenges because of these drastic conditions of environments (Ahmed and Schmitz, 2011). According to the Global Climate Risk Index, Pakistan has been placed at 12th position among countries that have been severely affected by harsh environmental impacts (Ali *et al.*, 2022). However, harsh environmental conditions like high temperatures, high rains and other stresses are making it difficult to produce food on a large scale (Shahzad *et al.*, 2021). All the environmental factors are interlinked with each other either individually or by combining with other factors. These factors have a large impact on the morphology, biochemistry, physiology, and plant species production (Madani *et al.*, 2019; Al-Khayri *et al.*, 2022). High/low temperature, water logging, water stress, salt stress are main abiotic stresses that can destroy tissue cells in plants and also damage cereal crops (Bita and Gerats, 2013). According to dos Santos *et al.* (2022) heat stress is an utmost climatic abiotic stress that have most adverse impacts on plants. High temperature stress is considered more dangerous than drought stress because it significantly affects various plant organs at several stages of their life cycle (Riaz *et al.*, 2021). Plants are sessile and cannot move therefore there are greater chances of damage by changes occurring in their surroundings (Medina *et al.*, 2021). Plants can survive in an optimum temperature but if temperature is increased more than optimum value, then growth of plants can be negatively affected. It can cause reduction in germination of seeds, fruiting, pollens, and in productivity (Sehgal *et al.*, 2018).

Wheat is high energy crop for human population sown on an area of 8825 thousand hectares, as it contains energy compounds like proteins, carbohydrates, sugars, and fibers (Hussain *et al.*, 2023). It has great role in global cereal production (28%), trade (41%) and total yield about 24.946 million tonnes (Yadav *et al.*, 2022). In 40 countries, wheat is providing 85% calories and 82% proteins (Pandey *et al.*, 2019). Wheat is more sensitive during reproductive stages than other crops and 15-20 °C temperature is optimum for normal growth. If temperature is high during reproductive stage, then it can disturb the reproductive physiology and cause decrease in yield (Prasad and Djanaguiraman, 2014).

In order to handle such harsh circumstances, plants have adopted several regulatory processes, such as heat shock proteins. These processes help plants to withstand drastic circumstances (Akter and Rafiqul Islam, 2017). Figure 1 shows responsive mechanism of plants regarding different abiotic stresses. However, to cope with present challenges faced by wheat and to enhance yield production, different technologies have been introduced and nano technology is one of the most advanced fields for this purpose (Li *et al.*, 2015). Effective control of irrigation systems helps in cultivation of wheat when faced with challenges like heat stress (Tack *et al.*, 2017). Utilization of phytohormones is also another phenomenon in promoting plant growth. Moreover, it helps plants cope with a variety of abiotic and biotic stresses (Hossain *et al.*, 2021). Khan *et al.* (2020) reported that silicon introduction in tomatoes resulted in increased heat tolerance because silicon helped in improving antioxidants and regulated HSPs (Heat Shock Proteins). Similarly, Kothari and Lachowiec (2021) found that brassinosteroids mitigated negative impacts of heat shocks (HS) in cereals crops. Under heat and drought conditions, selecting stay-green (SG) genotypes is an effective strategy to enhance crop yield. This strategy

involves choosing plant varieties that can maintain their green leaves and sustain photosynthesis for an extended period, even in the presence of HS. By prolonging the period of grain filling, these plants can achieve increased yield (Kamal *et al.*, 2019).

This review article aims to comprehensively examine the effects of heat stress on wheat, elucidate its basic mechanisms, and present modern techniques for reducing heat stress in wheat. Furthermore, this article delves into the heat stress impact on various attributes of wheat, offering valuable insights for addressing food shortages. It also imparts fundamental knowledge and significant advancements in strategies to alleviate HS in wheat. This whole section is the explanation of table of content.

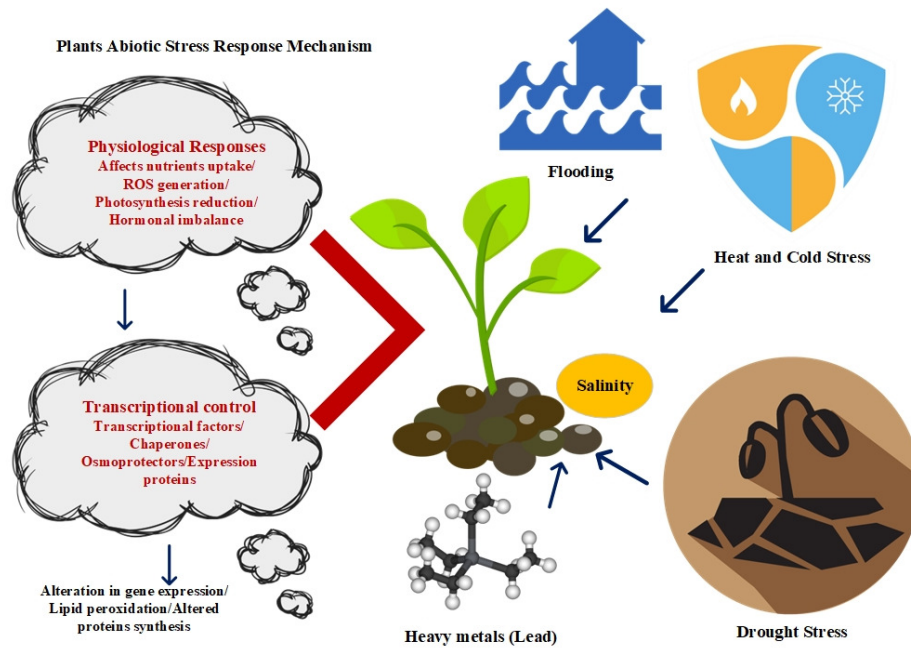


Figure 1. Plants response mechanisms to various abiotic stressors

Heat Stress Effect on Plants

Plants can sense changes in their environment and respond accordingly. Under HS, plants detect this condition by their plasma membrane. Plants respond to heat stress by opening their calcium channels, allowing the influx of calcium ions. This stress cause reduced growth due to increased water loss from plant cells (Rodríguez *et al.*, 2005). Laizer *et al.* (2019) and Lipiec *et al.* (2013) in their review also explained the harsh impacts of heat on multiple facets of plants physiology and metabolism. High temperature stress disrupts important cellular regulatory mechanisms, like respiration, photosynthetic machinery, transport of water, and absorption of nutrients irrespective of the length of heat stress. Table 1 illustrates the consequences of HS on plants during various growth stages. These effects can result in cell death caused by proteins, enzymes, nucleic acid, and plasma membrane denaturation. Such disruptions significantly impact the regular operations like physiology and plant metabolism (Faiz *et al.*, 2020). Heat stress inhibits the development of floral buds and results in flower abortion. Furthermore, heat stress can persuade oxidative type of secondary stress.

Plants have evolved various responses to mitigate the effects of heat and protect themselves. Based on transcriptomics and proteomics, plants might be grouped into two classes, considering genes and proteins involved in heat stress response. The first category consists of signaling elements like transcription factors and protein kinases (Zheng *et al.*, 2022). To some extent a plant can tolerate heat stress as they start to produce signaling genes for the alteration of metabolism but with the passage of time plants metabolic pathways are disturbed by heat which harms different tissues (Rehman *et al.*, 2023). According to Bharti *et al.* (2021)

transcription factors and protein kinases contributes to HS reduction through expression of genes and regulation of cellular signaling pathways. The second category consists of functional genes like heat shock proteins (HSPs) (Todaka *et al.*, 2012). Under HS, production of heat stress transcription factors is triggered in plants. These transcription factors promote the production of HSPs which help in regulating HS response (Kotak *et al.*, 2007). According to Khan and Shahwar (2020) HSPs helps in numerous activities of cells, such as protein folding, stabilization, and degradation. When cells are subjected to HS, it increases the synthesis of HSPs which ultimately prevents the denaturation and aggregation of proteins. Under heat stress situations, this protective mechanism ensures the maintenance of protein optimal functioning and structure.

Table 1. Effect of heat stress (HS) throughout different growth stages of plants

Crops	Scientific Name	Heat treatment	Growth stage	Major effect	References
Mustard	<i>Brassica nigra</i>	25-40 °C (day/night)	Seedling stage	Reduced vigor indices, survival percentages, antioxidant activity, and proline content	Sakpal <i>et al.</i> (2023)
Sugarcane	<i>Saccharum officinarum</i>	15 °C, 28 °C, and 40 °C (0, 4, 8, 12, and 24 hours)	65 days after planting	chlorophyll a and total chlorophyll indices increased, increased rate of respiration, enzyme denaturation	dos Santos Panta <i>et al.</i> (2022)
Tomato	<i>Solanum lycopersicum</i>	28 °C (Day time)	Seedling, Reproductive	photosynthesis, electrolyte conductivity, proline, Reduction in fruit parameters	Rajametov <i>et al.</i> (2021)
Maize	<i>Zea mays</i>	40 °C for 6 hours	15 days after sowing	Reduced plant weight, increased leaf temperature, Proline, total soluble sugars and amino acid contents increased	Ayub <i>et al.</i> (2021)
Chili pepper	<i>Capsicum annuum</i>	38/30 °C (day/night)	Reproductive stage, maturity and harvesting level	Reduction in fruit width and weight, enhanced abnormal seeds per fruit.	Pagamas and Nawata (2008)
Sorghum	<i>Hordeum vulgare</i>	40/30 °C (day/night)	65 DAS to maturity stage	Chlorophyll level, chlorophyll <i>a</i> fluorescence decreased, decreased antioxidant enzyme activity and photosystem II (PSII) photochemistry, increased reactive oxygen species content, damage to thylakoid membrane, and reduction in yield	Djanaguiraman <i>et al.</i> (2010)
Rice	<i>Oryza sativa</i>	32 °C (night temperature)	Reproduction	Grain yield, grain length, gain width, and gain weight decreased, increased spikelet sterility	Mohammed and Tarpley (2010)
Tobacco	<i>Nicotiana tabacum</i>	43 °C, 2 h	Early growth stages	Stomatal conductance, AQY (Apparent Quantum Yield), net photosynthetic rate and CE (Carboxylation Efficiency) decreased. Antioxidant enzymes activities decreased.	Tan <i>et al.</i> (2011)

Notes: DAS: Days After Sowing, AQY: Apparent Quantum Yield, CE: Carboxylation Efficiency

Wheat response towards heat

Wheat growth is affected by HS due to alteration of important processes like photosynthesis, respiration, proteins, antioxidants enzymes, water relations, and yield (Dutta *et al.*, 2023). It is affected by heat stress in two ways directly and indirectly. Directly, heat stress cause denaturation of proteins, aggregation of proteins and enhanced membrane fluidity while indirectly it causes poor germination of seeds, reduced growth, increased leaf senescence and reduced photosynthesis (Aiqing *et al.*, 2018; Djanaguiraman *et al.*, 2018). According to Heckathorn *et al.* (2013) high temperatures have directly affected wheat roots by causing cellular damage, affecting root growth and function. Direct heat stress caused physiological disruptions in root cells, such as protein denaturation, membrane damage, and metabolic imbalances. According to findings recorded by Alam *et al.* (2014); Iqbal *et al.* (2019); Nesar *et al.* (2022) heat might lead to pre- and post-harvest damages in plants. It can result in various detrimental effects, including leaves scorching and sunburns on the entire plant body, leaf abscission, root and shoot growth hinderance, discoloration of fruits, and low crop yield. These effects highlight the vulnerability of plants to high temperatures and the potential impact on agricultural productivity. Heat stress affects metabolic activities in wheat by triggering changes at hormonal levels. The altered hormone levels lead to stomatal closure, changes in gene expression, enzyme activities, and perturbations in hormonal crosstalk. These effects collectively influence various metabolic processes, compromising wheat morphology and yield during heat stress. According to Khan *et al.* (2013) and Lenzone and Knight (2019) plants have a responsive mechanism towards heat, involving calcium ions accumulation and ROS. Alternatively, this affects phytohormones like SA (Salicylic Acid) and JA (Jasmonic Acid). These phytohormones help in plant defense systems. However, in wheat plants, HS leads to a decrease in grains number per spike, their weight and tiller numbers. These observations highlight the HS negative impact on wheat yield-related parameter (Plaut *et al.*, 2004; Afzal *et al.*, 2020). Harsh situations caused low wheat yield because these conditions have harmful impacts on germination of seeds, and physio-biochemical processes (Kheiri *et al.*, 2021; Kheiri *et al.*, 2022).

Figure 2 showing the heat stress impact on wheat. Wheat may exhibit changes in protein expression patterns, with some proteins being upregulated or downregulated under heat stress. These alterations in protein expression can impact the overall cellular functions and the plant capacity to minimize heat stress. According to Usman *et al.* (2014) HS disrupted normal synthesis as well as expression of proteins in wheat plants. These proteins regulate various cellular processes, including metabolism, signaling, and stress responses. Similarly Poudel *et al.* (2021) confirmed that HS alters proteins expression, deteriorate mitochondria disrupting ATP formation and provide less oxygen to embryos. These findings state that HS negatively affects wheat metabolic activities. HS effect on various attributes of wheat is described below in detail.

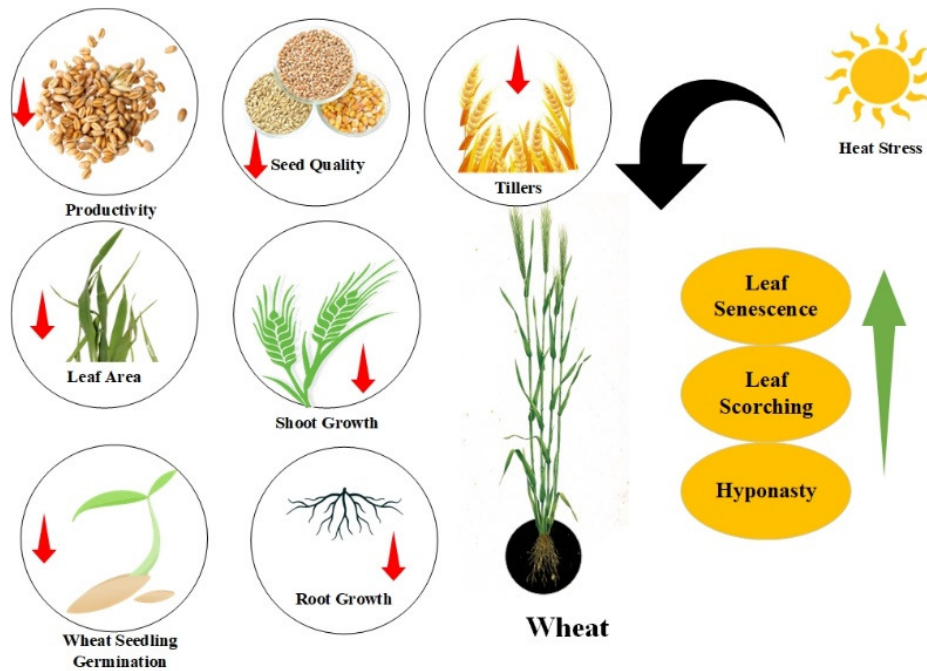


Figure 2. Effect of heat stress on wheat (The upward arrow means increase, and downward arrow means decrease)

Wheat Morphology

Growth

Growth and development include stages like germination of seed, emergence of shoots, roots, stem, flowering, pollination, fertilization, and yield. Heat has very harmful impacts on all these stages (Buttar *et al.*, 2020; Fleitas *et al.*, 2020). When plants sense any change in the environment, they tend to change their metabolism and adapt themselves according to the changing conditions (Rangan *et al.*, 2020). Different studies were made to investigate heat impact on wheat at different stages and it is cleared that at high temperature about 45 °C germination of seed is declined, and embryo is dead (Essemine *et al.*, 2010; Hasanuzzaman *et al.*, 2013; Lal *et al.*, 2021). Diurnal temperature variations, such as high temperature at daytime (37 °C) and lower temperature at night (28 °C) are observed to minimize period of grain filling and they affect the maturity level of plants. It has been found that 26 °C is considered a threshold temperature, indicating that temperatures above this threshold can have significant impacts on formation of grains and maturation (Zhao *et al.*, 2007; Dubey *et al.*, 2020).

Physiology of Wheat

HS exerts detrimental influence on wheat physiology. It diminishes seed germination rates, prolongs the germination period, reduces seed vigor, inhibits radicle and plumule growth, and can induce abnormal growth patterns in plants (Hasanuzzaman *et al.*, 2013). According to Mirza (2021) under HS seed germination of wheat was inhibited. Similarly, Debnath *et al.* (2022) in their review paper also explained that heat stress affected seed vigor, and plumule growth. Germination serves as the initial stage that can be influenced by various types of stresses, including heat stress. Heat stress has the potential to impede the germination process,

leading to delays. Moreover, it significantly disrupts the biochemical mechanisms involved in germination, ultimately resulting in a reduction of growing time (Kamrun *et al.*, 2010; Nadeem *et al.*, 2018). Sattar *et al.* (2020) explained that wheat flag leaf provides tolerance against abiotic stresses and has assimilation power for carbohydrates but at high temperature flag leaf wilts and its area is dropped. Heat also has negative impacts on the number of tillers of wheat plant and it is investigated that due to high temperature they reduced from 2.3 to 1.7 per plant. Flowering is an important trait for wheat adaptation during unfavorable conditions (Zahra *et al.*, 2021). Normally, flowering and grain filling period of wheat is 20 days but under heat stress it accelerates by reducing period with 12 days and cause shorting of life cycle which leads to reduced weight and size of wheat grain (Paudel *et al.*, 2021).

Photosynthesis

Plant productivity is determined by a biochemical mechanism occurring in plants known as photosynthesis. Major reason of low productivity in plants during HS conditions is detrimental effect it has on photosynthesis (Zahra *et al.*, 2023). It is investigated that heat causes decreased protein and relative water contents (RWC), activity of PS II (Photosystem II), and chlorophyll (Chen *et al.*, 2017). Younis *et al.* (2020) revealed in their study that heat decreases PS II activity and results in low photosynthesis and ultimately low production. PS II is a site where injury is incurred by different types of environmental stresses like heat stress in photosynthesis. Under high temperature, byproducts formed during photosynthesis are reduced because of instability of membrane and cannot be transferred to other plant parts (Poudel *et al.*, 2020). Heat stress leads to structural changes in chloroplasts, including changes in the organization of thylakoid membranes, grana swelling and structure loss (Ashraf and Hafeez, 2004). Photosynthesis is also disturbed by heat stress due to because of specific proteins reductions such as Rubisco binding proteins and their subunits (Sumesh *et al.*, 2008). According to Sparrow-Muñoz *et al.* (2023) Rubisco is not affected by heat stress directly, but high temperature causes negative effects on activase enzyme of Rubisco which help in Rubisco modulation. This modulation of Rubisco results in reduced photosynthesis in wheat. Include some more research findings on harsh impacts of heat on wheat physiology viz, stomatal conductance, cell membrane stability, biochemical enzyme activities etc.

Water relations

Under changing environmental conditions like high temperature, water relation status of plants is very sensitive. When the temperature is high, there is more loss of water leading to dehydration in plants and ultimately death. Heat stress causes depletion of bonds in water molecules which have negative impact on soil temperature and transpiration process in plants (Fortunato *et al.*, 2023). Water deficit in plants is brought through high temperature in two ways. Firstly, a condition when a plant loses more water through its aerial portions than it takes up through its roots and stomata get closed, leading to a high rate of transpiration. Secondly, at high temperature process of vaporization in soil is enhanced which cause inhibition of roots extension downwards and less water is absorbed by roots (Tao *et al.*, 2016). Heat stress can directly disturb wheat metabolic pathways by increasing respiration rate, impaired photosynthesis, decreasing osmotic potential and sugar level and can cause water deficit. According to Sattar *et al.* (2020) heat disrupted water relations in wheat because of increased rates of transpiration and reduced water uptake.

Oxidative damage

HS cause ROS formation (Reactive Oxygen Species) in wheat which leads towards oxidative damage. Higher ROS production cause unbalanced redox homeostasis which damages the membrane and more electrolytes are leaked from membrane that disturbs functioning of cell (Sharma *et al.*, 2012). ROS formation takes place in the chloroplast region. But recent studies showed that ROS is also generated in mitochondria (Suzuki, 2023). These two studies present the same result. Therefore, write one statement for these two

references. They cause radicals formation and these radicals react with all biomolecules and cellular components of plants that cause disturbance in metabolism (Møller *et al.*, 2007). Wheat crop have evolved a number of defensive systems to combat ROS generation. These mechanisms help in ROS scavenging, protect membranes and organelles from being damaged by ROS. Similarly, Lipid peroxidation is caused by denaturation of proteins and this denaturation is result of heat stress. Due to this lipid peroxidation, heat stress induces oxidative stress in wheat (Camejo *et al.*, 2006).

Yield

One major factor that negatively affects productivity is abiotic stress, including wheat, with a global average reduction of over 50% (Buttar *et al.*, 2020). Wheat crop is accounting for 2.2% of GDP of Pakistan and known as king of cereals (Usman, 2016). HS has severe hazardous effects on wheat productivity cultivated in low-altitude regions worldwide, where approximately 100Mha wheat is cultivated. According to Morgounov *et al.* (2018) a 6% reduction in wheat production was recorded by increase in one-degree Celsius temperature.

Different yield related attributes such as no. of tillers, grains, plant height, spike length, weight of grain have effect on wheat yield (Bhattarai *et al.*, 2017). The Federal committee on agriculture meeting has reported that in 2021-22 from 8.99 million hectares about 26.8 million tonnes wheat is produced which is showing 2.5% loss of yield from last year. Similarly, Ali *et al.* (2011) revealed that HS cause decrease in wheat productivity by minimizing tillers numbers. Loss of yield at higher temperature is due to the decreased Rubisco formation and its substrates. According to Posch *et al.* (2019) proper functioning of Rubisco is a major process for greater yield and heat stress results in disturbing Rubisco activity. In tropical regions wheat yield is more affected because its life cycle is completed faster. It is reported that HS changes grain filling time duration and inhibit kernel growth of wheat which leads to loss of yield up to 7% (El Sabagh *et al.*, 2019).

Wheat biochemistry

Wheat biochemistry is affected by denaturation of enzymes due to heat stress (Rubisco, Rubisco Activase (RCA), ATP Synthase, Starch Synthase). The primary component of wheat is starch which consists of amylopectin and amylose. Most important indicator of starch quality is amylose level. During heat stress amylose and amylopectin levels are decreased (Sharma *et al.*, 2015). Sehgal *et al.* (2018) HS can affect multiple aspects of starch metabolism in wheat grains, leading to a decrease in amylose and amylopectin levels. The accelerated starch degradation, altered enzyme activity, impaired granule formation, and increased respiration rates contribute to the reduction in these polysaccharides. Similarly, Liu *et al.* (2011) reported that under heat enzymes involved in starch synthesis are denatured that results in reduction of starch content in grain.

Respiration

Growth and survival of plants depends on respiration and mitochondrial respiration is an important factor which has impact on productivity of wheat during heat stress. High rate of respiratory homeostasis is shown by wheat and rice (Rai *et al.*, 2020). Under heat stress photosynthesis is inhibited and respiration rate is increased. Temperature under 0 °C to 35 °C, respiration process tends to increase but at higher temperature (>50 °C), respiration process is decreased, and its mechanism is stopped. Reduced respiration can result in low yield and impaired growth of wheat. According to Bavita *et al.* (2012) the fluctuation in respiration process disrupts the movement of nutrients from the leaves to the grains, which cause inhibition of plant growth, development, and ultimately crop productivity. This indicates that HS significantly affects the wheat respiration process.

HS Resistance Mechanism in Wheat

Heat tolerance described as capacity of plants to grow, survive, and produce viable yields during high temperature conditions (Maj *et al.*, 2023). Production of HSPs and SG (Stay Green) are important for HS tolerance in wheat (Poudel and Poudel, 2020). According to Sable and Agarwal (2018) and Wu *et al.* (2022) the induction of HSPs helps plants cope with heat stress by maintaining cellular homeostasis, protecting proteins from denaturation, and facilitating proper protein folding and assembly. Additionally in wheat plant genetic components like QTL genes help in HS tolerance (Haider *et al.*, 2021). As Rabara *et al.* (2021) found that these genes are involved in alleviating HS by regulating physiology and biochemistry that enable plants to withstand high temperatures. Plants have developed several adaptive mechanisms during heat stress. Avoidance, escape or tolerance are some common defensive mechanisms of wheat plant during heat stress (Janni *et al.*, 2020). Avoidance helps plants to tolerate any type of stress. Additionally, plants attempt to finish their reproductive cycle during favorable time in order to endure periods of HS (Giordano *et al.*, 2021). Abdelrahman *et al.* (2017) in their review also explained that plant avoidance mechanisms involve adaptive strategies that help plants to minimize negative impacts of heat stress. Another stress mitigating mechanism is the small size of leaves which helps plants to overcome HS. Under HS small leaves can effectively survive than large leaves because in respiration process small leaves face less resistance on surface in expelling heat outside (Salman *et al.*, 2019). Shashikumara *et al.* (2022) reported that wheat leaves have a natural tendency to roll or fold during periods of heat stress, which can reduce exposure to direct sunlight and minimize heat stress. This leaf movement, coupled with changes in leaf angle and orientation, can help regulate leaf temperature and protect the photosynthetic apparatus from thermal damage. These mechanisms are described below in detail.

HSPs: Key players for heat resistance

Functioning of proteins depends upon their folding and synthesis and any type of misfolding negatively affect their function. Under HS conditions proteins are denatured and folding is disturbed (Sharma *et al.*, 2019). Depending on their molecular masses, functioning and amino acids sequence HSPs are grouped in several categories. These include HSP100, HSP90, HSP70, HSP60, and other small families (Gupta *et al.*, 2013). In stressed conditions such as heat stress every family has a specific function as shown in Table 2. When a plant sense high temperature then signals are transferred to heat shock transcription factors. These HSFs get attached with HSE (heat shock elements) in DNA leading to show gene expression (Al-Wahaibi, 2011).

Table 2. Distinct HSP (Heat Shock Proteins) classes and their functional role in overcoming heat stress (HS)

HSPs Classes	Molecular weight (kDa)	Representative members	Role	References
Hsp27	12-43	α A-Crystallin (CRYAA), α B-Crystallin (CRYAB)	protein folding and stability, protein degradation, signal transduction, stress tolerance	Mondal <i>et al.</i> (2023)
Hsp10	10	Chaperonin 10 or CPN10	precise protein folding, cooperation with hsp60, heat and salt stress tolerance	Abasi <i>et al.</i> (2023)
Hsp60	60	Group I (CCT)	protein folding and assembly	Hu <i>et al.</i> (2022)
Hsp70	68-75	Hsp/Hsc70 Hsp70 Bip1 Hsp91	serves as a molecular chaperone, ensuring balance of processes in cells, and regulates the activation of various factors involved in signal transduction pathways when confronted with HS.	Barna <i>et al.</i> (2018)

Chaperonin/Hsp60	55–64	Group I (Cpn602) Group II (CCT3)	Role in supporting plastid proteins like Rubisco, guaranteeing the correct folding of proteins during their transportation to chloroplasts and mitochondria, and preventing assemblage of proteins when exposed to HS	Usman <i>et al.</i> (2014)
Hsp90	82–90	Hsp90-1 Hsp90-5 Hsp90-6 Hsp90-7	Collaboratively with HSP70 works to reduce HS in plants, exhibit associated activity to other chaperones in response to HS, involves genetic buffering and the maturation of upstream signalling molecules related to stress response.	Kaur <i>et al.</i> (2019)
Hsp100	100–104	Hsp100, Hsp101	Engaged in the renaturation process of heat denatured proteins, restoring their functionality, and enabling them to resume their biological activities. Also facilitates the degradation of proteins that have been irreversibly damaged by HS, enhance the survival rate of cells during severe or prolonged stress conditions.	Jee (2016)
Small Hsp (sHsp)	15–30	Hsp 17.6 Hsp17.9 Hsp21 Hsp22 Hsp22.3 Hsp235 Hsp26.25	Capacity to bind with partially folded or denatured substrate proteins, preventing irreversible unfolding or improper protein assembly, undergoes heat-induced assembly into functional stress granules or heat shock granules. Play a crucial role in providing cellular protection during heat stress.	Bakthisaran <i>et al.</i> (2015)

Notes: kDa: Kilo Dalton, Hsp: Heat shock protein, HS: Heat Stress, Hsp/Hsc70: Heat shock protein/heat shock cognate 70, CCT: chaperonin containing TCP-1, Bip1: Immunoglobulin Binding Protein, Cpn602 and CCT3: Chaperone family heat shock proteins

Heat stress initiates genes expressions that encode for HSPs. These proteins act as chaperones which protect proteins from denaturation as mechanism of HSPs is shown in Figure 3. Similarly, according to Yadav *et al.* (2020) thermotolerance in wheat is due to the presence and expression of HSP18.1 and HSP17.9. These specific low molecular weight-heat shock proteins (LMW-HSPs) help in protecting wheat cells from heat stress and ensuring the proper functioning of cellular processes. Overall, the correlation between thermotolerance and the expression of HSP18.1 and HSP17.9 suggests that these HSPs have role in wheat plant response to HS, potentially contributing to its ability to survive and adapt under heat stress conditions.

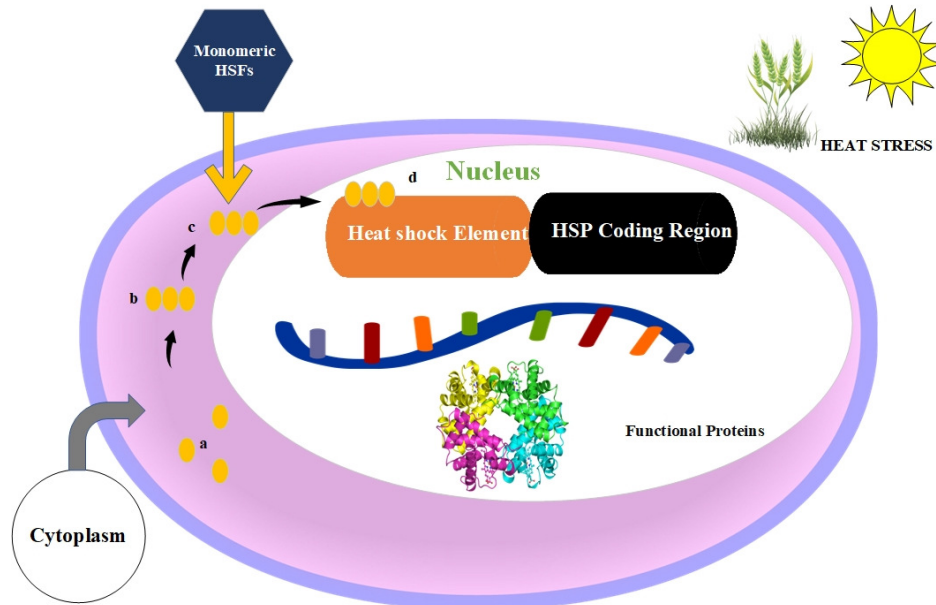


Figure 3. Mechanism of HSPs (Heat Shock Proteins)

HSP: Heat Shock Protein, HSFs: Heat Shock Factors

Wheat membrane fluidity: A smart hack

Altered membrane fluidity is a critical factor for HS resistance in plants. The plasma membrane of plants is very sensitive towards change in environmental conditions and any effect to membrane can cause disturbance in metabolic functioning (Ul Hassan *et al.*, 2021). Bhunia *et al.* (2016) found that plant cell membrane contains high content of unsaturated fatty acids that make plants capable of surviving under low temperatures. Similarly, during high temperature saturated fatty acids level is increased. Both types of fatty acids (saturated and unsaturated) are controlled by an enzyme called lipid desaturase. This enzyme maintains membrane fluidity by regulating different chemical reactions in thylakoid membrane under changing temperature. Likewise according to Yamamoto (2016) lipids forms a matrix which helps in proper functioning of photosynthetic pigments of PS I and PS II in thylakoids. It is reported that membrane fluidity helps plants in maintaining ion transport, enhancing enzymes activity, maintains protein's structure, ROS scavenging and oxidative stress management under high temperature (Rawat *et al.*, 2021). Moreover, Plants have also waxy coating layer on their external surface which act as protector under harsh conditions like heat stress and also minimize loss of water from plants surface (Bhunia *et al.*, 2018). Cuticular waxes are very long chains of fatty acids and their derivatives. It is investigated that these waxes have important contribution in reducing temperature under HS in wheat (Mohammed *et al.*, 2018).

Wheat transcription factors: Functions and mechanisms

Transcription factors have worked as primary regulators of gene expression in plants when exposed to heat stress. They can repress or express gene expression by blocking or recruiting RNA polymerase to gene promoter region (Hussain *et al.*, 2021). Some molecular components like transcription factors are involved in plants' response towards changing environment. However, temperature regulation expression is shown by heat shock transcription factors. According to Barna *et al.* (2018) instead of controlling HSPs, HSFs shows expression of non-HSP genes. These HSPs bind heat shock responsive genes and elements which in the form of proteins show expression and produce tolerance against heat stress in wheat. Currently, about 20 heat shock transcription factors are discovered including *AP2/ERF* (*APETALA2*/Ethylene Responsive Factor) that includes *TaDREB2*, *TaERF1*, and *TaWRKY*. These factors regulate gene expression for salinity, pathogen,

and drought tolerance. Similarly, *MYB* (Myeloblastosis) regulates genes for grain development and diseases resistance. Another *NAC* (*TaNAC2*, *TaNAC29*, and *TaNAC69*) regulates genes for heat and salinity resistance. Additionally, *bZIP* (*TaABF1*, *TaABIS*, and *TaFDL2*) regulates genes for drought and low temperature stress resistance while *WRKY* (*aWRKY10*, *TaWRKY33*, and *TaWRKY71*) regulates genes for biotic and abiotic resistance (Figure 4).

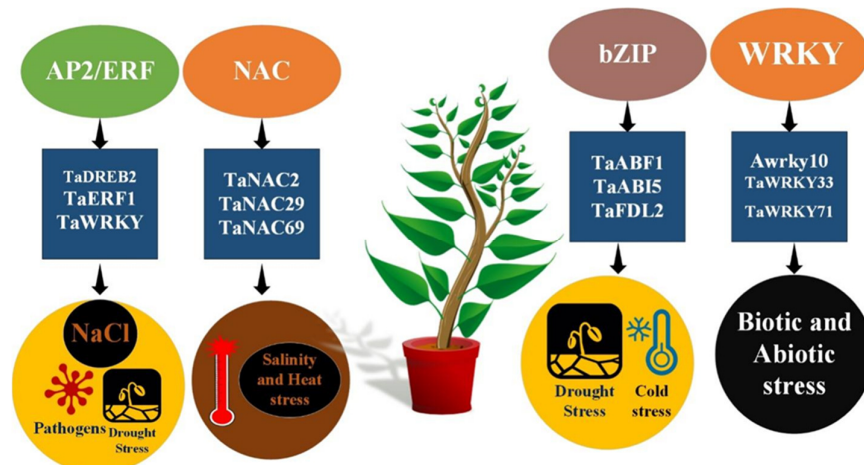


Figure 4. Wheat Transcription Factors and their function regarding biotic and abiotic stresses

Notes: *AP2/ERF*: *APETALA2*/Ethylene Responsive Factor, *TaDREB2*: Triticum aestivum Dehydration Responsive Element-Binding protein 2, *TaERF1*: Triticum aestivum Ethylene Responsive Factor 1, *TaWRKY*: Triticum aestivum *WRKY* (a family of transcription factors), *NAC*: *NAM*, *ATAF*, and *CUC* (*NAC*) domain-containing protein, *TaNAC2*: Triticum aestivum *NAC* 2, *TaNAC29*: Triticum aestivum *NAC* 29, *TaNAC69*: Triticum aestivum *NAC* 69, *bZIP*: Basic Leucine Zipper, *TaABF1*: Triticum aestivum *ABRE*-Binding Factor 1, *TaABIS*: Triticum aestivum *ABA* Insensitive 5, *TaFDL2*: Triticum aestivum Flowering Locus D 2, *WRKY*: a family of transcription factors, *aWRKY10*: *Wheat WRKY* 10, *TaWRKY33*: Triticum aestivum *WRKY* 33, *TaWRKY71*: Triticum aestivum *WRKY* 71

Wheat Management Strategies: Innovations and Best Practices

Heat stress is a growing problem that negatively affects the growth and development of plants. Several techniques have been developed in plants which mitigate heat stress in wheat. These techniques are briefly discussed below.

Creating heat resistant wheat varieties: An omics technologies roadmap

Many effective methods are employed to reduce biotic and abiotic stress in plants. These includes genomics, transcriptomics, proteomics, and metabolomics (Figure 5) (Tiwari *et al.*, 2021). Gene's function is investigated in proteomics technique which shows that identified genes are involved in transcription, translation, regulation, phosphorylation, or in signaling of lipids. These genes activate heat shock proteins which help in inducing HS tolerance (Comastri *et al.*, 2018). According to Kaur *et al.* (2021) the transcriptomics technique has been employed to investigate alterations in gene expression within cereal crops like maize, barley, rice under abiotic stress. Therefore, advanced transcriptomics techniques can be a useful strategy to produce heat tolerance in wheat by genes expression.

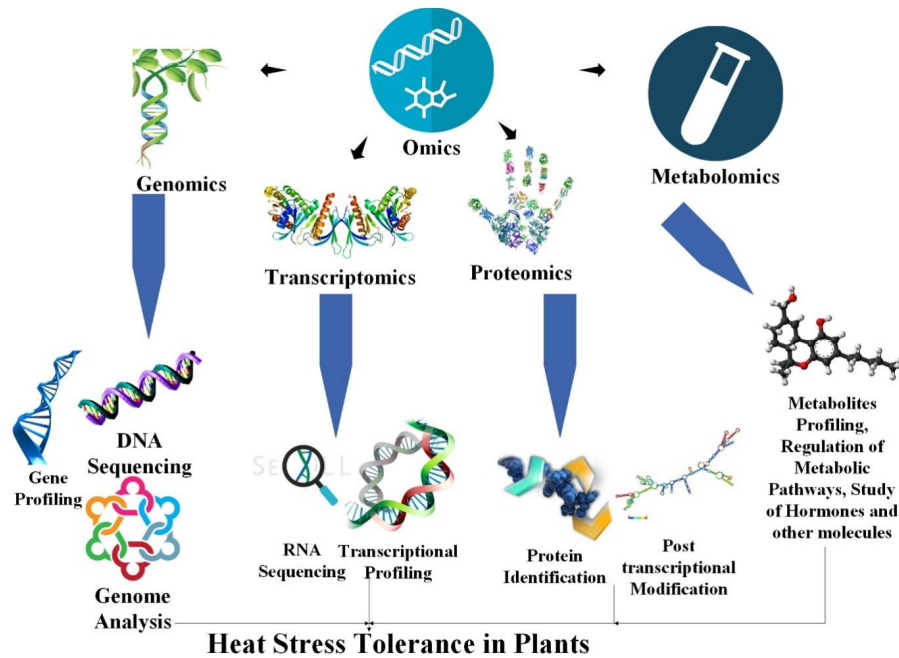


Figure 5. Omics techniques for heat stress tolerance in plants

Another technique, quantitative proteomics analysis reported some new proteins named SAAP (stress associated active proteins). Approximately, 4272 SAAPs have been identified in wheat. These proteins produce adaptation in wheat to tolerate heat stress by heat shock response, antioxidant defense, protein folding, energy metabolism, and signal transduction mechanism (Kumar *et al.*, 2019). Jan *et al.* (2023) revealed that proteomics provides insights into functional aspects of proteins and their involvement in various biological processes. Therefore, studying proteomic changes for stress conditions can assist in identifying stress-responsive proteins and pathways, thereby enhancing our understanding of stress tolerance mechanisms in plants. Similarly in tobacco plants SAPs showed plants natural or basal resistance against pathogen infections by over expression of OsSAP1 (Tyagi *et al.*, 2014). Therefore, quantitative proteomics can also be a helpful strategy to cope with heat stress.

QTL mapping

Crop production is increased by making several progresses in molecular biology which helped in improving crops. Different types of progress have been made like QTL (Quantitative Trait Locus) mapping, MAS (Marker-Assisted Selection), map-based gene cloning, and genome editing (Hasan *et al.*, 2021). QTL mapping technique was used to increase heat tolerance in wheat plant previously. Jha *et al.* (2014) identified specific regions in genomes of various plants that are associated with HS resistance. They found genetic markers linked to different traits related to a plant's susceptibility to heat, including yield traits like fruit set or grain filling rate. Similarly, Ali *et al.* (2013) found three QTLs and markers associated with HS resistance located on chromosomes 1B, 2B, and 5A by using linkage analysis. Therefore, QTL mapping technique with MAS can be useful for identifying wheat HS tolerant genotypes.

Breeding strategy to develop heat tolerant wheat varieties

In past, breeding and selection were applied for production of desired traits of plants and now it is being used for breeding wheat cultivars (Bradshaw, 2017). According to Jagadish *et al.* (2012) IIRRI (International Rice Research Institute) has developed heat-tolerant varieties of *Oryza sativa* such as 'IR64 sub1' through

breeding which combines submergence tolerance with heat tolerance. A major source of genetic variability for wheat plants to adapt drastic conditions like heat stress are landraces. Different genotypes of wheat have been bred from landraces e.g. bread wheat variety 'Aragon 03' in Spain (Ullah *et al.*, 2022). To reduce negative effects of heat on wheat, advanced breeding techniques can be useful. New breeding techniques have been developed for wheat cultivars adaptation to abiotic stress which include genetic modification (Zafar *et al.*, 2020).

Crop domestication, which is the initial stage of plant breeding, involves alterations in physical as well as physiological characteristics of plants to meet human requirements (Krug *et al.*, 2023). However, the process of domestication leads to a decrease in genetic diversity due to the similar lines' selection and breeding with desirable traits. Due to selective breeding cultivated crops possess a limited set of genes and alleles compared to their wild ancestors. This loss of genetic diversity has resulted in a decrease in the capacity of domesticated crops to tolerate environmental stress (Driedonks *et al.*, 2016). However, according to Capasso *et al.* (2021) it has been shown that many wild relatives and traditional landraces still retain higher levels of stress tolerance but more study is required on genetic diversity loss. Similarly, Yumurtaci (2015) described that wild relatives of cultivated crops possess genetic traits that make wheat more tolerant to heat stress. By crossing these wild varieties with cultivated ones, breeders can introduce heat stress tolerance genes into domesticated crops. Therefore, crop domestication with new biotechnological breeding techniques will be useful to identify traits of wild ancestor of wheat crops suitable for heat tolerance.

MAGIC (Multi-parent Advanced Generation Inter-Cross) population

Multi-parent Advanced Generation Inter-Cross is another breeding approach that involves creating populations by crossing multiple parents with each other over several generations. This method is commonly used in crop breeding. The purpose of MAGIC populations is to increase genetic diversity and recombination, allowing for the mapping of complex characters and improving varieties. MAGIC population technique offers a viable method for enhancing heat tolerance in wheat varieties during their development. As Bandillo *et al.* (2013) developed four multi-parent populations that consist of improved rice varieties with desirable attributes for stress resistance, productivity, and quality. Similarly, Huynh *et al.* (2018) also developed MAGIC population from 8 founder parents that carried biotic and abiotic stress resistance traits related to cowpea. Consequently, the employment of the MAGIC strategy in wheat breeding programs can result in synthesis and advancement of heat tolerant varieties.

Table 3. Different omics techniques in contribution to mitigation of heat stress

Strategy	Phase	Temperature (°C)	Activities	References
Transcriptomics	Rice seedlings stage	45	Evaluation of heat tolerance in rice varieties. Identification of heat response genes	He <i>et al.</i> (2023)
Integrated transcriptomics and proteomics	Jajoba leaves	28	Determination of differentially abundant proteins and genes	Zheng <i>et al.</i> (2022)
Transcriptomics and proteomics	<i>Triticum aestivum</i> yield	30-40	Determination of genes and proteins with differential expression	Wu <i>et al.</i> (2021)
Transcriptome analysis	<i>T. aestivum</i> awn	42	Characterization of transcriptome changes	Chaudhary <i>et al.</i> (2021)
Transcriptomes	Reproductive phase	32-36	Analysis of gene expression patterns during flowering and grain development	Kumar <i>et al.</i> (2021)

Lipidomics	Kernal development and flowering stage	32	Investigation of lipid composition and metabolism	Djanaguiraman <i>et al.</i> (2020)
Metabolomics (LC/HRMS)	Post flowering spikelet	35	Profiling of metabolites using LC/HRMS	Thomason <i>et al.</i> (2018)

Notes: LC/HRMS: Liquid Chromatography High Resolution Mass Spectrometry

Phytoprotectants application

At present, to reduce harsh effects of abiotic stresses in plants different types of chemicals are applied exogenously (Upreti and Sharma, 2016). In wheat plant different phytoprotectants including arginine, putrescine, and α -tocopherol have been used. These molecules activate enzymatic and non-enzymatic antioxidants which manage heat stress (Asthir, 2015). Studies have reported that abscisic acid exhibits favorable stress tolerant properties as a phytohormone in plants (Hamayun *et al.*, 2010; Ali *et al.*, 2020; Rehman *et al.*, 2022). Ethylene is popular as growth regulator plant hormone under stressful environment. (Include some findings on role of ethylene in mitigation of HS in wheat). Observations have reported that abscisic acid application leads to enhance grain filling process, kernel weight, and overall yield under HS wheat (Ni *et al.*, 2018). Plant growth hormones like brassinosteroids help plants in mitigating heat stress and produce adaptations of heat stress tolerance. According to Albertos *et al.* (2022) brassinosteroids are steroids that control morphological adaptive changes under stressed conditions like HS by regulating synthesis of Hsps. Therefore, phytohormones application might be a powerful approach to cope with HS in wheat.

Climate-Smart agronomic practices

This strategy includes special practices for any cropping system like changing planting time, and nutrient management. In the practice of altering planting time, seeds are typically sown in dry soil before the rainy season. On receiving water, seeds start imbibition process. These practices are very helpful in minimizing harsh impacts of climatic changes (Steward *et al.*, 2018). According to Nesar *et al.* (2022) early planting helps plants to avoid the most intense heat stress periods by reducing the risk of yield losses associated with heat-induced sterility and impaired grain filling but it also depends on some factors like climate, specific cultivar selection as well as soil conditions. According to Caubel *et al.* (2018) artificial intelligence technologies can be applied to improve prediction of the rainy season that will help in imbibition of seeds. Therefore, early planting with selection of suitable and specific variety of wheat can be a good practice to reduce effects of HS in wheat and to increase yield because early planted wheat can complete its growth cycle, including grain filling, before the onset of extreme heat conditions.

Another strategy is managing nutrient levels to minimize heat impacts. According to Mendanha *et al.* (2018) nitrogen level adjustment can alleviate HS in wheat by enhancing stomatal activity, chlorophyll level, as well as photosynthesis. Likewise, Hasanuzzaman *et al.* (2018) explained that during HS environment potassium orthophosphate application can be very helpful as it activates several metabolic processes occurring in wheat crop like enhancing water relation which help in HS tolerance. Similarly, at flowering stage of wheat foliar application of boron can increase antioxidants activities which results in minimizing HS (Eisvand *et al.*, 2018). These studies show that nutrients application in wheat can be helpful to alleviate HS as these nutrients like boron activate defense system of wheat.

CRISPR/Cas9 Technology

CRISPR/Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats) is a revolutionary genetic tool which consists of DNA segments, with Cas9 being the enzyme that functions as a molecular pair of scissors. This powerful and adaptable tool is extensively employed worldwide for DNA editing purposes in diverse organisms including animals and plants (Zhang *et al.*, 2021). CRISPR/Cas9 brought significant revolution in

genetics and plant breeding by enabling major crop genomes editing to enhance productivity, quality, and their ability to tolerate abiotic (heat, drought, salt), and biotic stresses (insects, weeds, diseases Figure 6) (Parmar *et al.*, 2017). In this technique targeted changes are made to genes through insertion, deletion, and knock in/out mutations, thereby improving the crop's capacity to scavenge ROS. A gene named OsNLT3 has been discovered through this technique in rice crops that involved in enhancing HS resistance (Liu *et al.*, 2020; Raza *et al.*, 2021). This gene contains a *NAC* transcription factor that triggers a regulatory mechanism. Tian *et al.* (2022) employed a comprehensive strategy in wheat by combining CRISPR/Cas9 based gene editing, polysome profiling, RNA-sequencing analysis, and protein-protein interactions. Their findings unveiled the significance of a gene called *TaMBF1c*, which is upregulated during heat stress. *TaMBF1c* helps in wheat response towards HS by regulation of translation process (Yadav *et al.*, 2022).

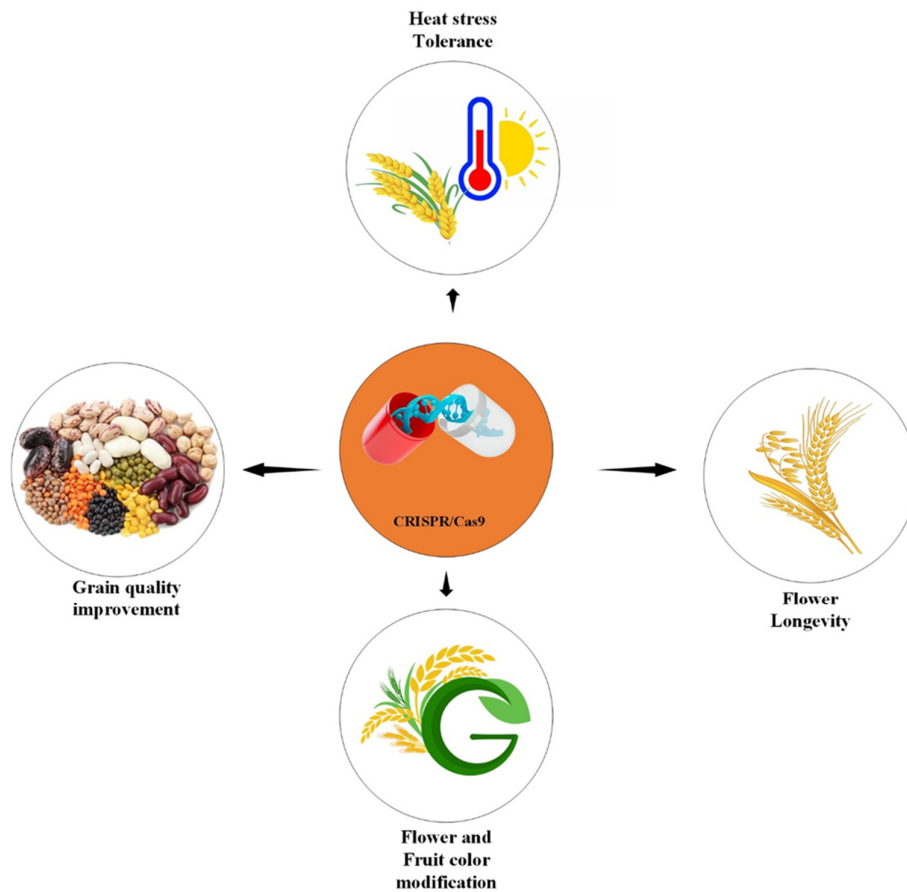


Figure 6. CRISPR/Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats) role in heat stress resistance and improving different traits of wheat

Future Perspective

Omics technologies like genomics, transcriptomics, proteomics, and metabolomics have shown great potential in understanding how wheat responds to heat stress at a molecular level. Further advancements in these technologies might help for genes determination, metabolic pathways and proteins regarding to HS tolerance in wheat. Integrating omics data with advanced breeding approaches can help in synthesizing heat tolerant wheat varieties with higher yield and resilience. MAS and genomic selection approach can speed up

this process by identifying and incorporating genomic regions associated with heat stress tolerance. Researchers can enhance heat tolerance in wheat by exploring various germplasm resources and introducing new Quantitative Trait Loci (QTLs) into breeding programs to expand the genetic basis. Breeding techniques like MAGIC populations aid in discovering new combinations of genes and introducing desirable traits. In addition to breeding techniques, CRISPR/Cas9 strategy can also enhance the creation of varieties with heat tolerance by targeting and modifying genes involved in response to HS. Implementing climate smart agronomic practices mitigate impact of HS on wheat production. Practices like cover cropping, mulching, and agroforestry systems enhance soil moisture retention and create a microclimate that reduces heat stress on wheat plants. To provide an additional layer of protection, phytoprotectants such as antioxidants, Osmo-protectants, and plant growth regulators can be applied. Biochemical priming techniques, including seed priming with specific compounds or microbial inoculants have shown promising results in improving HS tolerance in wheat. Similarly, providing knowledge and training to farmers through educational programs empowers them to adopt proper irrigation practices, nutrient management, and climate smart technologies. By interlinking these strategies, we can develop heat tolerant wheat varieties through advanced breeding techniques, genomic research, and gene editing technologies. Combined with climate smart agronomic practices, such as improved irrigation, soil management, and protective compounds utilization, we can enhance HS resilience in wheat and can mitigate its impacts on yield.

Currently these effective strategies are costly, and it is difficult for a common farmer to adopt them therefore more research is needed so that these strategies become easily available. As nowadays refrigerators, air conditioners are used in every house, offices, and buildings. They are becoming a big source of global warming and increasing temperature as well as destroying the climate. Therefore, more study is needed to prepare these eco-friendly electrical devices.

Conclusions

The primary factors contributing to reduced plant growth and productivity are the alterations in the environment. Heat stress has negatively affected wheat crops at both germination and reproductive stages. Low seed quality and reduced crop yield have been reported because of these climatic conditions. To handle these situations, nutrient application, omics approaches, QTL mapping, breeding and other techniques are very helpful. The integration of omics technologies, advanced breeding techniques, and climate-smart agronomic practices are powerful emerging strategies which assist in mitigating heat stress effect on wheat crop by developing heat tolerant varieties. Furthermore, advanced technology systems like MAGIC and CRISPR/Cas9 accelerate the gene editing process to develop heat tolerant cultivars. Through utilization of these techniques different heat resistance varieties of crop plants already have been developed but there is still needed to develop more heat resistance genetic varieties of wheat through an advanced breeding system by employing these techniques. Similarly, to change climate and provide suitable environment for wheat crops to grow and produce high yield, education should be given to farmers about proper irrigation system and nutrient application. Overall, these strategies are best solution to enhance crop yield and develop heat stress resistance in wheat.

Authors' Contributions

Conceptualization: AM and JMA, Writing original draft: ZUA and MSU. Reviewing and editing: AM, HFNA, BAK, MIA, OA, BA, WFS, AAR, Funding acquisition; JMA. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

References

- Abasi F, Raja NI, Ehsan M, Ali H, Shahbaz M (2023). Adaptation strategies with respect to heat shock proteins and antioxidant potential; an era of food security and climate change. *International Journal of Biological Macromolecules* 128379. <https://doi.org/10.1016/j.ijbiomac.2023.128379>
- Abdelrahman M, El-Sayed M, Jogaiah S, Burrett DJ, Tran LSP (2017). The stay-green trait and phytohormone signaling networks in plants under heat stress. *Plant Cell Reports* 36:1009-1025. <https://doi.org/10.1007/s00299-017-2119-y>
- Afzal I, Akram MW, Rehman HU, Rashid S, Basra SMA (2020). Moringa leaf and sorghum water extracts and salicylic acid to alleviate impacts of heat stress in wheat. *South African Journal of Botany* 129:169-174. <https://doi.org/10.1016/j.sajb.2019.04.009>
- Ahmed M, Schmitz M (2011). Economic assessment of the impact of climate change on the agriculture of Pakistan. *Business and Economic Horizons (BEH)* 4(1232-2016-101145):1-12. <http://dx.doi.org/10.15208/beh.2011.1>
- Aiqing S, Somayanda I, Sebastian SV, Singh K, Gill K, Prasad PVV, Jagadish SVK (2018). Heat stress during flowering affects time of day of flowering, seed set, and grain quality in spring wheat. *Crop Science* 58(1):380-392. <https://doi.org/10.2135/cropsci2017.04.0221>
- Akter N, Rafiqul Islam M (2017). Heat stress effects and management in wheat. A review. *Agronomy for Sustainable Development* 37(5):37. <https://doi.org/10.1007/s13593-017-0443-9>
- Alam MN, Bodruzzaman M, Hossain MM, Sadekuzzaman M (2014). Growth performance of spring wheat under heat stress conditions. *International Journal of Agricultural Research* 4(6):91-103.
- Albertos P, Düandar G, Schenk P, Carrera S, Cavalius P, Sieberer T, Poppenberger B (2022). Transcription factor BES1 interacts with HSFA1 to promote heat stress resistance of plants. *The EMBO Journal* 41(3):e108664. <https://doi.org/10.15252/embj.2021108664>
- Ali A, Syed AAW, Khaliq T, Asif M, Aziz M, Mubeen M (2011). Effects of nitrogen on growth and yield components of wheat. (Report). *Science International (Lahore)* 24:331-332.

- Ali MA, Hassan M, Mehmood M, Kazmi DH, Chishtie FA, Shahid I (2022). The potential impact of climate extremes on cotton and wheat crops in southern Punjab, Pakistan. *Sustainability* 14(3):1609. <https://doi.org/10.3390/su14031609>
- Ali MB, Ibrahim AMH, Malla S, Rudd J, Hays DB (2013). Family-based QTL mapping of heat stress tolerance in primitive tetraploid wheat (*Triticum turgidum* L.). *Euphytica* 192(2):189-203. <https://doi.org/10.1007/s10681-012-0824-8>
- Ali S, Hayat K, Iqbal A, Xie L (2020). Implications of abscisic acid in the drought stress tolerance of plants. *Agronomy* 10(9):1323. <https://doi.org/10.3390/agronomy10091323>
- Al-Khayri JM, Alshegaihi RM, Mahgoub EI, Mansour E, Atallah OO, Sattar MN, ... Aldaej MI, Hassanin AA (2022). Association of high and low molecular weight glutenin subunits with gluten strength in tetraploid durum wheat (*Triticum turgidum* spp. *durum* L.). *Plants* 12(6):1416. <https://doi.org/10.3390/plants12061416>
- Al-Khayri JM, Alwutayd KM, Safhi FA, Alqahtani MM, Alshegaihi RM, Abd El-Moneim D, ... Hassanin AA (2023). Assessment of intra- and inter-genetic diversity in tetraploid and hexaploid wheat genotypes based on omega, gamma and alpha-gliadin profiles. *PeerJ* 11:e16330. <https://doi.org/10.7717/peerj.16330>
- Al-Whaibi MH (2011). Plant heat-shock proteins: a mini review. *Journal of King Saud University-Science* 23(2):139-150. <https://doi.org/10.1016/j.jksus.2010.06.022>
- Ashraf M, Hafeez, M (2004). Thermotolerance of pearl millet and maize at early growth stages: growth and nutrient relations. *Biologia Plantarum* 48(1):81-86. <https://doi.org/10.1023/B:BIOP.0000024279.44013.61>
- Asthir B (2015). Protective mechanisms of heat tolerance in crop plants. *Journal of Plant Interactions* 10(1):202-210. <https://doi.org/10.1007/s10535-015-0539-5>
- Ayub M, Ashraf MY, Kausar A, Saleem S, Anwar S, Altay V, Ozturk M (2021). Growth and physio-biochemical responses of maize (*Zea mays* L.) to drought and heat stresses. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology* 155(3):535-542. <https://doi.org/10.1080/11263504.2020.1762785>
- Bakhtisaran R, Tangirala R, Rao CM (2015). Small heat shock proteins: Role in cellular functions and pathology. *Biochimica et Biophysica Acta (BBA)-Proteins and Proteomics* 1854(4):291-319. <https://doi.org/10.1016/j.bbapap.2014.12.019>
- Bandillo N, Raghavan C, Muyco PA, Sevilla MAL, Lobina IT, Dilla-Ermita CJ, ... Mauleon R (2013). Multi-parent advanced generation inter-cross (MAGIC) populations in rice: progress and potential for genetics research and breeding. *Rice* 6(1):1-15. <https://doi.org/10.1186/1939-8433-6-11>
- Barna J, Csermely P, Vellai T (2018). Roles of heat shock factor 1 beyond the heat shock response. *Cellular and Molecular Life Sciences* 75:2897-2916. <https://doi.org/10.1007/s00018-018-2836-6>
- Bavita A, Puneet KR, Navtej SB, Virinder SS (2012). Genotypic variation for high temperature tolerance in relation to carbon partitioning and grain sink activity in wheat. *American Journal of Plant Sciences* 2012.
- Bharti J, Sahil Mehta S, Ahmad S, Singh B, Padhy AK, Srivastava N, Pandey V (2021). Mitogen-activated protein kinase, plants, and heat stress. *Harsh environment and plant resilience: molecular and functional aspects* 323-354. https://doi.org/10.1007/978-3-030-65912-7_13
- Bhattarai RP, Ojha BR, Thapa DB, Kharel R, Ojha A, Sapkota M (2017). Evaluation of elite spring wheat (*Triticum aestivum* L.) genotypes for yield and yield attributing traits under irrigated condition. *International Journal of Applied Sciences and Biotechnology* 5(2):194-202. <http://doi.org/10.3126/ijasbt.v5i2.17615>
- Bhunia RK, Chakraborty A, Kaur R, Maiti MK, Sen SK (2016). Enhancement of α -linolenic acid content in transgenic tobacco seeds by targeting a plastidial ω -3 fatty acid desaturase (*fad7*) gene of *Sesamum indicum* to ER. *Plant Cell Reports* 35(1):213-226. <https://doi.org/10.1007/s00299-015-1880-z>
- Bhunia RK, Showman LJ, Jose A, Nikolau BJ (2018). Combined use of cutinase and high-resolution mass-spectrometry to query the molecular architecture of cutin. *Plant Methods* 14(1):1-17. <https://doi.org/10.1186/s13007-018-0384-6>
- Bitá CE, Gerats T (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science* 4:273. <https://doi.org/10.3389/fpls.2013.00273>
- Bradshaw JE (2017). Plant breeding: past, present and future. *Euphytica* 213:1-12. <https://doi.org/10.1007/s10681-016-1815-y>

- Buttar ZA, Wu SN, Arnao MB, Wang C, Ullah I, Wang C, (2020). Melatonin suppressed the heat stress-induced damage in wheat seedlings by modulating the antioxidant machinery. *Plants* 9(7):809. <https://doi.org/10.3390/plants9070809>
- Camejo D, Jiménez A, Alarcón JJ, Torres W, Gómez JM, Sevilla F (2006). Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. *Functional Plant Biology* 33(2):177-187. <https://doi.org/10.1071/FP05067>
- Capasso G, Santini G, Petraretti M, Esposito S, Landi S (2021). Wild and traditional barley genomic resources as a tool for abiotic stress tolerance and biotic relations. *Agriculture* 11(11):1102. <https://doi.org/10.3390/agriculture11111102>
- Caubel J, Garcia de Cortazar-Atauri I, Vivant AC, Launay M, de Noblet-Ducoudré N (2018). Assessing future meteorological stresses for grain maize in France. *Agricultural Systems* 159:237-247. <https://doi.org/10.1016/j.agsy.2017.02.010>
- Chaudhary C, Sharma N, Khurana P (2021). Decoding the wheat awn transcriptome and overexpressing TaRca1 β in rice for heat stress tolerance. *Plant Molecular Biology* 105(1):133-146. <https://doi.org/10.1007/s11103-020-01073-0>
- Chen YE, Zhang CM, Su YQ, Ma J, Zhang, ZW, Yuan M, ... Yuan S (2017). Responses of photosystem II and antioxidative systems to high light and high temperature co-stress in wheat. *Environmental and Experimental Botany* 135:45-55. <https://doi.org/10.1016/j.envexpbot.2016.12.001>
- Comastri A, Janni M, Simmonds J, Uauy C, Pignone D, Nguyen HT, Marmioli N (2018). Heat in wheat: exploit reverse genetic techniques to discover new alleles within the *Triticum durum* shsp26 family [original research]. *Frontiers in Plant Science* 9. <https://doi.org/10.3389/fpls.2018.01337>
- Debnath S, Chakraborty M, Kumawat R (2022). Physiological responses of plants under high temperature stress. *Biotechnology Research Today* 4:347-349.
- Djanaguiraman M, Boyle DL, Welti R, Jagadish SVK, Prasad PVV (2018). Decreased photosynthetic rate under high temperature in wheat is due to lipid desaturation, oxidation, acylation, and damage of organelles. *BMC Plant Biology* 18(1):55. <https://doi.org/10.1186/s12870-018-1263-z>
- Djanaguiraman M, Narayanan S, Erdayani E, Prasad PVV (2020). Effects of high temperature stress during anthesis and grain filling periods on photosynthesis, lipids and grain yield in wheat. *BMC Plant Biology* 20(1):268. <https://doi.org/10.1186/s12870-020-02479-0>
- Djanaguiraman M, Prasad PV, Seppanen M (2010). Selenium protects sorghum leaves from oxidative damage under high temperature stress by enhancing antioxidant defense system. *Plant Physiology and Biochemistry* 48(12):999-1007. <https://doi.org/10.1016/j.plaphy.2010.09.009>
- dos Santos TB, Ribas AF, de Souza SGH, Budzinski IGF, Domingues DS (2022). Physiological responses to drought, salinity, and heat stress in plants: A review. *Stresses* 2(1):113-135. <https://doi.org/10.3390/stresses2010009>
- Driedonks N, Rieu I, Vriezen WH (2016). Breeding for plant heat tolerance at vegetative and reproductive stages. *Plant Reproduction* 29(1):67-79. <https://doi.org/10.1007/s00497-016-0275-9>
- Dubey R, Pathak H, Chakrabarti B, Singh S, Gupta DK, Harit RC (2020). Impact of terminal heat stress on wheat yield in India and options for adaptation. *Agricultural Systems* 181:102826. <https://doi.org/10.1016/j.agsy.2020.102826>
- Dutta D, Karmakar S, Hossain A, Sadhukhan R, Atta K, Pramanick S (2023). Wheat and abiotic stress challenges: An overview. *Abiotic Stresses in Wheat* 1:1-13. <https://doi.org/10.1016/B978-0-323-95368-9.00006-0>
- Eisvand HR, Kamaei H, Nazarian F (2018). Chlorophyll fluorescence, yield and yield components of bread wheat affected by phosphate bio-fertilizer, zinc and boron under late-season heat stress. *Photosynthetica* 56(4):1287-1296. <https://doi.org/10.1007/s11099-018-0829-1>
- El Melki MN, Al-Khayri JM, Aldaej MI, Almaghasla MI, El Moueddeb K, Khelifi S (2023). Assessment of the effect of climate change on wheat storage in Northwestern Tunisia: control of *Rhizopertha dominica* by aeration. *Agronomy* 13(7):1773. <https://doi.org/10.3390/agronomy13071773>
- El Sabagh A, Hossain A, Barutcular C, Islam MS, Awan S, Galal A, ... Meena R (2019). Wheat (*Triticum aestivum* L.) production under drought and heat stress—adverse effects, mechanisms and mitigation: A review. *Applied Ecology and Environmental Research* 17(4):8307-8332 http://dx.doi.org/10.15666/aeer/1704_83078332

- Essemine J, Ammar S, Bouzid S (2010). Impact of heat stress on germination and growth in higher plants: Physiological, biochemical and molecular repercussions and mechanisms of defence. *Journal of Biological Sciences* 10(6):565-572. <https://doi.org/10.3923/jbs.2010.565.572>
- Faiz H, Ayyub CM, Khan RW, Ahmad R (2020). Morphological, physiological and biochemical responses of eggplant (*Solanum melongena* L.) seedling to heat stress. *Pakistan Journal of Agricultural Sciences* 57(2). <http://doi.org/10.21162/PAKJAS/20.9433>
- Fleitas MC, Mondal S, Gerard GS, Hernández-Espinosa N, Singh RP, Crossa J, Guzmán C (2020). Identification of CIMMYT spring bread wheat germplasm maintaining superior grain yield and quality under heat-stress. *Journal of Cereal Science* 93:102981. <https://doi.org/10.1016/j.jcs.2020.102981>
- Fortunato S, Lasorella C, Dipierro N, Vita F, de Pinto MC (2023). Redox signaling in plant heat stress response. *Antioxidants* 12(3):605. <https://doi.org/10.3390/antiox12030605>
- Giordano M, Petropoulos, SA, Roupheal Y (2021). Response and defence mechanisms of vegetable crops against drought, heat and salinity stress. *Agriculture* 11(5):463. <https://doi.org/10.3390/agriculture11050463>
- Gupta N, Agarwal S, Agarwal V, Nathawat N, Gupta S, Singh G (2013). Effect of short-term heat stress on growth, physiology and antioxidative defence system in wheat seedlings. *Acta Physiologiae Plantarum* 35(6):1837-1842. <https://doi.org/10.1007/s11738-013-1221-1>
- Haider S, Iqbal J, Naseer S, Yaseen T, Shaukat M, Bibi H, ... Mahmood T (2021). Molecular mechanisms of plant tolerance to heat stress: current landscape and future perspectives. *Plant Cell Reports* 40(12):2247-2271. <https://doi.org/10.1007/s00299-021-02696-3>
- Hamayun M, Khan SA, Khan AL, Shin JH, Ahmad B, Shin DH, Lee IJ (2010). Exogenous gibberellic acid reprograms soybean to higher growth and salt stress tolerance. *Journal of Agricultural and Food Chemistry* 58(12):7226-7232. <https://doi.org/10.1021/jf101221t>
- Hasan N, Choudhary S, Naaz N, Sharma N, Laskar RA (2021). Recent advancements in molecular marker-assisted selection and applications in plant breeding programmes. *Journal of Genetic Engineering and Biotechnology* 19(1):1-26. <https://doi.org/10.1186/s43141-021-00231-1>
- Hasanuzzaman M, Bhuyan MB, Nahar K, Hossain MS, Mahmud JA, Hossen MS, ... Fujita M (2018). Potassium: a vital regulator of plant responses and tolerance to abiotic stresses. *Agronomy* 8(3):31. <https://doi.org/10.3390/agronomy8030031>
- Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M (2013). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International Journal of Molecular Sciences* 14(5):9643-9684. <https://doi.org/10.3390/ijms14059643>
- He GH, Xu JY, Wang YX, Liu JM, Li PS, Chen M, ... Xu ZS (2016). Drought-responsive WRKY transcription factor genes TaWRKY1 and TaWRKY33 from wheat confer drought and/or heat resistance in *Arabidopsis*. *BMC Plant Biology* 16:1-16. <https://doi.org/10.1186/s12870-016-0806-4>
- Heckathorn SA, Giri A, Mishra S, Bista D (2013). Heat stress and roots. *Climate Change and Plant Abiotic Stress Tolerance* 109-136. <https://doi.org/10.1002/9783527675265.ch05>
- Hossain A, Skalicky M, Brestic M, Maitra S, Ashraf Al Alam M, Syed MA, ... Islam T (2021). Consequences and mitigation strategies of abiotic stresses in wheat (*Triticum aestivum* L.) under the Changing Climate. *Agronomy* 11(2):241. <https://doi.org/10.3390/agronomy11020241>
- Hu C, Yang J, Qi Z, Wu H, Wang B, Zou F, ... Liu Q (2022). Heat shock proteins: biological functions, pathological roles, and therapeutic opportunities. *MedComm* 3(3):e161. <https://doi.org/10.1002/mco2.161>
- Hussain N, Abbas A, Hammad M, Rehman A, Ali T, Ashraf S, Javed M (2023). Evaluation of wheat lines for yield and its components under different ecological zones. *Journal of Physical, Biomedical and Biological Sciences* 2023(1):9-9.
- Hussain Q, Asim M, Zhang R, Khan R, Farooq S, Wu J (2021). Transcription factors interact with ABA through gene expression and signaling pathways to mitigate drought and salinity stress. *Biomolecules* 11(8):1159. <https://doi.org/10.3390/biom11081159>
- Huynh BL, Ehlers JD, Huang BE, Muñoz-Amatriaín M, Lonardi S, Santos JRP, ... Roberts PA (2018). A multi-parent advanced generation inter-cross (MAGIC) population for genetic analysis and improvement of cowpea (*Vigna unguiculata* L.). *The Plant Journal* 93(6):1129-1142. <https://doi.org/10.1111/tpj.13827>

- Iqbal M, Raja NI, Mashwani ZUR, Hussain M, Ejaz M, Yasmeen F (2019). Effect of silver nanoparticles on growth of wheat under heat stress. *Iranian Journal of Science and Technology Transactions A: Science* 43:387-395. <https://doi.org/10.1007/s40995-017-0417-4>
- Iqbal M, Raja NI, Yasmeen F, Hussain M, Ejaz M, Shah M (2017). Impacts of heat stress on wheat: a critical review. *Advances in Crop Science and Technology* 5(1):1-9. <http://dx.doi.org/10.4172/2329-8863.1000251>
- Jagadish S, Septiningsih E, Kohli A, Thomson M, Ye C, Redona E, ... Ismail A (2012). Genetic advances in adapting rice to a rapidly changing climate. *Journal of Agronomy and Crop Science* 198(5):360-373. <https://doi.org/10.1111/j.1439-037X.2012.00525.x>
- Jan N, Rather AMUD, John R, Chaturvedi P, Ghatak A, Weckwerth W, ... Mir RR (2023). Proteomics for abiotic stresses in legumes: present status and future directions. *Critical Reviews in Biotechnology* 43(2):171-190. <https://doi.org/10.1080/07388551.2021.2025033>
- Janni M, Gulli M, Maestri E, Marmiroli M, Valliyodan B, Nguyen HT, Marmiroli N (2020). Molecular and genetic bases of heat stress responses in crop plants and breeding for increased resilience and productivity. *Journal of Experimental Botany* 71(13):3780-3802. <https://doi.org/10.1093/jxb/eraa034>
- Jee H (2016). Size dependent classification of heat shock proteins: a mini-review. *Journal of Exercise Rehabilitation* 12(4):255. <https://doi.org/10.12965/jer.1632642.321>
- Jha UC, Bohra A, Singh NP (2014). Heat stress in crop plants: its nature, impacts and integrated breeding strategies to improve heat tolerance. *Plant Breeding* 133(6):679-701. <https://doi.org/10.1111/pbr.12217>
- Kamal NM, Gorafi YSA, Abdelrahman M, Abdellatef E, Tsujimoto H (2019). Stay-Green Trait: A prospective approach for yield potential, and drought and heat stress adaptation in globally important cereals. *International Journal of Molecular Sciences* 20(23):5837. <https://doi.org/10.3390/ijms20235837>
- Kamrun N, Kamal Uddin A, Masayuki F (2010). Phenological variation and its relation with yield in several wheat (*Triticum aestivum* L.) cultivars under normal and late sowing mediated heat stress condition. *Notulae Scientia Biologicae* 2(3). <http://dx.doi.org/10.15835/nsb234723>
- Kaur B, Sandhu KS, Kamal R, Kaur K, Singh J, Röder MS, Muqaddasi QH (2021). Omics for the improvement of abiotic, biotic, and agronomic traits in major cereal crops: Applications, challenges, and prospects. *Plants* 10(10):1989. <https://doi.org/10.3390/plants10101989>
- Kaur R, Sinha K, Bhunia RK (2019). Can wheat survive in heat? Assembling tools towards successful development of heat stress tolerance in *Triticum aestivum* L. *Molecular Biology Reports* 46(2):2577-2593. <https://doi.org/10.1007/s11033-019-04686-x>
- Khan A, Khan AL, Imran M, Asaf S, Kim YH, Bilal S, ... Lee IJ (2020). Silicon-induced thermotolerance in *Solanum lycopersicum* L. via activation of antioxidant system, heat shock proteins, and endogenous phytohormones. *BMC Plant Biology* 20(1):1-18. <https://doi.org/10.1186/s12870-020-02456-7>
- Khan MIR, Iqbal N, Masood A, Per TS, Khan NA (2013). Salicylic acid alleviates adverse effects of heat stress on photosynthesis through changes in proline production and ethylene formation. *Plant Signaling & Behavior* 8(11):e26374. <https://doi.org/10.4161/psb.26374>
- Kheiri M, Deihimfard R, Kambouzia J, Moghaddam SM, Rahimi-Moghaddam S, Azadi H (2022). Impact of heat stress on rainfed wheat growth and yield under semi-arid, semi-humid and mediterranean climates in Iran condition. *International Journal of Plant Production* 16(1):29-40. <https://doi.org/10.1007/s42106-021-00179-9>
- Kheiri M, Soufizadeh S, Movahhed Moghaddam S, Ghaffari A (2021). Exploring the impact of weather variability on phenology, length of growing period, and yield of contrast dryland wheat cultivars. *Agricultural Research* 10(4):556-568. <https://doi.org/10.1007/s40003-020-00523-x>
- Kotak S, Larkindale J, Lee U, von Koskull-Döring P, Vierling E, Scharf KD (2007). Complexity of the heat stress response in plants. *Current Opinion in Plant Biology* 10(3):310-316. <https://doi.org/10.1016/j.pbi.2007.04.011>
- Kothari A, Lachowicz J (2021). Roles of brassinosteroids in mitigating heat stress damage in cereal crops. *International Journal of Molecular Sciences* 22(5):2706. <https://doi.org/10.3390/ijms22052706>
- Krug AS, BM Drummond E, Van Tassel DL, Warschefsky EJ (2023). The next era of crop domestication starts now. *Proceedings of the National Academy of Sciences* 120(14):e2205769120. <https://doi.org/10.1073/pnas.2205769120>

- Kumar RR, Dubey K, Arora K, Dalal M, Rai GK, Mishra D, ... Praveen S (2021). Characterizing the putative mitogen-activated protein kinase (MAPK) and their protective role in oxidative stress tolerance and carbon assimilation in wheat under terminal heat stress. *Biotechnology Reports* 29:e00597. <https://doi.org/10.1016/j.btre.2021.e00597>
- Kumar RR, Singh K, Ahuja S, Tasleem M, Singh I, Kumar S, ... Praveen S (2019). Quantitative proteomic analysis reveals novel stress-associated active proteins (SAAPs) and pathways involved in modulating tolerance of wheat under terminal heat. *Functional & Integrative Genomics* 19(2):329-348. <https://doi.org/10.1007/s10142-018-0648-2>
- Laizer HC, Chacha MN, Ndakidemi PA (2019). Farmers knowledge, perceptions and practices in managing weeds and insect pests of common bean in Northern Tanzania. *Sustainability* 11(15):4076. <https://doi.org/10.3390/su11154076>
- Lal MK, Tiwari RK, Gahlaut V, Mangal V, Kumar A, Singh MP, ... Zinta G (2021). Physiological and molecular insights on wheat responses to heat stress. *Plant Cell Reports* 1-18. <https://doi.org/10.1007/s00299-021-02784-4>
- Lenzoni G, Knight MR (2019). Increases in absolute temperature stimulate free calcium concentration elevations in the chloroplast. *Plant and Cell Physiology* 60(3):538-548. <https://doi.org/10.1093/pcp/pcy227>
- Li ZS, Li B, Zheng Q, Li H (2015). Review and new progress in wheat wide hybridization for improving the resistance to biotic and abiotic stresses. In *Advances in wheat genetics: from genome to field*. Springer Tokyo, pp 377-385. https://doi.org/10.1007/978-4-431-55675-6_43
- Lipiec J, Doussan C, Nosalewicz A, Kondracka K (2013). Effect of drought and heat stresses on plant growth and yield: a review. *International Agrophysics* 27(4). <https://doi.org/10.2478/intag-2013-0017>
- Liu P, Guo W, Jiang Z, Pu H, Feng C, Zhu X, ... Little C (2011). Effects of high temperature after anthesis on starch granules in grains of wheat (*Triticum aestivum* L.). *The Journal of Agricultural Science* 149(2):159-169. <https://doi.org/10.1017/S0021859610001024>
- Liu XH, Lyu YS, Yang W, Yang ZT, Lu SJ, Liu JX (2020). A membrane-associated NAC transcription factor OsNTL3 is involved in thermotolerance in rice. *Plant Biotechnology Journal* 18(5):1317-1329. <https://doi.org/10.1111/pbi.13297>
- Ma J, Tang X, Sun B, Wei J, Ma L, Yuan M, ... Chen KM (2022). A NAC transcription factor, TaNAC5D-2, acts as a positive regulator of drought tolerance through regulating water loss in wheat (*Triticum aestivum* L.). *Environmental and Experimental Botany* 196:104805. <https://doi.org/10.1016/j.envexpbot.2022.104805>
- Madani B, Mirshekari A, Imahori Y (2019). Chapter 19 - Physiological responses to stress. In: Yahia EM (Ed). *Postharvest Physiology and Biochemistry of Fruits and Vegetables*. Woodhead Publishing. pp 405-423. <https://doi.org/10.1016/B978-0-12-813278-4.00020-8>
- Maj W, Pertile G, Fraç M (2023). Soil-borne neosartorya spp.: a heat-resistant fungal threat to horticulture and food production—an important component of the root-associated microbial community. *International Journal of Molecular Sciences* 24(2):1543. <https://doi.org/10.3390/ijms24021543>
- Medina E, Kim SH, Yun M, Choi WG (2021). Recapitulation of the function and role of ROS generated in response to heat stress in plants. *Plants* 10(2):371. <https://doi.org/10.3390/plants10020371>
- Mendanha T, Rosenqvist E, Hyldgaard B, Ottosen CO (2018). Heat priming effects on anthesis heat stress in wheat cultivars (*Triticum aestivum* L.) with contrasting tolerance to heat stress. *Plant Physiology and Biochemistry* 132:213-221. <https://doi.org/10.1016/j.plaphy.2018.09.002>
- Mirza SR (2021). 23. Seed priming enhanced seed germination traits of wheat under water, salt and heat stress. *Pure and Applied Biology (PAB)* 4(4):650-658. <http://dx.doi.org/10.19045/bspab.2015.44025>
- Mohammed AR, Tarpley L (2010). Effects of high night temperature and spikelet position on yield-related parameters of rice (*Oryza sativa* L.) plants. *European Journal of Agronomy* 33(2):117-123. <https://doi.org/10.1016/j.eja.2009.11.006>
- Mohammed S, Huggins TD, Beecher F, Chick C, Sengodan P, Mondal S, ... Hays DB (2018). The role of leaf epicuticular wax in the adaptation of wheat (*Triticum aestivum* L.) to high temperatures and moisture deficit conditions. *Crop Science* 58(2):679-689. <https://doi.org/10.2135/cropsci2017.07.0454>
- Møller IM, Jensen PE, Hansson A (2007). Oxidative modifications to cellular components in plants. *Annals of Botany* 58:459-481. <https://doi.org/10.1146/annurev.arplant.58.032806.103946>
- Mondal S, Karmakar S, Panda D, Pramanik K, Bose B, Singhal RK (2023). Crucial plant processes under heat stress and tolerance through heat shock proteins. *Plant Stress* 10:100227. <https://doi.org/10.1016/j.stress.2023.100227>

- Morgounov A, Sonder K, Abugalieva A, Bhadauria V, Cuthbert RD, Shamanin V, ... DePauw RM (2018). Effect of climate change on spring wheat yields in North America and Eurasia in 1981-2015 and implications for breeding. *PLoS One* 13(10):e0204932. <https://doi.org/10.1371/journal.pone.0204932>
- Nadeem M, Li J, Wang M, Shah L, Lu S, Wang X, Ma C (2018). Unraveling field crops sensitivity to heat stress: mechanisms, approaches, and future prospects. *Agronomy* 8(7):128. <https://doi.org/10.3390/agronomy8070128>
- Nesar NA, Hameedi A, Attri M, Kumar R, Bochalya RS, Stanikzai RG, Srivastava H (2022). Terminal heat stress and its mitigation options through agronomic interventions in wheat crop: A review. *International Journal of Environment and Climate Change* 12(11):131-139. <http://dx.doi.org/10.9734/IJECC/2022/v12i1130955>
- Ni Z, Li H, Zhao Y, Peng H, Hu Z, Xin M, Sun Q (2018). Genetic improvement of heat tolerance in wheat: Recent progress in understanding the underlying molecular mechanisms. *The Crop Journal* 6(1):32-41. <https://doi.org/10.1016/j.cj.2017.09.005>
- Pagamas P, Nawata E (2008). Sensitive stages of fruit and seed development of chili pepper (*Capsicum annuum* L. var. *Shishito*) exposed to high-temperature stress. *Scientia Horticulturae* 117(1):21-25. <https://doi.org/10.1016/j.scienta.2008.03.017>
- Pandey GC, Geetika M, Pradeep S, Vinay S, (2019). Terminal heat tolerance in wheat: an overview. *Journal of Cereal Research* 11(1):1-16. <http://dx.doi.org/10.25174/2249-4065/2019/79252>
- Parmar N, Singh KH, Sharma D, Singh L, Kumar P, Nanjundan J, ... Thakur AK (2017). Genetic engineering strategies for biotic and abiotic stress tolerance and quality enhancement in horticultural crops: a comprehensive review. *3 Biotechnology* 7:1-35. <https://doi.org/10.1007/s13205-017-0870-y>
- Patil P, Shrivastav SP, Landge R, Patil K, Salunkhe H (2022). Heat stress and tolerance in wheat: A review. *The Pharma Innovation Journal* SP-11:362-368.
- Paudel S, Pokharel NP, Adhikari S, Poudel S (2021). heat and drought stress effect in wheat genotypes: A review. *Food and Agri Economics Review (FAER)* 1(2):77-79. <http://doi.org/10.26480/faer.02.2021.77.79>
- Plaut Z, Butow BJ, Blumenthal CS, Wrigley CW (2004). Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. *Field Crops Research* 86(2):185-198. <https://doi.org/10.1016/j.fcr.2003.08.005>
- Posch BC, Kariyawasam BC, Bramley H, Coast O, Richards RA, Reynolds MP, ... Atkin OK (2019). Exploring high temperature responses of photosynthesis and respiration to improve heat tolerance in wheat. *Journal of Experimental Botany* 70(19):5051-5069. <https://doi.org/10.1093/jxb/erz257>
- Poudel H, Khanal B, Poudel K, Dhungana M, Pandey R, Dhungana S (2021). Effect of heat stress in wheat: A review. *Agriculture Environment* 2:63.
- Poudel MR, Ghimire S, Dhakal KH, Thapa DB, Poudel HK (2020). Evaluation of wheat genotypes under irrigated, heat stress and drought conditions. *Journal of Biology and Today's World* 9(1):1-12. <http://doi.org/10.35248/2322-3308.20.9.212>
- Prasad PV, Djanaguiraman M (2014). Response of floret fertility and individual grain weight of wheat to high temperature stress: sensitive stages and thresholds for temperature and duration. *Functional Plant Biology* 41(12):1261-1269. <https://doi.org/10.1071/FP14061>
- Rabara RC, Msanne J, Basu S, Ferrer MC, Roychoudhury A (2021). Coping with inclement weather conditions due to high temperature and water deficit in rice: an insight from genetic and biochemical perspectives. *Physiologia Plantarum* 172(2):487-504. <https://doi.org/10.1111/ppl.13272>
- Rai KK, Pandey N, Rai SP (2020). Salicylic acid and nitric oxide signaling in plant heat stress. *Physiologia Plantarum* 168(2):241-255. <https://doi.org/10.1111/ppl.12958>
- Rajametov SN, Yang EY, Jeong HB, Cho MC, Chae SY, Paudel N (2021). Heat treatment in two tomato cultivars: a study of the effect on physiological and growth recovery. *Horticulturae* 7(5):119. <https://www.mdpi.com/2311-7524/7/5/119>
- Rangan P, Furtado A, Henry R (2020). Transcriptome profiling of wheat genotypes under heat stress during grain-filling. *Journal of Cereal Science* 91:102895. <https://doi.org/10.1016/j.jcs.2019.102895>
- Rawat N, Singla-Pareek SL, Pareek A (2021). Membrane dynamics during individual and combined abiotic stresses in plants and tools to study the same. *Physiologia Plantarum* 171(4):653-676. <https://doi.org/10.1111/ppl.13217>
- Raza A, Tabassum J, Kudapa H, Varshney RK (2021). Can omics deliver temperature resilient ready-to-grow crops? *Critical Reviews in Biotechnology* 41(8):1209-1232. <https://doi.org/10.1080/07388551.2021.1898332>

- Rehman A, Khan I, Farooq M (2023). Secondary metabolites mediated reproductive tolerance under heat stress in plants. *Journal of Plant Growth Regulation*. <https://doi.org/10.1007/s00344-023-11161-2>
- Rehman RS, Ali M, Ali Zafar S, Hussain M, Pasha A, Saqib Naveed M, ... Waseem M (2022). Abscisic acid mediated abiotic stress tolerance in plants. *Asian Journal of Research in Crop Science* 7(1):1-17. <https://doi.org/10.9734/ajrcs%2F2022%2Fv7i130128>
- Riaz MW, Yang L, Yousaf MI, Sami A, Mei XD, Shah L, ... Ma C (2021). Effects of heat stress on growth, physiology of plants, yield and grain quality of different spring wheat (*Triticum aestivum* L.) genotypes. *Sustainability* 13(5):2972. <https://doi.org/10.3390/su13052972>
- Rodríguez M, Canales E, Borrás-Hidalgo O (2005). Molecular aspects of abiotic stress in plants. *Biocología Aplicada* 22(1):1-10.
- Sable A, Agarwal SK (2018). Plant heat shock protein families: essential machinery for development and defense. *Journal of Biological Sciences and Medicine* 4(1):51-64.
- Sakpal A, Yadav S, Choudhary R, Saini N, Vasudev S, Yadava DK, ... Yadav SK (2023). Heat-stress-induced changes in physio-biochemical parameters of mustard cultivars and their role in heat stress tolerance at the seedling stage. *Plants*, 12(6):1400. <https://doi.org/10.3390/plants12061400>
- Salman M, Majeed S, Rana IA, Atif RM, Azhar MT (2019). Novel breeding and biotechnological approaches to mitigate the effects of heat stress on cotton. *Recent approaches in omics for plant resilience to climate change* 251-277. https://doi.org/10.1007/978-3-030-21687-0_11
- Sattar A, Sher A, Ijaz M, Ul-Allah S, Rizwan MS, Hussain M, ... Cheema MA (2020). Terminal drought and heat stress alter physiological and biochemical attributes in flag leaf of bread wheat. *PLoS One* 15(5):e0232974. <https://doi.org/10.1371/journal.pone.0232974>
- Sehgal A, Sita K, Siddique KH, Kumar R, Bhogireddy S, Varshney RK, ... Nayyar H (2018). Drought or/and heat-stress effects on seed filling in food crops: impacts on functional biochemistry, seed yields, and nutritional quality. *Frontiers in Plant Science* 9:1705. <https://doi.org/10.3389/fpls.2018.01705>
- Shahzad A, Ullah S, Dar AA, Sardar MF, Mehmood T, Tufail MA, ... Haris M (2021). Nexus on climate change: Agriculture and possible solution to cope future climate change stresses. *Environmental Science and Pollution Research* 28:14211-14232. <https://doi.org/10.1007/s11356-021-12649-8>
- Sharma D, Mamrutha H, Gupta VK, Tiwari R, Singh R (2015). Association of SSCP variants of HSP genes with physiological and yield traits under heat stress in wheat. *Research on Crops* 16(1). <http://dx.doi.org/10.5958/2348-7542.2015.00020.0>
- Sharma D, Singh R, Tiwari R, Kumar R, Gupta VK (2019). Wheat responses and tolerance to terminal heat stress: a review. *Wheat Production in Changing Environments* 149-173. https://doi.org/10.1007/978-981-13-6883-7_7
- Sharma P, Jha AB, Dubey RS, Pessaraki M (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *Journal of Botany* 2012:217037. <https://doi.org/10.1155/2012/217037>
- Shashikumara P, Gajghate R, Bhatt Devate N, Harikrishna, Mamrutha H, Gopalareddy K, Singh G (2022). Heat stress in wheat: Adaptation strategies. In: *Thermotolerance in Crop Plants*. Springer, pp 1-21. https://doi.org/10.1007/978-981-19-3800-9_1
- Sparrow-Muñoz I, Chen TC, Burgess SJ (2023). Recent developments in the engineering of Rubisco activase for enhanced crop yield. *Biochemical Society Transactions*. <https://doi.org/10.1042/BST20221281>
- Steward PR, Dougill AJ, Thierfelder C, Pittelkow CM, Stringer LC, Kudzala M, Shackelford GE (2018). The adaptive capacity of maize-based conservation agriculture systems to climate stress in tropical and subtropical environments: A meta-regression of yields. *Agriculture, Ecosystems & Environment* 251:194-202. <https://doi.org/10.1016/j.agee.2017.09.019>
- Sumesh K, Sharma-Natu P, Ghildiyal M (2008). Starch synthase activity and heat shock protein in relation to thermal tolerance of developing wheat grains. *Biologia Plantarum* 52(4):749-753. <https://doi.org/10.1007/s10535-008-0145-x>
- Suzuki N (2023). Fine tuning of ros, redox and energy regulatory systems associated with the functions of chloroplasts and mitochondria in plants under heat stress. *International Journal of Molecular Sciences* 24(2):1356. <https://doi.org/10.3390/ijms24021356>

- Tack J, Barkley A, Hendricks N (2017). Irrigation offsets wheat yield reductions from warming temperatures. *Environmental Research Letters* 12(11):114027. <http://doi.org/10.1088/1748-9326/aa8d27>
- Tan W, wei Meng Q, Brestic M, Olsovska K, Yang X (2011). Photosynthesis is improved by exogenous calcium in heat-stressed tobacco plants. *Journal of Plant Physiology* 168(17):2063-2071. <https://doi.org/10.1016/j.jplph.2011.06.009>
- Tao Zq, Chen Yq, Li C, Zou Jx, Yan P, Yuan Sf, ... Sui P (2016). The causes and impacts for heat stress in spring maize during grain filling in the North China Plain. A review. *Journal of Integrative Agriculture* 15(12):2677-2687. [https://doi.org/10.1016/S2095-3119\(16\)61409-0](https://doi.org/10.1016/S2095-3119(16)61409-0)
- Thomason K, Babar MA, Erickson JE, Mulvaney M, Beecher C, MacDonald G (2018). Comparative physiological and metabolomics analysis of wheat (*Triticum aestivum* L.) following post-anthesis heat stress. *PLoS One* 13(6):e0197919. <https://doi.org/10.1371/journal.pone.0197919>
- Tian X, Qin Z, Zhao Y, Wen J, Lan T, Zhang L, ... Zhao A (2022). Stress granule-associated TaMBF1c confers thermotolerance through regulating specific mRNA translation in wheat (*Triticum aestivum*). *New Phytologist* 233(4):1719-1731. <https://doi.org/10.1111/nph.17865>
- Tiwari RK, Lal MK, Kumar R, Chourasia KN, Naga KC, Kumar D, ... Zinta G (2021). Mechanistic insights on melatonin-mediated drought stress mitigation in plants. *Physiologia Plantarum* 172(2):1212-1226. <https://doi.org/10.1111/ppl.13307>
- Todaka D, Nakashima K, Shinozaki K, Yamaguchi-Shinozaki K (2012). Toward understanding transcriptional regulatory networks in abiotic stress responses and tolerance in rice. *Rice* 5(1):1-9. <https://doi.org/10.1186/1939-8433-5-6>
- Tyagi H, Jha S, Sharma M, Giri J, Tyagi AK (2014). Rice SAPs are responsive to multiple biotic stresses and overexpression of OsSAP1, an A20/AN1 zinc-finger protein, enhances the basal resistance against pathogen infection in tobacco. *Plant Science* 225:68-76. <https://doi.org/10.1016/j.plantsci.2014.05.016>
- Ul Hassan M, Rasool T, Iqbal C, Arshad A, Abrar M, Abrar MM, ... Fahad S (2021). Linking plants functioning to adaptive responses under heat stress conditions: a mechanistic review. *Journal of Plant Growth Regulation* 1-18. <https://doi.org/10.1007/s00344-021-10493-1>
- Ullah A, Nadeem F, Nawaz A, Siddique KHM, Farooq M (2022). Heat stress effects on the reproductive physiology and yield of wheat. *Journal of Agronomy and Crop Science* 208(1):1-17. <https://doi.org/10.1111/jac.12572>
- Upreti K, Sharma M (2016). Role of plant growth regulators in abiotic stress tolerance. In: *Abiotic Stress Physiology of Horticultural Crops*. Springer, pp 19-46. https://doi.org/10.1007/978-81-322-2725-0_2
- Usman M (2016). Contribution of agriculture sector in the GDP growth rate of Pakistan. *Journal of Global Economics* 4(2):1-3. <https://doi.org/10.4172/2375-4389.1000184>
- Usman MG, Rafii M, Ismail M, Malek M, Latif MA, Oladosu Y (2014). Heat shock proteins: functions and response against heat stress in plants. *International Journal of Science and Technology Research* 3(11):204-218.
- Wu B, Qiao J, Wang X, Liu M, Xu S, Sun D, (2021). Factors affecting the rapid changes of protein under short-term heat stress. *BMC Genomics* 22(1):263. <https://doi.org/10.1186/s12864-021-07560-y>
- Wu J, Gao T, Hu J, Zhao L, Yu C, Ma F (2022). Research advances in function and regulation mechanisms of plant small heat shock proteins (sHSPs) under environmental stresses. *Science of the Total Environment*: 154054. <https://doi.org/10.1016/j.scitotenv.2022.154054>
- Yadav A, Singh J, Ranjan K, Kumar P, Khanna S, Gupta M, ... Sirohi A (2020). Heat shock proteins: master players for heat-stress tolerance in plants during climate change. *Heat stress tolerance in plants: physiological, molecular and genetic perspectives* 189-211. <https://doi.org/10.1002/9781119432401.ch9>
- Yadav MR, Choudhary M, Singh J, Lal MK, Jha PK, Udawat P, ... Prasad PVV (2022). Impacts, tolerance, adaptation, and mitigation of heat stress on wheat under changing climates. *International Journal of Molecular Sciences* 23(5):2838. <https://doi.org/10.3390/ijms23052838>
- Yamamoto Y (2016). Quality control of photosystem ii: The mechanisms for avoidance and tolerance of light and heat stresses are closely linked to membrane fluidity of the thylakoids [Review]. *Frontiers in Plant Science* 7. <https://doi.org/10.3389/fpls.2016.01136>
- Younis A, Khattab H, Emam M (2020). Impacts of silicon and silicon nanoparticles on leaf ultrastructure and TaPIP1 and TaNIP2 gene expressions in heat stressed wheat seedlings. *Biological Plant* 64:343-352. <https://doi.org/10.32615/bp.2020.030>

- Yumurtaci A (2015). Utilization of wild relatives of wheat, barley, maize and oat in developing abiotic and biotic stress tolerant new varieties. *Emirates Journal of Food and Agriculture* 01-23. <http://dx.doi.org/10.9755/ejfa.v27i1.17852>
- Zafar SA, Hameed A, Ashraf M, Khan AS, Qamar Zu, Li X, Siddique KHM (2020). Agronomic, physiological and molecular characterisation of rice mutants revealed the key role of reactive oxygen species and catalase in high-temperature stress tolerance. *Functional Plant Biology* 47(5):440-453. <https://doi.org/10.1071/FP19246>
- Zahra N, Hafeez MB, Ghaffar A, Kausar A, Zeidi MA, Siddique KHM, Farooq M (2023). Plant photosynthesis under heat stress: Effects and management. *Environmental and Experimental Botany* 206:105178. <https://doi.org/10.1016/j.envexpbot.2022.105178>
- Zahra N, Wahid A, Hafeez MB, Ullah A, Siddique KH, Farooq M (2021). Grain development in wheat under combined heat and drought stress: Plant responses and management. *Environmental and Experimental Botany* 188:104517. <https://doi.org/10.1016/j.envexpbot.2021.104517>
- Zhang D, Zhang Z, Unver T, Zhang B (2021). CRISPR/Cas: A powerful tool for gene function study and crop improvement. *Journal of Advanced Research* 29:207-221. <https://doi.org/10.1016/j.jare.2020.10.003>
- Zhao H, Dai T, Jing Q, Jiang D, Cao W (2007). Leaf senescence and grain filling affected by post-anthesis high temperatures in two different wheat cultivars. *Plant Growth Regulation* 51:149-158. <https://doi.org/10.1016/j.sajb.2019.04.009>
- Zheng L, Wu W, Chen Q, Zhang G, Gao F, Zhou Y (2022). Integrated transcriptomics, proteomics, and metabolomics identified biological processes and metabolic pathways involved in heat stress response in jojoba. *Industrial Crops and Products* 183:114946. <https://doi.org/10.1016/j.indcrop.2022.114946>



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