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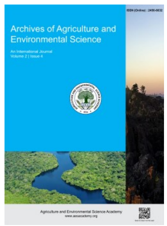

REVIEW ARTICLE

CrossMark

Impact and tolerance mechanism of heat stress in wheat (*Triticum aestivum* L.): A review

Suchi Bhatt*, Smirti Sharma and Sashi Bhusan Kumar Yadav

Institute of Agriculture and Animal Science, Tribhuvan University, Nepal
*Corresponding author's E-mail: suchi.zbhatt@gmail.com

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ABSTRACT

Wheat is one of the major cereal crops preferred by world's population. About 55% of world's population depend on wheat to meet their 20% calorie requirement. Wheat being a winter crop grows best in 15-25 degree Celsius of temperature range. But due to increasing global warming climatic requirement of wheat is not fulfilled and suffer different abiotic stresses such as heat, drought, salinity, cold, excess water etc. Among which heat stress is one of the major abiotic stresses faced by wheat. It has different morphological, biochemical and physiological consequences on wheat for instance poor grain quality, decreased grain number and weight, decreased photosynthesis due to disruption in chlorophyll structure and function, reduced starch content due to poor efficiency of enzyme required in biosynthesis. To cope up with all these impacts of heat stress wheat has developed various tolerance mechanisms such as release of heat shock protein, antioxidant defense mechanism, membrane thermostability, stay green, omics approaches etc. Heat shock protein helps to prevent death of cell, accumulation of denatured protein, refolding of protein, transmission of heat shock responses etc. While omics approaches help in gene profiling, protein identification etc. knowledge about both the effect and tolerance mechanism of heat stress in wheat helps to develop heat tolerant varieties with collaborative effort of plant breeder, physiologist etc. that helps to maintain food security.

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INTRODUCTION

Wheat (*Triticum aestivum*) is considered as one of the major cereal crops preferred by most of the population worldwide (Karki *et al.*, 2021) with yearly production of 781.31 million metric tons throughout the world (World Food and Agriculture – Statistical Year book 2023, 2023). It belongs to family Poaceae contributing about 50% of the world grain trade and 30% of world grain production (Akter & Rafiqul Islam, 2017). The worldwide volume of production of 2020-21 marketing year was more than 768.9 million metric tonnes (USDA, 2021). While in Nepal it was 2,210 thousand tonnes in year 2020, which is 5.73% up on annual basis (USDA, 2020). The gross production of wheat worldwide is 800.2 million metric ton (MMT) (Sowell & Swearingen, 2023). While in Nepal wheat is third most important cereal crop after rice and maize with 2,144,568 metric tons of production in 716,978 hectares of land (Statistical-Information-on-Nepalese-Agriculture-2078-79-2021-22, n.d.). Total of cereal cultivating area, wheat covers 19% of it contributing 7.14% to AGDP (Agriculture Gross Domestic Product) in year 2021 (Datta Bhatta *et al.*, 2020). In Nepal approx.25% of wheat cultivating area is facing heat stress (Nyaupane *et al.*, 2023). In almost 40 countries of the world, wheat is considered as basic food which provides proteins and calories of 82% and 85% to the earth's population, respectively (Chaves *et al.*, 2013; Sharma *et al.*, 2019). It is an excellent source of protein (6-26%) as well as starch (60-70%) **(**Paudel *et al.*, 2021**).** Approximately it consists of 78% carbohydrate, 2% fat, 14% protein and 2.5%

minerals and vitamins for instance thiamine, niacin, riboflavin, and other (Iqbal *et al.*, 2022). Almost 55% of the world's population relies on wheat to meet their 20% of the calorie requirement (Guarin *et al.*, 2022). It is used to prepare pasta, cereals, alcoholic drinks, bakery products (Orlovsky *et al.*, 2019) while residues of wheat are used to make biologically active additives for livestock (Netsvetaev *et al.*, 2020).

Cultivation of wheat is usually preferred at 15- 25° temperature range both in dry and cold weather and hence repeated irrigation is most for optimum growth and output as well as the grains quality. But being a winter crop, it is susceptible to heat stress condition at almost every phase of development especially at its reproductive phase (Sinha & Kumar, 2022). While the increasing rate of atmospheric mean temperature with 0.18 degree centigrade is significantly affecting quantity of wheat produced (Rebecca Lindsey *et al.*, 2024). Wheat is said to suffer from heat stress when temperature increase from 22 degree centigrade (Djanaguiraman *et al.*, 2020). By the year 2050, it is predicted that the population will reach 9 billons globally (Akter & Rafiqul Islam, 2017) whose demand can only be fulfilled by increasing yield and productivity of wheat (Grote *et al.*, 2021). As a consequence of global climate change, concerns are growing around the world about the effect of increasing temperature on wheat production (Poudel, 2020). Wheat which is farmed in tropical and subtropical region of the world and are subjected to variety of abiotic stresses (Poudel, 2020). The principal abiotic stresses are high temperature, drought, salinity, low temperature, chemical, and water excess. However, the major abiotic factors impacting worldwide production of wheat are drought and heat stress (Lesk *et al.*, 2016; Liu *et al.*, 2016). Evapotranspiration is increased due to heat stress which ultimately results in drought (Lamaoui *et al.*, 2018).Wheat growth is stunted by heat stress as it interferes with several physiological and biochemical phenomena, while the developmental phase of plant is critical in exhibiting susceptibility of various cultivars and species to high temperature. Decline in yield has also been observed due to heat stress as it inhibits seed germination. A sophisticated process that is controlled by various genes which governs physiological and biochemical characters is known as heat tolerance (Pandey *et al.*, 2019). To withstand high temperature stress wheat adopts various strategies such as morphological and phenological as well as avoidance or acclimation which includes altering leaf angle, modification of lipid composition and utilization of transpiration for cooling (Dwivedi *et al.*, 2018).

MATERIALS AND METHODS

Information was collected by surfing various related research, review articles. No primary data were used. Secondary data were collected through research papers, reviews, annual reports etc.

IMPACT OF HEAT STRESS ON DIFFERENT FACTORS OF WHEAT

The increase in air temperature over a critical point for a certain time frame that is adequate to produce injury or irreparable damage to agricultural crop in general is high temperature stress (Dhakal *et al.*, 2021). Wheat requires different temperature at its different stage of development as shown in (Table 1) so if temperature raise above 22 degrees centigrade it faces heat stress (Djanaguiraman *et al.*, 2020). In this section the effect of heat stress on different factors of wheat are discussed i.e., morphology, physiology, biochemical, growth and development.

Morphological

Heat stress has detrimental impacts at different growth phases of wheat including germination, leaf and stem development, root growth, emergence, formation of tiller, production of dry matter, exertion of panicle, fertilization, pollination, growth of seed, yield and also quality (Huang *et al.*, 2012; Iqbal *et al.*, 2017). Heat stress causes wheat plants to lose their fresh and dry biomass including length of root and shoot, also area and number of leaves (Iqbal *et al.*, 2019). It also affects several developmental stages of wheat such as flowering, anthesis, grain filling and ripening (Rahman *et al.*, 2009). Wheat leaves get rolled due to heat stress (Hassan *et al.*, 2021).

Germination

The major consequence of high temperature on multiple crops including wheat is poor crop establishment and seed germination hinderance (Akter & Rafiqul Islam, 2017).The percentage of seed germination is increased under stable soil moisture when the temperature is above base temperature (Bashyal *et al.*, 2021) but it decreases suddenly when the temperature rises above the optimum range.

Table 1. Optimum temperature at different stages of growth of wheat (Khan *et al.*, 2020).

Stages	Minimum temperature (°C)	Optimum temperature	Maximum temperature
Germination of seed	3.5-5.5±0.44	20-25±1.2	35 ±1.02
Growth of root	3.50±_0.73	17.2 ±0.87	24.0±1.21
Growth of shoot	4.50±0.76	18.5 ± 1.90	20.1 ± 0.64
Initiation of leaf	1.50±0.52	20.5 ± 1.25	23.5 ± 0.95
Terminal spikelet	2.50±0.49	16.0 ± 2.30	20.0 ± 1.60
Anthesis	10.0±1.12	23.0 ± 1.75	26.0 ± 1.01
Duration of grain filling	13.0±1.45	26 ± 1.53	30.0 ± 2.13

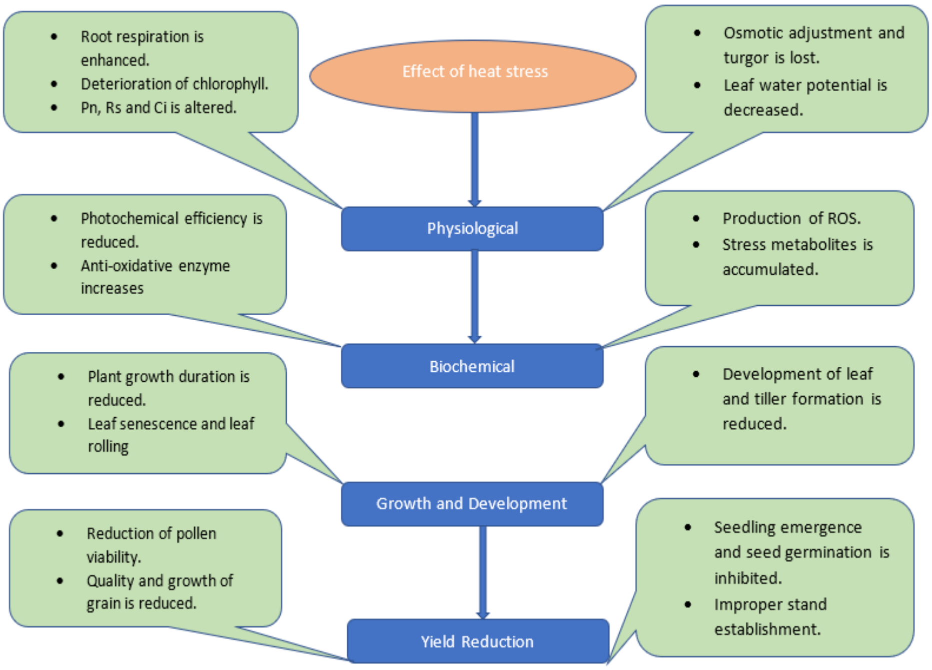

Figure 1. *Major effects of heat stress on plants growth and development; [Where, Pn= photosynthesis Rs= stomatal conductance Ci=intercellular CO2 concentration] (Akter & Rafiqul Islam, 2017).*

Plant size

The meristem of plant is significantly affected by heat stress and decline the growth of plant through shedding and leaf senescence, also by decreasing photosynthesis (Bashyal *et al*., 2021). This drop-in photosynthetic activity leads to decreased biomass yield, which in turn inhibits elongation of stem (Akter & Rafiqul Islam, 2017). The increased temperature also reduces water content of cell which ultimately reduces growth (Bashyal *et al*., 2021).

Tiller formation

High temperature accelerates growth of wheat by allowing it to enter in jointing stage followed by reproductive stage sooner than usual crop, leading to shorter tillering period (Karki *et al*., 2021) which results in reduction of number of tillers lowering the total crop yield (Kajla *et al*., 2015; Khan *et al*., 2020). Heat stress reduces survivability of effective tillers and hence reduces yield (Akter & Rafiqul Islam, 2017). The productive tillers per plant is also reduced when the day temperature is 30 degrees centigrade followed by night temperature of 25 degree centigrade (Bashyal *et al*., 2021). Heat stress reduces the tiller number and grain yield by 15.38% and 53.57%, respectively.

Pollination and fertilization

Decreased number of pollen grains on stigma is one of the major reasons under heat stress for reduced fertilization (Prasad & Djanaguiraman, 2014). Increase in temperature reduces fertility of pollen and development of pollen tube which inhibit pollen growth and hinder ovary growth leading to poor fertilization and decline in setting of seed (Kaushal *et al*., 2016).

Grain number and size

High temperature limits the embryo development during anthesis resulting in lower grain number and test weight (Poudel *et al*., 2017). The grain size of wheat is also reduced resulting in lowered thousand grain weight of wheat (Zhang *et al*., 2017). When the temperature is high i.e., 33-40 degree centigrade for three successive days during anthesis and grain filling the size, number and wight of grain is reduced extremely leading to formation of large number malformed grains (Balla *et al*., 2019).

Grain yield and quality

Grain yield is one of the major traits of crop which is determined by various elements such as number of grains/spikes, thousand grain weight (TGW), number of tillers/meter square, plant height and spike length (Bhattarai *et al*., 2017). Grain yield is sensitive to high temperature to such an extent that if the temperature rises for even a single day grain yield is reduced due to the damage of plant organs (Riaz *et al*., 2021). High temperature affects not only the grain yield but also the grain quality by reducing the accumulation of gluten, carbohydrate and proteins (Bahadur Poudel & Ram Poudel, 2020). The yield is reduced from 4.1% to 6% if the temperature increases by 1 degree centigrade (Dhakal *et al*., 2021).

Effect on physiology

Heat stress affects physiological processes such as water and nutrient relationship, photosynthesis, respiration, leaf senescence (Lal *et al*., 2021). Photosynthesis and respiration are particularly affected physiological processes as heat stress harms photosystem II and lead to deterioration of chlorophyll since excess production of Reactive Oxygen Species (ROS) damages thylakoid membrane (Sattar *et al*., 2020).

Water relation

Water status of plant is most unpredictable with changing ambient temperature, as it dehydrates plant tissue, limiting growth and development (Akter & Rafiqul Islam, 2017). Soil water content threshold is raised due to heat stress i.e., the amount of water that plants can take (Haworth *et al*., 2018). Insufficiency of water is caused by two ways; firstly, higher atmospheric temperature causes higher transpiration rate i.e., more water is lost through aerial parts of the plants than it is absorbed via roots ultimately resulting in poor photosynthetic capacity (Bashyal *et al*., 2021) Secondly, high soil temperature causes high soil moisture vaporization which inhibits the downward movement of roots and decline hydraulic conductivity of root (Bashyal *et al*., 2021). Higher temperature causes higher vapor pressure deficits, leading to increased evaporation rates (Farooq *et al*., 2011).

Photosynthesis

Photosynthesis is a complex, temperature-sensitive physiological process (Zahra *et al*., 2023). Photosynthesis of wheat is most efficient at temperature between 20° and 30° C while it decreases when temperature is raised above 30° C (Narayanan, 2018). Thylakoid membrane and PS-II are the heat unstable component which when damaged by heat cause chlorophyll loss (Ni *et al*., 2017). Chloroplast functions as a metabolic center for photosynthesis, and they play an important role in detecting heat stress and promoting specific physiological adaptive reactions via retrograde signaling (Chen *et al*., 2018; Li *et al*., 2017; Pollastri *et al*., 2021). Heat stress reduces photosynthesis by disrupting chloroplast structure and function, reducing chlorophyll concentration, inactivating chloroplast enzymes, decreasing leaf area expansion, and causing premature leaf senescence which eventually reduces yield (Akter & Islam, 2017) (Narayanan, 2018). Ribulose-1,5-bisphosphate carboxylase which is responsible for carbon fixation during photosynthesis is inhibited by heat stress (Kumar *et al*., 2016). Due to lower membrane integrity the photosynthetic products that needs to be transferred to different pant section is reduced under heat stress (Poudel *et al*., 2020). The solubility of oxygen and carbon dioxide is increased and so the photorespiration but photosynthesis is decreased due to high temperature (Karki *et al*., 2021).

Respiration

Heat stress alters mitochondrial activity by affecting respiration (Acharya *et al*., 2021). With increase in temperature rate of respiration increase to such an extent that photosynthesis is not able to compensate the losses caused due to respiration and leads to carbon famine (Narayanan, 2018). Respiration rate rises exponentially from temperature 0 to 35/40 degree centigrade, reaches to plateau in between 40 to 50 degrees centigrade, and beyond 50-degree centigrade starts to decline due to breakdown of respiratory mechanism (Iqbal et *al*., 2017).

Effect on biochemistry

Wheat is mostly composed of starch which includes amylose and amylopectin, among which amylose content is the major factor determining starch quality whose variation affects starch properties (Bahadur Poudel & Ram Poudel, 2020). While the high temperature reduces the starch content of grain by one-third to its endosperm starch due to poor efficiency of enzymes required in biosynthesis of starch (Feng *et al*., 2014) Whereas the enzymes involved in biosynthesis of starch are ADP-Glucose Pyro phosphorylase (AGPase) (Bahadur Poudel & Ram Poudel, 2020) and starch synthase while the starch synthase are of two types i.e., soluble starch synthase and granular bound starch synthase (Sharma *et al*., 2019).Grain protein content is increased in heat stress condition with the increase in essential amino acids, sedimentation index and leaf nitrogen content (Akter & Rafiqul Islam, 2017). While there is reduction in grain size and deposition of starch due to poor activity of soluble synthase at temperature of around 40 degrees centigrade (Chauhan *et al*., 2011). The deposition of reactive oxygen species such as superoxide radical (O_2^-), oxygen (O^{-1}), hydrogen peroxide (H_2O_2) and hydroxyl ion (OH) are mostly favored in heat stress (Lai & He, 2016). These reactive species in chloroplasts, peroxisomes and mitochondria impair metabolism by oxidizing lipids, proteins and nucleic acid leading structural damage of cell (Qaseem *et al*., 2019).

Tolerance mechanism

Wheat plants have developed various ways to deal with high temperature such as escaping, stay green and also, they produce special kind of protein called heat shock protein to protect themselves (Sharma *et al*., 2019). An overview of tolerance mechanism to heat stress at physiological, biochemical, and morphological behavior can be helpful in developing better breeding technique to improve wheat crop.

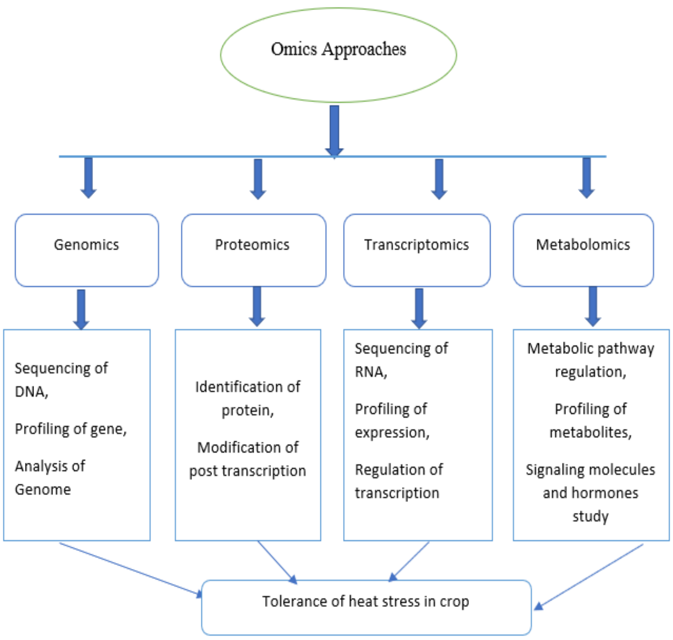

Figure 2. *Approaches of omics for tolerance of heat stress in wheat (Hasanuzzaman et al., 2013a)*

Physiological

Canopy temperature depression: Canopy temperature difference is defined as the variance between the temperature within the canopy and the current air temperature (Deva *et al.*, 2020). It serves as an important indicator for the adaptability of genotype under heat stress condition (Urban *et al.*, 2018). During heat stress CTD has significant role in maintaining the physiological basis of wheat yield. Cool canopy serves as significant principle of physiology for heat tolerance during the period of grain filling in wheat (Munjal & Rana, 2003). CTD works best where vapor pressure deficit (VPD) is high which is related to low relative humidity and warm air temperature (Medina *et al.*, 2019). Vapor pressure deficit refers to the combined effect of air temperature and relative humidity which on change controls the rate of transpiration of wheat (Belko *et al.*, 2013).

Membrane thermostability: Heat stress cause changes in the tertiary and quaternary structure of protein membranes which leads to increased loss of electrolyte and finally resulting in reduced membrane stability (Sarkar, Aminul Islam, *et al.*, 2021). High temperature speed up kinetic energy triggering the molecules to be more mobile by breaking the chemical bond in the membrane, as a result lipid bilayers become more fluid due to raise in unsaturated fatty acids or denaturation of protein (Higashi & Saito, 2019; Savchenko *et al.*, 2002).

Molecular

Omics approaches: Omics is defined as the study of cellular processes on large scale along with their control over functional, genetics and structural component (Sarkar *et al.*, 2021). The major elements of omics such as genomics, proteomics, transcriptomics and metabolomics have led us to observe the response of crops towards environmental stresses more precisely, efficiently and comprehensively (Zhou *et al.*, 2022). Knowledge related to gene structure, interconnected networks, functions including biochemical and metabolic processes are provided by genomics (Varshney *et al.*, 2018). The analysis of genomic complements of proteins or proteomics is a technique widely used in identification of changes occurred in expression of protein and to measure quantity of protein in crop in response to abiotic stresses (Mazzeo *et al.*, 2018; Mu *et al.*, 2017; Zhang *et al.*, 2017; Zhao *et al.*, 2016) Transcriptomics is defined as a field which involves investigation of expressed portions of genome i.e., transcripts using a wide range of technologies for instance microarrays, RT qPCR and next generation sequencing (Wang *et al.*, 2019) The quantity and location of transcripts at specific stages of growth and development provides deeper insights especially of various abiotic stress such as heat stress (Yadav *et al.*, 2022). The plant metabolome consists of primary and secondary metabolites (Zhou *et al.*, 2022). Primary metabolites are necessary in facilitating the synthesis of sugars, lipid and amino acids while secondary metabolites along with atropine, phytic acid, carotene and flavonoids also include ROS, coenzymes and antioxidants (Razzaq *et al.*, 2019).

Biochemical

Antioxidant defense: The harmful molecules present within the subcellular compartments is referred as reactive oxygen species (ROS) (Caverzan *et al.*, 2016).Under heat stress condition plant produce unwanted reactive oxygen species such as singlet oxygen(O_2), superoxide(O_2) (Slimen *et al.*, 2014) and hydroxy radical (OH) (Bahadur Poudel & Ram Poudel, 2020). In typical cell there is balance between production and removal of reactive oxygen species which is called as redox homeostasis (Caverzan *et al.*, 2016). Antioxidant defense system is divided into two types in wheat i.e., enzymatic and non-enzymatic (Sattar *et al.*, 2020).Superoxide dismutase (SOD), glutathione peroxidase (GPX), catalase (CAT), peroxidase (POX), ascorbate peroxidase and glutathione reductase (GR) are involved in enzymatic antioxidant whereas ascorbic acid, tocopherols, glutathione, phenolic compounds and carotenoids are divided under non- enzymatic antioxidant (Yadav *et al.*, 2022). All these antioxidants play vital role in removing ROS (Table 2).

Table 2. Functions of different antioxidants in removing ROS.

Antioxidant	Functions	References
Enzymatic		
Superoxide dismutase (SOD)	It helps in breakdown of superoxide anion (O_2) into molecular oxygen (O_2) and hydrogen peroxide (H_2O_2).	Bahadur Poudel & Ram Poudel (2020)
Glutathione peroxidase (GPX)	It helps to remove hydrogen peroxide (H_2O_2).	Bahadur Poudel & Ram Poudel (2020)
Catalase (CAT)	It facilitates in conversion of hydrogen peroxide (H_2O_2) in water (H_2O) and oxygen.	Das & Roychoudhury (2014)
Ascorbate peroxidase (APX)	Helps in removal of hydrogen peroxide by converting it into DHA and water	Das & Roychoudhury (2014)
Non- enzymatic		
Ascorbic acid (AA)	With the help of ascorbate peroxidase (APX) detoxifies hydrogen peroxide (H_2O_2)	Das & Roychoudhury (2014)
Reduced Glutathione (GSH)	Helps in removal of hydroxyl, hydrogen peroxide, singlet oxygen, etc.	Bahadur Poudel & Ram Poudel (2020)
Flavonoids	It also helps in removal of singlet oxygen, H_2O_2 and hydroxyl.	Agati *et al.* (2012)

Table 3. Different HSPs & their roles under heat stress condition.

Types of HSPs	Functions of HSPs	References
Small HSPs	Prevent cell death (apoptosis) and keeps microfilament steady.	Sah & Sherpa (2021)
HSP40	After the formation of completely refolded protein, small heat shock proteins are released by HSP40, HSP70and HSP100.	Hasanuzzaman *et al.* (2013b)
HSP60	Prevent accumulation of denatured protein and helps in refolding of protein.	Sharma *et al.* (2019c)
HSP70	Folding protein is correctly assisted and newly produced protein is kept stable by preventing the formation of clump together.	Park & Seo (2015)
HSP90	It facilitates transmission of signal related with heat shock responses.	Xu *et al.* (2012)
HSP100	It is a process dependent on ATP &helps in degradation of aggregate protein.	Sharma *et al.* (2019c)

Heat shock protein: Heat shock gene expression is stimulated by heat stress which encodes heat shock protein (HSPs) (Rangan *et al.*, 2020). The special kind protein that is formed when cells go thorough changes in protein synthesis due to high temperature exposure is known as heat shock proteins (Bimal Roka *et al.*, 2022) They are the water soluble and provides heat stress tolerance to plants probably through hydrating cellular structure (Yadav *et al.*, 2022). On the basis of molecular weight in kilo Dalton (kDa) heat shock protein is divided into different classes of which small heat shock proteins (sHSPs) are most commonly found in plant (Wu *et al.*, 2022). Under environmental stress, wheat decreases the synthesis of normal protein while increases the transcription and translation of heat shock proteins (HSPs) and establish a comprehensive protein quality control system that actively helps to maintain proper protein folding that is prone to aggregation, while ensuring their functionality even in stress conditions (Banerjee & Roychoudhury, 2018; Ul Haq *et al.*, 2019).

Morphological

Stay green: Stay green has an important role in tolerance to abiotic stress as it is an important trait of genetic improvement and is affected by the rate at which chlorophyll degrades which affect photosynthesis resulting in reduced yield (Yadav *et al.*, 2022). There are 2 types of stay green characters, firstly the functional traits which maintains the photosynthetic activity either by slowing down the rate of senescence i.e., type B or by delaying the start of senescence i.e., type A, secondly the non-functional traits or cosmetic traits in which the senescence occurs at its normal rate while photosynthetic activity is declined, but the color of the leaf is maintained as there occurs the failure of chlorophyll degradation pathway i.e., type C (Abdelrahman *et al.*, 2017).

Conclusion

Wheat is one of the important cereals consumed by majority of people worldwide. But nowadays increasing thermal stress has become one of the major limitations in wheat production. This review article has mainly focused on the heat stress induced effect. It explains how germination, emergence, tiller numbers, protein synthesis, activities of various enzymes are affected by heat stress. Knowing about all these effects we can be able to select stress tolerance varieties of wheat. We can also identify the various genetic technology, agronomic practices to overcome the complexities of heat stress. The knowledge of heat stress can become one of the coping mechanisms for future against heat stress. The detailed study of heat stress at molecular level help to develop stress-tolerant varieties with collaborative effort of plant breeders, plant physiologists etc. It also to enhance food security and minimize malnutrition worldwide.

DECLARATIONS

Authors contribution: Conceptualization and design: S.S., Writing—original draft preparation, review and editing: S.B.K.Y. S.B. All authors have read and agreed to the published version of the manuscript.

Conflict of interest: The authors declare no conflict of interest.

Ethics approval: This study did not involve any animal or human participant and thus ethical approval was not applicable.

Consent for publication: All co-authors gave their consent to publish this paper in AAES.

Data availability: The data that support the findings of this study are available on request from the corresponding author.

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