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REVIEW

Physiological and molecular insights on wheat responses to heat stress

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Abstract
Increasing temperature is a key component of global climate change, affecting crop growth and productivity worldwide. Wheat is a major cereal crop grown in various parts of the globe, which is affected severely by heat stress. The morphological parameters affected include germination, seedling establishment, source-sink activity, leaf area, shoot and root growth. The physiological parameters such as photosynthesis, respiration, leaf senescence, water and nutrient relation are also affected by heat. At the cellular level, heat stress leads to the generation of reactive oxygen species that disrupt the membrane system of thylakoid, chloroplast and plasma membrane. The deactivation of the photosystem, reduction in photosynthesis and inactivation of rubisco affect the production of photoassimilates and their allocation. This ultimately affects anthesis, grain filling, size, number and maturity of wheat grains, which hamper crop productivity. The interplay of various systems comprising antioxidants and hormones plays a crucial role in imparting heat stress tolerance in wheat. Thus, implementation of various omics technologies could foster in-depth insights on heat stress effects, eventually devising heat stress mitigation strategies by conventional and modern breeding to develop heat-tolerant wheat varieties. This review provides an integrative view of heat stress responses in wheat and also discusses approaches to develop heat-tolerant wheat varieties.

Keywords Heat stress · Photosynthesis · Growth · Biomass · Climate change · Wheat

Introduction

Abiotic stresses are the primary culprit of crop losses worldwide, reducing the yield of crops including wheat by more than 50% (Ohama et al. 2017; Buttar et al. 2020). The rise in global temperature is a major threat to agriculture, negatively affecting wheat growth and development, which ultimately leads to a reduction in yield and productivity. The mean global temperature of the earth has been predicted to increase from 1.3 to 3.7 °C by the end of this century (IPCC 2013). One of the key developmental stages affected by heat stress is the reproductive stage (Rezaei et al. 2018), and a major constraint to breed heat-tolerant varieties (Hall 2010; Haque et al. 2014).

Wheat productivity is affected by heat stress in the arid, semiarid, tropical and subtropical region of the world (Rehman et al. 2009; IPCC 2013; Stocker et al. 2014). The rise in both daytime and high night temperatures are detrimental for the plant, particularly encountered at the reproductive stages. There is a diurnal asymmetry in the temperature trend over the past few decades leading to a more

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rapid increase in the night temperature. Besides reproductive stages, other stages such as seed germination, seedling emergence and its establishment are severely impacted by high temperature (El-Sarag and Ismaeil 2013; Zhang et al. 2016). Also, heat stress is detrimental for photosynthesis, inhibition of which leads to lower accumulation of photoassimilates resulting in decreased leaf area, shoot biomass and grain production (Buttar et al. 2020). In this review, we provide an integrative view of various morphological, biochemical and molecular processes affected by heat stress in wheat. Also, mitigation strategies including the implementation of the conventional and modern breeding approaches are discussed.

Growth and physiological responses of wheat to heat stress

High temperature affects almost every stage of wheat growth and development including seed germination, root and leaf emergence, stem growth, floral initiation, pollination, fertilization, seed yield and seed quality (Rezaei et al. 2018; Buttar et al. 2020; Fleitas et al. 2020) (Fig. 1). The duration and intensity of high temperature determine the severity of stress on plant developmental stages. Plants detect changes in the temperature and adjust their metabolism, protein conformation, cytoskeleton assembly and membrane fluidity (Rangan et al. 2020). Several studies are exploring the impact of high-temperature stress on wheat at different stages, showing that heat treatment of 45 °C at the seed germination stage cause embryo death and decline seedling establishment rate (Cheng et al. 2010), and reduce root/shoot length and dry mass, chlorophyll content and membrane stability index (Gupta et al. 2013). However, 26 °C was found to be a threshold temperature for the post-anthesis stage (Stone and Nicol et al. 1994), suggesting that terminal heat stress is highly deleterious to reproductive development (Dubey et al. 2020). Thus, the future focus should be to improve wheat production under terminal stress during grain filling stages (Farooq et al. 2014).

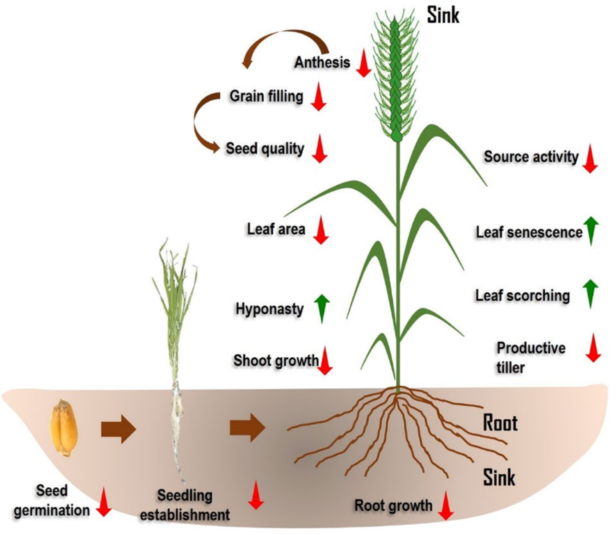


Fig. 1 Illustrative model showing the effect of heat stress on morphological characteristics of the wheat plant. In the initial phase of the development of wheat, the heat stress inhibits seed germination and seedling establishment. Due to high temperature, the inhibition of photosynthesis takes place due to which the source activity is decreased. This lead to having various morphological changes in both the vegetative (reduction in productive tillers) and reproductive part (reduction in anthesis) of the plant. Heat stress also affects leaf senescence and scorching by increasing their incidence. Due to the decrease in leaf area under heat stress, there is a reduction in the amount of photoassimilates produces which further hampers the shoot as well as root growth. Ultimately the reproductive part of the plant is highly affected due to its sensitivity against heat stress. Thus grain filling and seed qualities are affected which leads to a reduction in the production and productivity of wheat under heat stress. The upward arrow means increase, and downward arrow means decrease

High-temperature stress leads to architectural and phenotypic changes in the above ground part of the plant such as stem elongation and leaf extension (Patel and Franklin 2009). Also, prolongation of vegetative growth was observed while green leaf area and the number of productive tillers decreased drastically at 30/25 °C (day/night) (Djanaguiraman et al. 2010). Even a slight rise in temperature (1–2 °C) has been shown to reduce wheat yield significantly (Nahar et al. 2010). Late sowing of wheat causes a significant reduction in the ear length, the number of spikelets and fertile florets (Prasad et al. 2011). It has also been reported that exposure to heat stress at the early growth stages have an effect on later stages including dough and maturity, where shortening of kernel desiccation period has been linked with grain yield losses (Hasanuzzaman et al. 2013).

Wheat flag leaves undergo various morphological and physiological changes like leaf rolling to improve the efficiency of water metabolism (Hasanuzzaman et al. 2013). Exposure to extreme high-temperature causes programmed cell death within seconds or minutes and denaturation of vital enzymes such as Ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco), sucrose phosphate synthase, PEP carboxylase and invertase that are involved in photosynthesis and carbon assimilation. While prolonging heat exposure leads to organ injury and death, causing leaf shedding and floral abortion (Kumar et al. 2019a). The diurnal differences in the temperature such as 37 °C (day) and 28 °C (night) lead to the shortening of grain filling period and a maturity date in wheat. Also, a drastic reduction in grain size and yield together with the decline in the protein and starch contents has been reported (Hurkman et al. 2009). However, stress priming involving exposure of wheat to mild stress during the vegetative phase tend to have beneficial effects during reproductive phases (Fig. 1) (Mendanha et al.

2018; Poudel and Poudel 2020). The combination of high-temperature with drought tend to aggravate the stress effects, leading to a decrease in plant height, the number of tillers and dry matter production (Hossain et al. 2012). The overall effects of heat stress on morphological parameters of wheat are illustrated in Fig. 1. The temperature range for wheat seed germination is from 4 to 37 °C, where 12 °C to 25 °C is the optimal temperature range, however high temperature up to 40 °C adversely affects photosynthesis (Spilde 1989). Sing (2009) found that heat-tolerant wheat cultivars showed a significant increase in leaf area, leaf weight ratio, leaf area per shoot and leaf length, whereas their specific leaf weight, leaf width, plant height and total dry matter (TDM) got reduced (Sing 2009). Overall, these studies show that heat stress negatively affects the physiological function of wheat, which eventually hampers growth and development.

Photosynthesis, rubisco, rubisco activase and photorespiration

Photosynthesis is a biochemical mechanism whose efficiency determines plant productivity (Fig. 4). Photosynthesis is highly responsive to environmental fluctuations, hence serves as a global sensor of environmental stress. Ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) activity has long been described as the thermal inactivation site of the Calvin—Benson—Bassham cycle (Weis 1981). This inactivation is chiefly due to a feeble regulation of Rubisco activity by the heat-sensitive molecular chaperone Rubisco activase, Rca (Crafts-Brandner and Salvucci 2000; Salvucci and Crafts-Brandner 2004). Therefore, the modified initial activity of Rubisco from light-saturated, heat-stressed leaves is directly related to changes in the activity of Rubisco activase. However, Rubisco is not directly affected by a rise in temperature but the Rubisco activase enzyme, which helps within the modulation of Rubisco is severely affected by high-temperature stress suggesting that Rubisco activase is thermolabile. One of the limitations of Rubisco is its sensitivity to inhibition by the binding of sugar-phosphate derivatives that lock active sites into a closed conformation including the substrate RuBP when it binds to uncarbamylated active sites. Photosynthesis at high temperatures is not constrained by Rubisco itself, but by the lack of Rca to get rid of inhibitors and maintain Rubisco activity in vivo.

Restoring catalytic competence to Rubisco by removing inhibitory sugar-phosphate derivatives from the Rubisco active site is accomplished with a new chaperone enzyme, Rubisco activase (Rca) (Spreitzer and Salvucci 2002; Portis 2003; Wachter and Henderson 2015). The activation state of Rubisco in the leaves reflects the balance between keeping the Rubisco active sites in a closed, inactive conformation and the reactivation of these regions with conformational changes caused by Rubisco activase. Rca is an AAA + (ATPase associated with various cellular activities) (Neuwald et al. 1999) catalytic chaperone that uses the energy from ATP hydrolysis to remodel the active site of Rubisco. As such, Rca is considered to be one of the main causes of the decrease in photosynthetic function for plants exposed to above-optimum temperatures (Perdomo et al. 2017) due to its heat-labile nature and unable to keep pace with the rate of Rubisco deactivation with even moderate heat application, to a much greater than Rubisco (Salvucci and Crafts-Brandner 2004). The thermal stability of Rca is dependent on species and related to the climate in which a species has evolved (Wachter and Henderson 2015) with temperate species having Rca being thermolabile compared to tropical species.

Brestic et al. (2012) analyzed 30 winter wheat genotypes using prompt chlorophyll fluorescence kinetics for PSII thermostability and acclimation effects before and after dark heat treatment. Based on this all genotypes divided into different groups for low, intermediate, and high thermostability and concluded that the composition of lipids in thylakoid membranes seems to be important for heat thermostability. Law and Crafts-Brandner 1999 provided evidence that high temperature inhibits activase by disrupting subunit interactions. When taken together, the accumulated data from the gas exchange and biochemical analyses suggest that deactivation of Rubisco, caused at least in part by thermal inactivation of activase, is the primary cause of inhibition of photosynthesis under moderate heat stress (Crafts-Brandner and Salvucci 2002).

The wheat genome encodes for three Rca protein isoforms (Carmo-Silva et al. 2015) in which expression of TaRca1 produces a short isoform 1β (42.7 kDa), whereas TaRca2 produces either a short isoform 2β (42.2 kDa) or a long isoform 2α (46.0 kDa) by alternative splicing. Perdomo et al. 2017 described that out of these three isoforms 2β is insensitive to ADP inhibition and the other two forms are more sensitive. Scafaro et al. (2019) characterized gene expression and protein thermostability of the above three isoforms found in wheat and also compared wheat Rca with one of the two Rca isoforms from rice (OsRca-β) and other species adapted to warm environments. The TaRca2 isoforms were sensitive to heat degradation, with thermal midpoints (T_m) of 35 ± 0.3 °C and TaRca1-β was more temperature resistant, with a T_m of 42 °C, matched with rice OsRca-β. Eleven amino acids conserved in Rubisco activase (Rca) variants found in heat-adapted species increase the thermostability of wheat Rca by 7 °C. Kumar et al. (2019a) identified and cloned a putative Rca gene of 1402 bp from wheat cv. HD2985 using a transcriptomic approach. Degen et al. (2021) identified a single amino acid substitution (M159I) that fundamentally alters the thermal and regulatory properties of Rca in bread wheat (*Triticum aestivum* L.).

Therefore, improving the thermostability of Rca is considered one of the most promising ways to improve photosynthesis and hence the yield of crops potentially exposed to the detrimental effects of heat stress (Parry et al. 2011). The ability of the activase to keep Rubisco active appears to put a limit on the temperatures at which higher plants can photosynthesize (Salvucci and Crafts-Brandner 2004). The manipulation of the relative abundance of Rca isoforms, as well as the introduction of superior Rca forms through breeding or genetic engineering, offers the field to make Rubisco regulation in wheat more resistant to an increasingly hot and changeable climate (Degen et al. 2021).

The world abundant enzyme is Rubisco which is the important enzyme that is involved in the carboxylation of CO_2 in the plant. It is highly temperature-sensitive and the rate of photosynthesis decreases if Rubisco activity is decreased. It has two substrates, i.e., CO_2 and O_2. High temperature decreases the solubility of CO_2 and O_2, however, there is an increase in photorespiration rate (Prasad et al. 2004). Calvin cycle and electron transport in chloroplast are more susceptible to high-temperature stress. The reduction in wheat grain production and productivity under heat stress is dependent upon the availability of photoassimilates (Fig. 4). Wahid (2007) reported that photosynthesis is the most sensitive process under elevated temperature. The key enzyme of carboxylation is ribulose-bisphosphate-carboxylase which is inhibited under heat stress and also disrupt the integrity of the thylakoid membrane (Sehgal et al. 2018). High-temperature stress appears to be a major factor for source limitation which ultimately reduce the yield of wheat crop (Berry and Bjorkman 1980). Mendanha et al. (2018) in wheat reported that those plants which were not subjected to heat stress showed a linear increase in transpiration (A/T curves) as a result of the higher vapour pressure deficit (VPD) values, plants under heat stress did not change transpiration values with varying temperatures, and a decline in stomatal conductance following higher VPD values. Brestic et al. (2018) in their study with wheat observed that the selection for high yields was supplemented by the increase of photosynthetic productivity through the improvement of both leaf anatomical and biochemical traits including tolerance to non-optimal temperature conditions.The overproduction of reactive oxygen species, alteration of enzyme action and denaturation of heat shock proteins is the major culprit which leads to a reduction of photosynthetic efficiency of the wheat plant (Fig. 4).

Photosynthetic apparatus

The photosynthetic apparatus is the important constituent for light reaction in the chloroplast and is sensitive to abiotic stress like heat, drought, salinity, etc. Photosystem II (PSII), the cytochrome b6f complex (Cytb6f), and photosystem I (PSI) are the three integral protein complex embedded in the thylakoid membrane of the chloroplast, which forms the primary reaction center of photosynthesis. These complexes are connected in the series through the electron transport chain (ETC) (Rochaix 2011). Among the photosynthetic apparatus, PSII is the most sensitive photosynthetic apparatus which is present in the thylakoid membrane. The D1 protein present in PSII protein is sensitive to heat and light labile (Hauvaux 1993). A comparative analysis of various parameter is shown to have potential pf chlorophyll-a fluorescence-derived PS II and Rfd index as a sensor of heat stress and the sensitivity of Rfd index is used in screening wheat cultivar at an early development growth for seedling tolerance against heat stress. Under heat stress there increase in the fluidity of thylakoid which leads to a reduction in electron transport in PS II and its dislodging. An increase in chlorophyll fluorescence was found to be increased under high-temperature stress which leads to photosynthetic inhibition and electron flow in PSII (Fig. 2) (Macabuhay et al. 2018).

PS II is the most sensitive protein and is heterogeneous than other components like PS I and Cytb$_6$f with respect to structure and function. Based on different antenna size of PS II there are PS II alpha [α], PS II beta [β] and PS II gamma [γ] centres and on the acceptor/reducing side function, QB-reducing and QB-non-reducing centres have been proposed. It was reported that the increase in temperature from 25 °C to 45 °C in wheat leaves showed a decrease in γ centre while the increase in α and β centres of PS II. The β and γ centres were found to be increased at the cost of α centres and depending upon the environmental condition it is undoubtedly interconvertible (Mathur et al. 2014). The initial target of high-temperature stress is D1 protein in PS II. Apart from D1 protein the other component like oxygen-evolving complex (OEC), Rubisco, Cytochrome b559 (Cytb559) and plastoquinone (PQ) were also affected (Fig. 2) (Mathur et al. 2014). Haque et al. (2014) examined that after application of heat stress there was a difference between the cultivar in relation to inhibition and recovery of PS II function at different stages of the wheat plant. It was reported by Mohammadi et al. (2009) that the seedling of Karacadag and Firat wheat cultivars after exposure to heat stress at 37 °C and 45 °C for 8 h showed heat stress-induced inhibition of chlorophyll accumulation. Further, clear observation of the decrease in chlorophyll fluorescence and photosynthesis was reported in wheat cultivars. Cultivar Karacadag was found to have a lower reduction in the chlorophyll content under heat stress, thus it was reported to be heat tolerant and suitable for cultivation in a warmer region. Under high-temperature stress, there is an alteration in the thylakoid membrane (Fig. 2) (which is highly susceptible), disorganization of thylakoids, swelling of grana and loss of grana stacking takes place (Kosová et al. 2011).

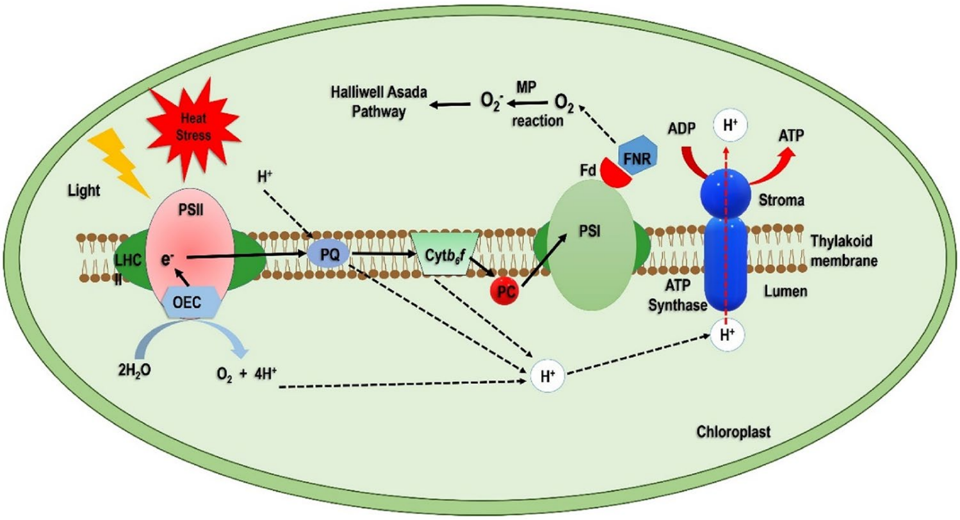


Fig. 2 Schematic model depicting reactive oxygen species (ROS) inactivation of photosystem and Mehler Peroxidase reaction (MP reaction). Under the normal light condition, the splitting of water (H_2O) takes place at the oxygen-evolving complex (OEC) and produces H^+ ions which are transferred across the membrane through ATP synthase. Under heat stress, ROS are produced from PSII due to its inactivation. The thylakoid membrane is damaged by the lipid peroxidation due to the ROS from PSII. The inactivation of PSII is mainly due to the damage and degradation of heat susceptible D1 protein. The superoxide radicals are produced from PSI via Mehler Peroxidase reaction. These superoxide radicals were further deactivated by plants own antioxidant mechanism known as the Helliwell-Asada pathway. Thus chloroplastic and thylakoid membrane damage may be protected in the heat-tolerant wheat plant through this mechanism

It was reported that under high-temperature stress there was a significant decrease in the chlorophyll content at all the growth stages viz., vegetative, reproductive and maturity stage of wheat. Almeselmani et al. (2012) found that the chlorophyll content of Indian cultivar C 306 and PBW-343 at anthesis and 15 days after anthesis was reduced. The chlorophyll content was reduced to 22.8 and 47.5% in C306 and 29.2 and 60.9% in PBW 343, respectively as compared to the normal temperature. The above lowering of chlorophyll content may be due to degradation or inhibition of porphobilinogen deaminase activity which leads to a reduction in protochlide content in the wheat plant when it is exposed to more than 42 °C (Tewari and Tripathy 1998).

Many investigations have already shown that in wheat and other crops PSII is not as thermally stable as PSI (Yan et al. 2013). As Rumeau et al. 2007 well explained that in response to heat stress conditions Plastid terminal oxidase (PTOX) regulates the cyclic pathways, thereby modulating electron pressure on Photosystem I (PSI) acceptor and preventing PSI from photoinhibition. Moderate high temperature accelerates PSI activity in vitro and in vivo, resulting in increased thylakoid proton conductance and CEF (cyclic electron flow) around PSI. Under conditions when PSII activity is severely reduced, above stimulation of proton conductance of cyclic electron flow around the PSI could be an adaptive process, producing ATP (Mathur et al. 2014; Ivanov et al. 2017). Chovancek et al. 2019 in wheat observed that lower activity of PSI could have been responsible for the decrease in the electron transport capacity after the transient heat wave period. Overall Brestic et al. 2016 concluded that inactivation of PSI under heat stress conditions could also be a defensive mechanism to prevent photooxidative damage of cell structures and chloroplast.

Leaf senescence

As discussed in the earlier section the heat stress leads to a decrease in vegetative shoot plant growth and leaf senescence is also accelerated with diminishing photosynthetic capacity in wheat crop (Shah and Paulsen 2005). During heat stress in the wheat plant there were structural changes in the chloroplast which was followed by vacuolar collapse and ultimately lead to loss of integrity in the plasma membrane and cellular homeostasis was interfered (Viswanathan and Khanna-Chopra 2001). It was also reported that under heat stress wheat plant experiences metabolic changes. The leaf senescence of the wheat plant was enhanced when exposed to heat during maturity due to loss of chloroplastic integrity, inhibition of PS II-mediated electron flow and destruction of the antenna pigments (Haque et al. 2014). However, Liu et al. (2017) reported that under heat stress of more than 34 °C the chlorophyll biosynthesis inhibition may hasten leaf senescence (Fig. 4). But the large variation in diurnal temperature was also found to be responsible for the promotion of flag leaf senescence in the wheat plant (Zhao et al. 2007). It was also suggested by Dhindsa et al. (1981) that leaf senescence can lead to cumulative membrane deterioration because of increasing lipid peroxidation level which is controlled by enzymes like superoxide dismutase (SOD) and catalase (Dhindsa et al. 1981).

Oxidative damage

Various environmental stress like heat, salinity, drought stress leads to the production of Reaction oxygen species (ROS) causing oxidative damage in the plant which ultimately leads to death. Under heat stress there is an accumulation of ROS which causes severe oxidative damage to the plant, thus inhibiting the growth and development. (Caverzan et al. 2016). Earlier studies suggest that heat stress in wheat showed multiple changes in many of the physiological

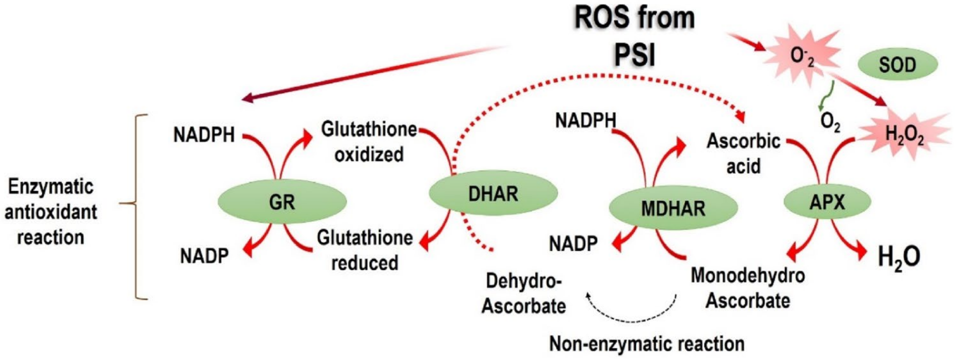
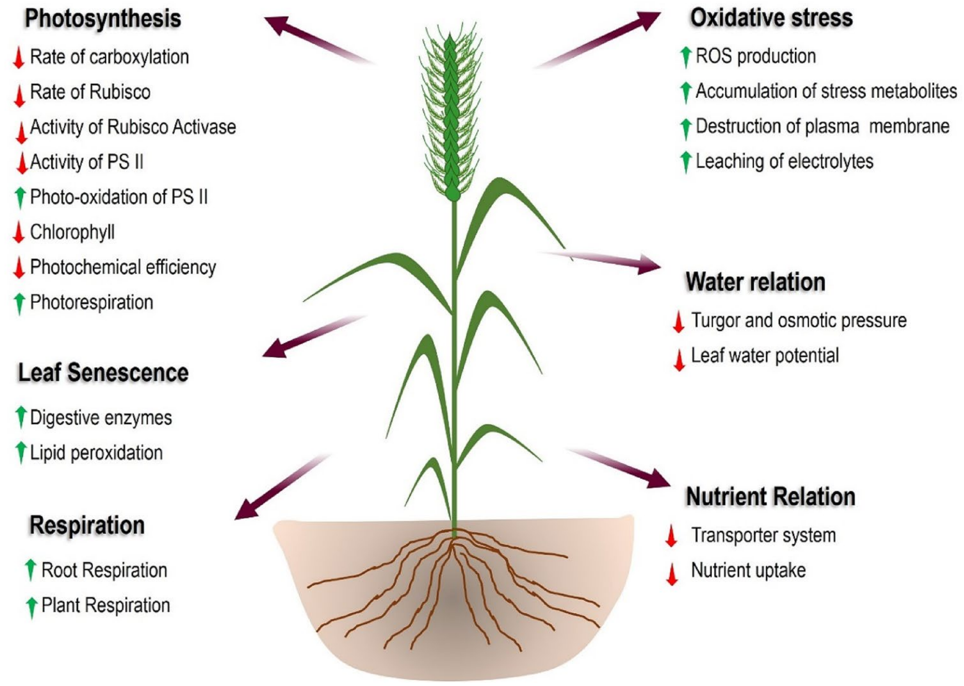


Fig. 3 Reactive oxygen species (ROS) scavenging conceptual mechanism (Halliwell-Asada Pathway). The superoxide molecules (O_2^-) which are produced from the photosystem is scavenged (detoxified) by superoxide dismutase (SOD) enzyme which is a ROS scavenging enzyme that leads to the production of peroxide molecule (H_2O_2). Which is further detoxified to H_2O using ascorbic peroxidase (APX) enzyme and ascorbic acid. This leads to an increase in the monodehydroascorbate (MDA) and dehydroascorbate (DHA) in the system. This is reduced by MDA reductase (MDAR), DHA reductase (DHAR), and glutathione reductase (GR) through enzymatic and non-enzymatic oxidant reactions. Thus under heat stress, the ROS produced from PSI and other membrane system leads to the deactivation of these molecules to prevent further damage

Fig. 4 An overview of the effect of heat stress on photosynthesis, oxidative stress, leaf senescence, water relation, respiration and nutrient relation in the wheat plant. The upward arrow means increase, and the downward arrow means decrease



parameters which include accumulation of osmolytes like proline, a quaternary molecule like glycine betaine, destruction of the plasma membrane, mitochondrial membrane and chloroplastic membrane by lipid peroxidation, H_2O_2 production, a secondary metabolic that involves in signalling under stress (Gupta et al. 2013; Kumar et al. 2019b). There were generation and accumulation of ROS which was induced by oxidative stress molecules viz., super-oxides (O^{2-}), hydroxyl radicals (OH^-) and hydrogen peroxide (H_2O_2) in wheat under heat stress (Fig. 3) (Kumar et al. 2019b). Heat stress elicits the production and accumulation of ROS and detoxification by antioxidant is very much necessary for protecting the plant from the detrimental effect of heat stress (Roy et al. 2017). In wheat when the temperature rises above 25 °C at the vegetative stage there was found to be a very high proline concentration of about 1.0 µmole/g FW. However, when the heat shock is treatment is given at 30, 35 and 40 °C for 2 h, the concentration of proline gradually decreases to 0.9, 0.79 and 0.66 µmole/g FW respectively (Kumar et al. 2012).

When ROS production increases over cellular scavenging capacity then there is an unbalancing in redox homeostasis which results in more damage to the membrane (Fig. 3). Thus more electrolytes are leaked from the damaged membrane and disrupting the function of the cell, which is known as oxidative stress (Sharma et al. 2012). The wheat plant develops various strategies to overcome the effect of ROS so that it can scavenge the ROS molecule and prevent the damage of the membrane and other organelles against it. Under oxidative stress, the production of ROS is accelerated which include the following molecules like superoxide anion ($O_2^{\bullet-}$), hydroxyl radical ($^{\bullet}OH$), as well as nonradical molecules like hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$) (Fig. 3) (Asada 2006). So to avoid damage caused by ROS to the various component of the cell, maintenance of growth and development, metabolism, the balance between the production and elimination of ROS is to be tightly regulated in the cell. The reduction in the carbon assimilation also reduces ROS generation, thus reducing the protein synthesis and inhibiting the repairing of damaged PS II. Moreover, this also leads to decrease in the efficiency of photosystem (Nishiyama et al. 2011). Thus temperature stress results in the development of oxidative damage which ultimately disproportionates the photosynthesis and respiration process in the plant (Fig. 4). The crucial stage in the life cycle of wheat is the reproductive stage and which may be affected by the accumulation of reactive oxygen species which is regulated by superoxide dismutase, catalase, ascorbate peroxidase, and peroxidase (Kumar et al. 2012). Thus, cell membrane damage can be prevented without leaching of electrolytes may be prevented.

Respiration

Respiration is the vital process that determines the growth and survival of the plant (Gifford 2003). The important parameter influencing production and productivity in the wheat plant under heat stress is mitochondrial respiration. With the increase in the temperature above optimum temperature, the gross photosynthesis is lowered or inhibited but there is an increase in respiration rate and photorespiration rate (Fig. 4). It was observed that the rate of respiration exponentially increases from 0 to 35 °C, and maintaining the plateau at 40–50 °C however, at a temperature more than 50 °C, the rate of respiration decreases and there is the destruction of respiratory mechanism and proteins. The increased respiration rate results in the reduction of availability and transport of photoassimilates from leaves to grain, thus hampering the plant growth and development (Asthir et al. 2012). Previously it was reported that in the short term exposure to drought in wheat can result in a decrease in the leaf area and root respiration (Backhausen et al. 2014). However, mitochondria show greater stability to heat stress and their activity significantly increases over a certain temperature range in which the plant is grown. But heat stress may also cause a more detrimental effect on chloroplast, which leads to disrupting growth and a decrease in maintenance respiration (Wang et al. 2018a, b). Almeselmani et al. (2012) reported that the rate of leaf respiration showed to be increased under high-temperature stress. PBW 343 variety which is heat susceptible variety showed a significantly higher rate of respiration as compared to control, however, C-306 variety showed a marginal higher respiration rate as compared to control. Due to respiratory losses under heat stress in the wheat grain, counterbalance the influx of photoassimilates which ultimately leads to a reduction in yield and production (Akter and Rafiqul Islam 2017). The above evidence makes us clear that increased respiration efficiency and its resistance against heat stress is beneficial and improves the growth and yield of wheat crop. Plant maintain homeostasis in the rate of respiration by altering their metabolism. The maintenance of a similar rate of respiration when grown at the control and elevated temperature is known as respiratory homeostasis. Rice and wheat show a high degree of respiratory homeostasis (Rai et al. 2019).

Water relations

Water status in the plant is very much crucial under changing climatic pattern and under high-temperature condition. The temperature of plant tissue is maintained by the water uptake and transpiration, thus water content in the tissue is stabilized. But the rise in temperature may prove to be lethal when there is less availability of water (Fahad et al. 2019). The parameter that is controlled during heat stress is leaf relative water content (LRWC), leaf water potential (LWP), rate of transpiration and stomatal conductance (SC) are influenced by leaf and canopy temperature (Fig. 4) (Farooq et al. 2011). There are limited reports on the dynamics of water and heat balance for wheat during grain filling and reproductive stages, however, dynamics in seedling was studied by Machado and Paulsen (2001). In dry condition and higher temperature, there are higher vapour pressure deficits which lead to a higher evapotranspiration rate. Due to transpiration, the temperature of a plant organ in the field is several degrees different from the atmospheric temperature. Due to high temperature, there is depletion in soil moisture content which ultimately leads to a decrease in LRWC and leaf water potential. Sairam et al. (2000) observed that the LRWC was significantly reduced under high temperature which affects the reproductive and grain filling stage. This stage is very crucial as water is needed for the stem as well as peduncle elongation to raise the ear through the unfolding leaf to the top of the canopy. The process of transpiration helps the wheat plant in heat avoidance which is the primary means for energy dissipation. In this sense, the plant which has more transpiration may be a good avoider. Water is also required for pollen ripening, cell expansion and growth of all part of the ear, rapid extension of stem filaments and fertilization grain growth and filling (Begcy et al. 2018).

Increasing hydraulic conductivity is beneficial in both leaves and root. Increased hydraulic conductivity leads to minimizing the change in water potential so that stomata can open for a longer period. Under heat stress, it was found that permeability of membranes was increased which may cause flower and grain to dehydrate due to an increase in the permeability of the membrane. If water shortage arises then the stomata begin to close and leaf temperature rises which may exceed the atmospheric temperature. When the soil water content is near to field capacity the parameter like leaf RWC and water potential were not affected by heat stress but water content was slightly affected by day/night temperature of 40/35 °C (Fig. 4). Transpiration rates also diminished with increasing temperature (from 15/10 to 40/35 °C) and plant growth was reported to be decreased (Machado and Paulsen 2001). Water flow inside the cell for the various metabolic process involved the crossing of water through membranes which may be facilitated by diffusion or by aquaporin. Under high-temperature stress, there was a greater degree of reduced water viscosity along with increased hydraulic conductivity of membrane and plant tissues due to an increase in the activity of aquaporin, membrane fluidity and permeability (Cochard et al. 2007). However, the evaporation from the leaf surface enhances leaf and canopy cooling, thus overheating may be ameliorated by higher rates of transpiration. However, the soil water content decreased significantly when the temperature imposed was 25 °C or more which was found to be more than soil evaporation. Martinez-Ballesta et al. (2009) reported that root functioning in water and nutrient uptake was found to be heat sensitive under elevated room temperature.

Nutrient relation

Very little information regarding the effect of high-temperature stress in relation to the nutrient status of the crop is available (Rennenberg et al. 2006). The activity of enzymes that are involved in nitrogen assimilation like nitrate reductase activity was found to be low under elevated temperature (Klimenko et al. 2006). It was reported that under high-temperature stress there was an increase in nitrogen content in both leaves and stem at flowering as well as during the maturity stage. But there was a significant decrease in the total sugar content in a shoot during both flowering and maturity stages (Sing 2009). It was also reported that the use of sulphur as a nutrient can be used to enhance the tolerance against elevated temperature. Under heat stress, sulphur metabolites maintain the redox state of the cell and protect the cell membrane, thylakoid membrane and cytoplasm from destruction which ultimately enhance the photosynthetic rate (Fig. 4) (Alghabari et al. 2019).

Epigenetic responses in wheat to heat stress

Genetic components (QTL/genes) involved in heat stress tolerance and their underlying molecular mechanisms have been well explored in wheat (Qin et al. 2008; Chauhan et al. 2011; Niu and Xiang 2018; Janni et al. 2020; Haider et al. 2021). However, the role of epigenetics (DNA methylation, histone modifications, chromatin remodelling, smRNA; small RNAs) in the regulation of heat stress-responsive genes have been still lacking in crop plants including, wheat (Begcy et al. 2018; Kong et al. 2020; Gahlaut et al. 2020). Below, we discuss some important epigenetic research associated with heat stress regulation in wheat.

In a genome-wide analysis of DNA-methylation in wheat, heat stress had a striking effect on gene expression, but there were only minimal differences in methylation patterns. However, in some cases methylation was associated with small changes in gene expression of important genes during heat stress (Gardiner et al. 2015). These results direct us that DNA methylation was associated with alterations in heat stress responsive genes and deserve further exploration. Recently, Gahlaut et al.(2020) identified 52 wheat cytosine-5 DNA methyltransferase (C5-MTases) in wheat. They also studied their expression profiling under drought stress and heat stress conditions. Notably, most of the TaC5-MTases genes responded to both of the stress conditions. But, in response to 6 h heat stress, genes like *TaDRM10-5A*, *TaDRM10-5B* and *TaDRM10-5D* were upregulated

(Gahlaut et al. 2020). In Arabidopsis, it was reported that histone modification (acetylation) of H3K9 and H3K14 of Heat Shock Factor A3 (HSFA3) and UV-Hypersensitive 6 (UVH6) by General Control Of Nonrepressed Protein 5 (GCN5) gene (a Histone acetyltransferase) provides tolerance to heat stress (Hu et al. 2015). In wheat also, it was found that *TaGCN5* gene up-regulated in response to heat stress and it suggested that GCN5-mediated heat stress tolerance may be conserved among wheat and Arabidopsis (Hu et al. 2015). Besides DNA methylation and histone modifications, the role of miRNAs (another important epigenetic component) in a heat stress-related signalling pathway were reported in wheat (Xin et al. 2010; Ragupathy et al. 2016; Gahlaut et al. 2018; Ravichandran et al. 2019). For instance, Xin et al. (2010) reported several heat-stress responsive miRNAs in wheat. They also validated that tae-miR156 was up-regulated and its putative target genes, i.e., SQUAMOSA promoter-binding (SBP) protein-like proteins (SPLs) were down-regulated in response to heat stress. In another study by Kumar et al. (2015), it was observed that six novel miRNA were heat stress-responsive in wheat. Recently, small RNAs and the degradome sequence analysis identified and validated heat stress-regulated miRNAs and their target genes in wheat (Ravichandran et al. 2019). In total, they identified 202 miRNAs and out of that, 36 miRNAs were differentially expressed upon heat stress. Further, they observed some of these miRNAs targets the heat stress response genes. For instance, miR156 targets SPLs protein, miR159 targets MYB transcription factor, and miR398 regulating superoxide dismutase (Ravichandran et al. 2019). However, further functional explorations into each member's role during heat stress via DNA methylation/miRNA machinery could enhance our knowledge and could be utilized in wheat improvement for heat stress tolerance.

Heat stress mitigation in wheat

The capacity of wheat plants to overcome heat stress may include common defence mechanisms mainly avoidance, escape, or tolerance (Janni et al. 2020). Avoidance is the acclimatization mechanism that makes the plants tolerant to the most deleterious effect of stress (Hasanuzzaman et al. 2013). In the escape mechanisms, the plants growth cycle is altered prior to the heat stress occurrence such as preceding reproduction and casting vegetative structures. However, tolerance is the mechanism that is certainly interesting for researchers as it depicts the endurance of wheat plants under stress. A heat-tolerant wheat plant is habitual to continue its growth cycle quite irrespective of ongoing stress (Barnabás et al. 2008). The discovery of heat stress-mediated morphological, physiological and molecular responses has guided the exhaustive research on how these plants combat heat stress by inherent genetic variation or creating artificial variations using genome editing or mutational breeding (Janni et al. 2020).

The contribution of 'Omics' in heat stress

The omics (genomics, transcriptomics, proteomics, and metabolomics) are a powerful tool to decipher the underlying molecular mechanisms of growth and development in plants under abiotic and biotic stress conditions (Tiwari et al. 2020a). The transcriptomic approach has been applied to decipher gene expression changes under abiotic stress conditions in cereals, such as rice (González-Schain et al. 2016), barley (Mangelsen et al. 2011), maize (Frey et al. 2015; Wei et al. 2017), wheat (Qin et al. 2008). Similarly, the advanced transcriptomic studies have elucidated the functions of relevant genes in wheat cultivars facing heat stress (Table 1). The identified genes for heat stress regulations in wheat are mostly involved in primary and secondary metabolism, transcription, translation, regulation, and phytohormone, calcium, sugar, and lipid signaling, or phosphorylation (P). The activation of heat stress responsive transcription factors, heat shock proteins (HSPs) and ROS scavenging activity plays a key role in heat stress adaptations in wheat plants (Comastri et al. 2018). The gene family of HSF has been already characterized in wheat. With rapid advancements in gene annotation, a specialized database 'HEATSTER' (http://www.cibiv.at/services/hsf/info#anfang) has been developed which can identify annotate the new HSF gene in plants (Berz et al. 2019). Wheat genome array-based heat stress-responsive transcriptome analysis revealed changes in expression of several genes representing HSF genes, Hsp genes, genes of phytohormone biosynthesis/signalling, sugar and calcium signal pathways, ribosomes and RNA metabolism and primary and secondary metabolism (Qin et al. 2008). Under the heat stress, a prominent reduction in expression of non-essential photosynthetic genes at flowering is an energy-saving strategy that maintains sugar metabolism and consequently protects pollen viability (Li et al. 2015).

Quantitative proteomic analysis has revealed the role of new stress associated active proteins (SAAP) in heat stress adaptations in wheat. There were approx 4272 identified SAAPs in wheat like HSP17, Rubisco, Rubisco activase (RCA), superoxide dismutase (SOD), catalase (CAT), oxygen-evolving extrinsic protein (OEEP), and calcium-dependent protein kinase (CDPK) (Kumar et al. 2019a). The two most perturbed pathways were the carbon assimilation pathway and starch metabolism. The post-transcriptional modifications (PTM) of proteins are also a significant adaptive mechanism of heat stress regulation in wheat (Chen et al. 2011).

Table 1 Omics studies performed at different growth stages during heat stress in wheat

Sr. no.	Technique applied	Tissue or growth stage	Simulation conditions	References
1	Transcriptomics and proteomics	Wheat grains	30 °C and 40 °C	(Wu et al. 2021)
2	Metabolomics, transcriptomics	At the filling stage of seeds	37 °C	(Wang et al. 2015)
3	Transcriptome analysis	Awns `	42 °C	(Chaudhary et al. 2021)
4	Metabolomics	Flowering	Up to 35 °C	(Narayanan et al. 2016)
5	Transcriptomics	Seedlings	Up to 42 °C	(Comastri et al. 2018)
6	Transcriptome	Flowering and grain development stage	32 °C and 36 °C	(Kumar et al. 2021)
7	Proteomics (MALDI TOF/TOF	Seedlings	35 °C	(Gupta et al. 2015)
8	Proteomics (iTRAQ LC–MS/MS)	Leaves, stems, and spikes, flag leaf	38 °C, and 37 °C	(Kumar et al. 2019a)
9	Proteomics (MALDI TOF/TOF MS/MS)	Plant leaf	32 °C	(Yousuf et al. 2017)
10	Proteomics (MALDI TOF/TOF MS/MS)	Post-anthesis	35 °C	(Zhang et al. 2018)
11	Proteomics	Flag Leaf	35 °C	(Wang et al. 2015)
12	Transcriptomics (wheat genome array)	Leaf	40 °C	(Qin et al. 2008)
13	Proteomics	Flag leaf, seedlings in anthesis stage	37/17 °C	(Lu et al. 2017)
14	Metabolomics (LC/HRMS	Spikelet post-anthesis	35 °C)	(Thomason et al. 2018)
15	Transcriptomics (RNA-seq)	Seedlings	40 °C, 20% (w/v)	(Liu et al. 2015)
16	Lipidomics ICP-MS	Plant leaf	35 °C	(Djanaguiraman et al. 2018)
17	Lipidomics ICP-MS	Pollen	35 °C	(Narayanan et al. 2018)
18	Lipidomics	Grain filling and anthesis stage	32 °C	(Djanaguiraman et al. 2020)

Heat stress-mediated metabolic reorganization in wheat plants to maintain homeostasis and essential metabolism has also been elucidated (Thomason et al. 2018). The study identified the metabolites showing the highest reduction under heat stress: anthranilate, dimethylmaleate, drummondol, guanine, galactoglycerol, and glycerone. The lipids which are regarded as major components of cell membranes and organelles are the first targets of heat mediated ROS generation as identified through lipidomics (Narayanan et al. 2016, 2018). Similar findings indicated that the reduced photosynthetic rate is because of lipid desaturation, oxidation (Djanaguiraman et al. 2018). Further, overexpression of the gene OsFBN1 (code for fibrillin) facilitates the lipids import to the chloroplast and the consequent grain filling during heat stress. The advanced omics-based approaches have given lots of understanding of the mechanism of heat stress on plants as well and plants survival mechanism. Further researches are required to exploit these stress adaptive transcription factors and HSPs to develop resistant cultivars. Besides, identifying novel non toxic chemicals and phytohormones which may scavenge ROS may lead to better stress tolerance in the prevalent cultivars.

Quantitative trait locus (QTLs) associated with heat stress

Heat stress tolerance is a multigenic trait, i.e., several genes with minor effects on the phenotype; besides, it also has high genotype-by-environment interactions and low heritability (Abou-Elwafa and Shehzad 2021). It creates an obstacle for wheat breeding for heat stress tolerance-related traits under field conditions. However, advances in genomics, bioinformatics tools and high throughput phenotyping have assisted in dissecting the genomic regions associated with various agronomic and physiological traits under heat stress in wheat. Serval genomic regions have been reported in wheat utilizing Interval mapping (IM) and linkage mapping (GWAS) for heat stress tolerance related traits like days to heading, thousand-grain weight, yield, grain filling duration (Paliwal et al. 2012; Jamil et al. 2019; Abou-Elwafa and Shehzad 2021), canopy temperature depression (Bennett et al. 2012), stay green and senescence-associated traits (Vijayalakshmi et al. 2010; Maulana et al. 2018), and chlorophyll content-related traits (Talukder et al. 2014a; Shirdelmoghanloo et al. 2016). In wheat, ~ 300 QTL/MTAs for different agronomic and physiological traits (data measured under heat stress conditions) have been reported (Gupta et al. 2020). However, most of these QTL/MTAs were minor (less than 10% PV, phenotypic variance) and unstable (detected in less 50% environments). Only a few QTLs were major and stable and phenotypic variance explained by these major stable QTLs for different traits measured under heat stress conditions ranged from 15 to 36.1% (summary of these QTL are given in Table 2). These stable major QTLs could be utilised for marker-assisted selection (MAS) in wheat

Table 2 Details of important QTL/SNPs associated with heat tolerance related traits in wheat

Sr. no.	Trait	QTL(linked marker)/MTA	Mapping Approach (QTL-IM[a]/GWAS[b])	PVE(%)[c]/R^2	References
1	Days to heading	S5B_586352552	GWAS	15.0	(Jamil et al. 2019)
2	Grain filling duration	*QHgfd.iiwbr-5A* (X1079678|F|0)	IM	22.0	(Sharma et al. 2017)
3	Grain number/spike	*QGnp-HS-R1* (AX-95652063)	IM	24.5	(Li et al. 2019)
4	Spike dry weight	BS00055584-51	GWAS	15.0	(Valluru et al. 2016)
5	Grain yield	*Q.Yld.aww-3B* (gwm0114)	IM	22.0	(Bennett et al. 2012)
		RAC875_c57371_238-6D	IM	26.6	(Li et al. 2019)
		Qtgw.iiwbr-2A (Xgwm122)	IM	23.7	(Tadesse et al. 2019)
		S6D_471249189	GWAS	17.0	(Jamil et al. 2019)
		QGyp-HS-R1 (AX-111105973)	IM	21.0	(Li et al. 2019)
6	Thousand Grain weight	*QHthsitgw.bhu-7B* (Xgwm745)	IM	20.0	(Paliwal et al. 2012)
		Kukri_c22235_1547-2A	IM	36.1	(Liu et al. 2019)
		S6B_680699350	GWAS	18.0	(Jamil et al. 2019)
7	Canopy temperature depression	*QHtctd.bhu-7B (Xgwm1025)*	IM	19.8	(Paliwal et al. 2012)
		Q.Ctgf.aww-3B (Xgwm0114B)	IM	21.0	(Bennett et al. 2012)
8	Leaf chlorophyll content	*QLCCHS.nri-2D*	GWAS	24.6	(Maulana et al. 2018)
		wsnp_Ra_c41135_48426638	IM	34.3	(Shirdelmoghanloo et al. 2016)
		QLCCHS.nri-4B.3	GWAS	17.5	(Maulana et al. 2018)
9	Seedling recovery (%)	*QSRHS.nri-2A*	GWAS	32.9	(Maulana et al. 2018)
10	Fv/Fm (maximum quantum efficiency of photosystem II)	*QHst.cph-3B.2* (Xgwm389)	IM	25.4	(Sharma et al. 2017)
11	Maximum rate of senescence	*QMrs.ksu-2A*(Xgwm356)	IM	19.0	(Vijayalakshmi et al. 2010)

[a] Interval mapping

[b] Genome wide association mapping

[c] *PVE* phenotypic variance explained

molecular breeding programs for the improvement of heat stress tolerance.

Breeding for heat tolerance: conventional and new breeding techniques

The ill effects of heat stress on wheat production are increased due to greater genetic uniformity resulting from the narrowing of the varieties grown in developed countries (Fu 2015). This warrants the increased efforts to explore new genetic resources and useful traits to counteract the ill effects of heat stress on wheat productivity. The current approaches of mitigating heat stress using breeding methods include (i) exploiting natural and/or artificial mutations; (ii) screening and identification of the available sources of tolerance or resistance; (iii) using the available genetic resources to produce new genetic material more tolerant to heat and (iv) genome editing tools to design the targeted crops.

It is well established that biotic stresses including heat stress responses are governed by the Quantitative trait loci (QTLs) distributed throughout the genome. In wheat, QTLs with heat tolerance have been mapped using QTL analysis, combined with (genome-wide association studies) GWAS and genotyping-by-sequencing (GBS). Major QTL regions associated with heat tolerance have been mapped on different chromosomes (Paliwal et al. 2012; Talukder et al. 2014b; Acuña-Galindo et al. 2015; Shirdelmoghanloo et al. 2016; Maulana et al. 2018).

Previously, a model to mitigate wheat heat stress was proposed which included traits such as partitioning of total assimilates light interception, and radiation use efficiency. All these traits are combined in the physiological breeding approach for additive gene effect on yield (Cossani and Reynolds 2012). Data sets of CIMMYT (International Maize and Wheat Improvement Center) were extensively analyzed which revealed that spring wheat breeding has shown enhanced genetic gains in warmer environments targeted against abiotic stress (Gourdji et al. 2013). To identify heat-tolerant genotypes in a breeding program, the performance of yield traits has been used under heat and non- stressed environments (Gaur et al. 2019). Recently, some new cultivars of wheat are released which are capable of tolerating severe heat stress. This was only possible due to the identification of critical genes governing heat tolerance (Tadesse et al. 2019).

New breeding techniques (NBTs) involving genetic modification through biotechnology is a powerful strategy that offers high level of crop adaptability to abiotic stresses. The date gathered through omics studies can be exploited to significantly improve the heat stress tolerance in wheat. Many studies have used transcription factor and other genes associated with abiotic stress tolerance as targets for development of transgenic varieties. Cereal crops including wheat, maize, and rice have been genetically modified to develop thermotolerance, by targeting HSPs and HSFs (Fu et al. 2008; Casaretto et al. 2016). The availability of genomic data for many crops together with modern genome editing tools has given a solid platform for breeding possibilities for any desirable trait (Jaganathan et al. 2018). Presently, clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9), is the most common technique available for genome editing which has also used been used in wheat protoplast to perform the targeted editing of stress-responsive transcription factor genes, wheat ethylene responsive factor 3 (TaERF3) and wheat dehydration responsive element-binding protein 2 (TaDREB2). Further studies are required in this direction to develop genome editing based new cultivars having multiple biotic and abiotic stress resistance. A breakthrough approach of mutation breeding is TILLING (targeting induced local lesions in the genome) which provides an easy way to identify mutations (lesions) in a target sequence irrespective of phenotypic effect. Comastri et al. (2018) identified four Hsp26 (sHsp26) alleles suitable for mitigating heat stress in durum wheat. Such kind of studies is also very elusive and demands exhaustive research. All of this suggests that in future a prominent advancement in crop improvement is expected, resulting in the development of new varieties with greater heat tolerance and wider adaptation to climate change.

Phytohormones and novel phytoprotectants

Currently, several exogenously applied growth-promoting osmoprotectants, signalling molecules and trace elements are tested on plants that neutralize the adverse effects of heat stress (Upreti and Sharma 2016). In most cases, exogenous applications of these biochemicals improve thermotolerance in wheat by managing the ROS and enhancing the antioxidant capacity (Akter and Rafiqul Islam 2017). Some of these phytoprotectants such as arginine, putrescine (Put), and α-tocopherol are highly effective in managing heat stress in wheat. Exogenous application of these molecules activates several enzymatic (superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase) and non-enzymatic (ascorbic acid, tocopherol, and glutathione) antioxidants (Asthir et al. 2012; Asthir 2015).

Sattar et al. 2020 observed that under terminal heat stress, the chlorophyll content in wheat was reduced by 47.8% compared with unstressed plants. Tian et al. 2020 found that TaOPR3 (heat-resistance associated protein) contributes to heat tolerance in wheat via regulating jasmonic acid levels. Janda et al. 2019 observed an enhanced amount of the free salicylic acid (SA) after moderate heat stress in wheat. External application of Salicylic acid in wheat alleviated heat stress by increasing proline production via the increase in γ-glutamyl kinase (GK) and decline in proline oxidase (PROX) activity, due to the elevation of water potential and osmotic potential necessary for sustaining photosynthetic activity (Khan et al. 2013; Afzal et al. 2020). From the above studies, it is proved that salicylic acid might also contribute to higher heat tolerance. Brassinosteroid's treatment in pre-and post-flowering stage in wheat plant resulted in an increased SOD and APX activity after exposure to heat stress (Kumari and Hemantaranjan 2019). In wheat, exogenous BR application increases fresh and dry weight, leaf area which may be traced to the BR application increasing both CO_2 fixation and RUBISCO activity (Kothari and Lachowiec 2021). The presence of melatonin significantly improved the heat tolerance of wheat seedlings by activating the ascorbate–glutathione cycle, increasing GR activities, induced the expression of ROS related genes (TaSOD, TaPOD, and TaCAT), and anti-stress responsive genes (TaMYB80, TaWRKY26, and TaWRKY39) (Buttar et al. 2020).

Recently, melatonin is emerging as a novel multifunctional phyoprotectant in mitigating abiotic and biotic stresses of crop plants (Tiwari et al. 2020a, b). Melatonin is involved in balancing the photosynthetic rate of a plant under heat stress (Ahammed et al. 2018). The increase in transcript level of heat shock proteins and autophagy-related genes was observed in melatonin-treated plants under heat stress. Recently, Buttar et al. 2020 reported the melatonin-mediated suppression of heat stress-induced damage in wheat seedlings. Treatments of 100 µM melatonin (MT) followed by exposure to heat stress efficiently reduced oxidative stress by reducing the lipid peroxidation content (represented as malondialdehyde (MDA) content), preventing the higher accumulation of hydrogen peroxide (H_2O_2) and enhancing proline (Pro) biosynthesis. The melatonin pretreated seedlings had shown increased activity of antioxidant enzymes, such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT). Additionally, melatonin modulated the antioxidant defence system by increasing glutathione reductase (GR) activities and activating the ascorbate–glutathione (AsA–GSH) cycle comprising ascorbate peroxidase (APX). Chlorophyll content was also increased in melatonin treated seedlings. So far there is only one study that highlights the role of this phytoprotectant in heat stress alleviation in wheat. Further studies will give a clear understanding of how well this molecule can be utilized in abiotic stress management in wheat.

Conclusion

The emission of greenhouse gases has resulted in the rise in the earth's temperature, which induces heat stress in plants. In recent decades, high temperature stress has proved detrimental for wheat production and productivity on global scale. High-temperature stress in wheat mainly affects the reproductive stages which include grain setting, duration and rate which ultimately affects the grain yield. Duration, timing and intensity of wheat stress determine the impact on grain yield and quality. To minimize the yield losses in a climate change scenario, breeders have to work on breeding of heat-tolerant varieties of wheat. The physiological basis of heat tolerance is better understood in wheat, but some research areas like partitioning of assimilates, phenotyping under heat stress and understanding nutrient response and its mechanism need further investigation. Moreover, the intesive studies highlighting the detrimental effect of heat stress in wheat and its in-depth mechanistic understanding of tolerance are elusive. More work is needed on the nutritional aspect with respect to nutrient transport and assimilation under heat stress. As climate change is a pressing global problem, monitoring and detection of heat stress by the latest remote sensing technologies could help to alleviate the lethal effects on wheat production and storage. Moreover, various experiments suggest that along with heat stress there is cross-talk between signalling pathways of other stresses, stress combination is often more detrimental to plant growth. Besides, exogenous application of phytoprotectants such as melatonin and salicylic acid have revealed more positive effect and provide tolerance under high temperature stress. Heat stress has a great impact on the reproductive system which ultimately decrease crop productivity in a complex manner, which involves the process of supply of photoassimilates to reproductive organs, stem reserve accumulation, gametogenesis, fertilization, embryogenesis, nutrient assimilation, respiration, photosynthesis, water relation and grain development. Moreover, the study of functional genomics approach might be a helpful tool to study the reponse of wheat to heat stress. The researcher around the globe should aim to generate heat-tolerant genotypes with higher yield under changing climatic condition. Thus, to get a holistic view on heat stress responses on wheat there is a need to implement omics approaches, output of which could be eventually utilized to devise heat stress mitigation strategies by conventional and modern breeding methods.

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Declarations

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References

Abou-Elwafa SF, Shehzad T (2021) Genetic diversity, GWAS and prediction for drought and terminal heat stress tolerance in bread wheat (*Triticum aestivum* L.). Genet Resour Crop Evol 68:711–728. https://doi.org/10.1007/s10722-020-01018-y

Acuña-Galindo MA, Mason RE, Subramanian NK, Hays DB (2015) Meta-analysis of wheat QTL regions associated with adaptation to drought and heat stress. Crop Sci 55:477–492. https://doi.org/10.2135/cropsci2013.11.0793

Afzal I, Akram MW, Rehman HU et al (2020) Moringa leaf and sorghum water extracts and salicylic acid to alleviate impacts of heat stress in wheat South African. J Bot 129:169–174. https://doi.org/10.1016/j.sajb.2019.04.009

Ahammed GJ, Xu W, Liu A, Chen S (2018) COMT1 silencing aggravates heat stress-induced reduction in photosynthesis by decreasing chlorophyll content, photosystem II activity, and electron transport efficiency in tomato. Front Plant Sci 9:998. https://doi.org/10.3389/fpls.2018.00998

Akter N, Rafiqul Islam M (2017) Heat stress effects and management in wheat. A review. Agron Sustain Dev 37:37. https://doi.org/10.1007/s13593-017-0443-9

Alghabari F, Shafqat W, Ahmad M et al (2019) Heat stress and plant development: role of sulphur metabolites and management strategies. Acta Agric Scand Sect B Soil Plant Sci 69:1–11. https://doi.org/10.1080/09064710.2019.1569715

Almeselmani M, Viswanathan PSD, Deshmukh PS, Chinnusamy V (2012) Effects of prolonged high temperature stress on respiration, photosynthesis and gene expression in wheat (*Triticum aestivum* L.) varieties differing in their thermotolerance. Plant Stress 6:25–32

Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol 141:391–396. https://doi.org/10.1104/pp.106.082040

Asthir B (2015) Protective mechanisms of heat tolerance in crop plants. J Plant Interact 10:202–210

Asthir B, Rai PK, Bains NS, Sohu VS (2012) Genotypic variation for high temperature tolerance in relation to carbon partitioning and grain sink activity in wheat. Am J Plant Sci 3:381–390. https://doi.org/10.4236/ajps.2012.33046

Backhausen JE, Scheibe R, Ahmad I et al (2014) Physiological, biochemical, and genome-wide transcriptional analysis reveals that elevated CO_2 mitigates the impact of combined heat wave and drought stress in *Arabidopsis thaliana* at multiple organizational levels. Plant Physiol Biochem 30:963–967. https://doi.org/10.1007/s11738-009-0415-z

Barnabás B, Jäger K, Fehér A (2008) The effect of drought and heat stress on reproductive processes in cereals. Plant Cell Environ 31:11–38. https://doi.org/10.1111/j.1365-3040.2007.01727.x

Begcy K, Weigert A, Egesa A, Dresselhaus T (2018) Compared to Australian Cultivars, European summer wheat (*Triticum aestivum*) overreacts when moderate heat stress is applied at the pollen development stage. Agronomy 8:99. https://doi.org/10.3390/agronomy8070099

Bennett D, Reynolds M, Mullan D et al (2012) Detection of two major grain yield QTL in bread wheat (*Triticum aestivum* L.) under heat, drought and high yield potential environments. Theor Appl Genet 125:1473–1485. https://doi.org/10.1007/s00122-012-1927-2

Berry J, Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. Annu Rev Plant Physiol 31:491–543

Berz J, Simm S, Schuster S et al (2019) Heatster: a database and web server for identification and classification of heat stress transcription factors in plants. Bioinform Biol Insights. https://doi.org/10.1177/1177932218821365

Brestic M, Zivcak M, Kalaji HM et al (2012) Photosystem II thermostability in situ: Environmentally induced acclimation and genotype-specific reactions in Triticum aestivum L. Plant Physiol Biochem 57:93–105. https://doi.org/10.1016/J.PLAPHY.2012.05.012

Brestic M, Zivcak M, Kunderlikova K, Allakhverdiev SI (2016) High temperature specifically affects the photoprotective responses of chlorophyll b-deficient wheat mutant lines. Photosynth Res 130:251–266. https://doi.org/10.1007/s11120-016-0249-7

Brestic M, Zivcak M, Hauptvogel P et al (2018) Wheat plant selection for high yields entailed improvement of leaf anatomical and biochemical traits including tolerance to non-optimal temperature conditions. Photosynth Res 136:245–255. https://doi.org/10.1007/s11120-018-0486-z

Buttar ZA, Wu SN, Arnao MB et al (2020) Melatonin suppressed the heat stress-induced damage in wheat seedlings by modulating the antioxidant machinery. Plants 9:1–17. https://doi.org/10.3390/plants9070809

Carmo-Silva E, Scales JC, Madgwick PJ, Maj P (2015) Optimizing Rubisco and its regulation for greater resource use efficiency. Plant Cell Environ 38:1817–1832. https://doi.org/10.1111/pce.12425

Casaretto JA, El-kereamy A, Zeng B et al (2016) Expression of OsMYB55 in maize activates stress-responsive genes and enhances heat and drought tolerance. BMC Genom. https://doi.org/10.1186/s12864-016-2659-5

Caverzan A, Casassola A, Brammer SP (2016) Antioxidant responses of wheat plants under stress. Genet Mol Biol 39:1–6. https://doi.org/10.1590/1678-4685-GMB-2015-0109

Chaudhary C, Sharma N, Khurana P (2021) Decoding the wheat awn transcriptome and overexpressing TaRca1β in rice for heat stress tolerance. Plant Mol Biol 105:133–146. https://doi.org/10.1007/s11103-020-01073-0

Chauhan H, Khurana N, Agarwal P, Khurana P (2011) Heat shock factors in rice (Oryza sativa L.): genome-wide expression analysis during reproductive development and abiotic stress. Mol Genet Genom 286:171–187. https://doi.org/10.1007/s00438-011-0638-8

Chen X, Zhang W, Zhang B et al (2011) Phosphoproteins regulated by heat stress in rice leaves. Proteome Sci. https://doi.org/10.1186/1477-5956-9-37

Cheng W, Sakai H, Yagi K, Hasegawa T (2010) Combined effects of elevated [CO_2] and high night temperature on carbon assimilation, nitrogen absorption, and the allocations of C and N by rice (*Oryza sativa* L.). Agric Meteorol 150:1174–1181. https://doi.org/10.1016/j.agrformet.2010.05.001

Chovancek E, Zivcak M, Botyanszka L et al (2019) Transient heat waves may affect the photosynthetic capacity of susceptible wheat genotypes due to insufficient photosystem I Photoprotection. Plants 8:282. https://doi.org/10.3390/plants8080282

Cochard H, Venisse J-S, Barigah TS et al (2007) Putative role of aquaporins in variable hydraulic conductance of leaves in response to light. Plant Physiol 143:122–133

Comastri A, Janni M, Simmonds J et al (2018) Heat in wheat: exploit reverse genetic techniques to discover new alleles within the *Triticum durum* shsp26 family. Front Plant Sci. https://doi.org/10.3389/fpls.2018.01337

Cossani CM, Reynolds MP (2012) Physiological traits for improving heat tolerance in wheat. Plant Physiol 160:1710–1718. https://doi.org/10.1104/pp.112.207753

Crafts-Brandner SJ, Salvucci ME (2000) Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. Proc Natl Acad Sci USA 97:13430–13435. https://doi.org/10.1073/pnas.230451497

Crafts-Brandner SJ, Salvucci ME (2002) Sensitivity of photosynthesis in a C_4 plant, maize, to heat stress. Plant Physiol 129:1773–1780. https://doi.org/10.1104/pp.002170

Degen GE, Orr DJ, Carmo-Silva E (2021) Heat-induced changes in the abundance of wheat Rubisco activase isoforms. New Phytol 229:1298–1311. https://doi.org/10.1111/nph.16937

Dhindsa RS, Plumb-dhindsa P, Thorpe TA (1981) Leaf senescence: correlated with increased levels of membrane permeability and lipid peroxidation, and decreased levels of superoxide dismutase and catalase. J Exp Bot 32:93–101. https://doi.org/10.1093/jxb/32.1.93

Djanaguiraman M, Prasad PVV, Seppanen M (2010) Selenium protects sorghum leaves from oxidative damage under high temperature stress by enhancing antioxidant defense system. Plant Physiol Biochem 48:999–1007. https://doi.org/10.1016/j.plaphy.2010.09.009

Djanaguiraman M, Boyle DL, Welti R et al (2018) Decreased photosynthetic rate under high temperature in wheat is due to lipid desaturation, oxidation, acylation, and damage of organelles. BMC Plant Biol. 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 Biol 20:1–12. https://doi.org/10.1186/s12870-020-02479-0

Dubey R, Pathak H, Chakrabarti B et al (2020) Impact of terminal heat stress on wheat yield in India and options for adaptation. Agric Syst. https://doi.org/10.1016/j.agsy.2020.102826

El-Sarag EI, Ismaeil RIM (2013) Evaluation of some bread wheat cultivars productivity as affected by sowing dates and water stress in semi-arid region. Asian J Crop Sci 5:167–178. https://doi.org/10.3923/ajcs.2013.167.178

Fahad S, Adnan M, Hassan S, et al (2019) Rice responses and tolerance to high temperature. In: Advances in rice research for abiotic stress tolerance. Elsevier, pp 201–224

Farooq M, Bramley H, Palta JA, Siddique KHM (2011) Heat stress in wheat during reproductive and grain-filling phases. CRC Crit Rev Plant Sci 30:491–507. https://doi.org/10.1080/07352689.2011.615687

Farooq M, Hussain M, Siddique KHM (2014) Drought stress in wheat during flowering and grain-filling periods. CRC Crit Rev Plant Sci 33:331–349. https://doi.org/10.1080/07352689.2014.875291

Fleitas MC, Mondal S, Gerard GS et al (2020) Identification of CIMMYT spring bread wheat germplasm maintaining superior grain yield and quality under heat-stress. J Cereal Sci. https://doi.org/10.1016/j.jcs.2020.102981

Frey FP, Urbany C, Hüttel B et al (2015) Genome-wide expression profiling and phenotypic evaluation of European maize inbreds at seedling stage in response to heat stress. BMC Genom. https://doi.org/10.1186/s12864-015-1282-1

Fu YB (2015) Understanding crop genetic diversity under modern plant breeding. Theor Appl Genet 128:2131–2142

Fu J, Momčilović I, Clemente TE et al (2008) Heterologous expression of a plastid EF-Tu reduces protein thermal aggregation and enhances CO_2 fixation in wheat (*Triticum aestivum*) following heat stress. Plant Mol Biol 68:277–288. https://doi.org/10.1007/s11103-008-9369-6

Gahlaut V, Baranwal VK, Khurana P (2018) miRNomes involved in imparting thermotolerance to crop plants. 3 Biotech 8:1–19

Gahlaut V, Samtani H, Khurana P (2020) Genome-wide identification and expression profiling of cytosine-5 DNA methyltransferases during drought and heat stress in wheat (*Triticum aestivum*). Genomics 112:4796–4807. https://doi.org/10.1016/j.ygeno.2020.08.031

Gardiner LJ, Quinton-Tulloch M, Olohan L et al (2015) A genome-wide survey of DNA methylation in hexaploid wheat. Genome Biol 16:273. https://doi.org/10.1186/s13059-015-0838-3

Gaur PM, Samineni S, Thudi M et al (2019) Integrated breeding approaches for improving drought and heat adaptation in chickpea (*Cicer arietinum* L.). Plant Breed 138:389–400

Gifford RM (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. Funct Plant Biol 30:171–183. https://doi.org/10.1071/FP02083

González-Schain N, Dreni L, Lawas LMF et al (2016) Genome-wide transcriptome analysis during anthesis reveals new insights into the molecular basis of heat stress responses in tolerant and sensitive rice varieties. Plant Cell Physiol 57:57–68. https://doi.org/10.1093/pcp/pcv174

Gourdji SM, Mathews KL, Reynolds M et al (2013) An assessment of wheat yield sensitivity and breeding gains in hot environments. Proc R Soc B Biol Sci. https://doi.org/10.1098/rspb.2012.2190

Gupta NK, Agarwal S, Agarwal VP et al (2013) Effect of short-term heat stress on growth, physiology and antioxidative defence system in wheat seedlings. Acta Physiol Plant 35:1837–1842. https://doi.org/10.1007/s11738-013-1221-1

Gupta OP, Mishra V, Singh NK et al (2015) Deciphering the dynamics of changing proteins of tolerant and intolerant wheat seedlings subjected to heat stress. Mol Biol Rep 42:43–51. https://doi.org/10.1007/s11033-014-3738-9

Gupta PK, Balyan HS, Sharma S, Kumar R (2020) Genetics of yield, abiotic stress tolerance and biofortification in wheat (*Triticum aestivum* L.). Theor Appl Genet 133:1569–1602

Haider S, Iqbal J, Naseer S et al (2021) Molecular mechanisms of plant tolerance to heat stress: current landscape and future perspectives. Plant Cell Rep 1:1–25. https://doi.org/10.1007/S00299-021-02696-3

Hall AE (2010) Breeding for heat tolerance. Plant breeding reviews. Wiley, Oxford, pp 129–168

Haque MS, Kjaer KH, Rosenqvist E et al (2014) Heat stress and recovery of photosystem II efficiency in wheat (*Triticum aestivum* L.) cultivars acclimated to different growth temperatures. Environ Exp Bot 99:1–8. https://doi.org/10.1016/J.ENVEXPBOT.2013.10.017

Hasanuzzaman M, Nahar K, Alam MM et al (2013) Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci 14:9643–9684. https://doi.org/10.3390/ijms14059643

Hauvaux M (1993) Rapid photosynthetic adaptation to heat stress triggered in potato leaves by moderately elevated temperatures. Plant Cell Environ 16:461–467. https://doi.org/10.1111/j.1365-3040.1993.tb00893.x

Hossain A, Teixeira da Silva JA, Lozovskaya MV, Zvolinsky VP (2012) High temperature combined with drought affect rainfed spring wheat and barley in South-Eastern Russia: I. Phenology and growth. Saudi J Biol Sci 19:473–487. https://doi.org/10.1016/j.sjbs.2012.07.005

Hu Z, Song N, Zheng M et al (2015) Histone acetyltransferase GCN 5 is essential for heat stress-responsive gene activation and thermotolerance in Arabidopsis. Plant J 84:1178–1191. https://doi.org/10.1111/tpj.13076

Hurkman WJ, Vensel WH, Tanaka CK et al (2009) Effect of high temperature on albumin and globulin accumulation in the endosperm proteome of the developing wheat grain. J Cereal Sci 49:12–23. https://doi.org/10.1016/j.jcs.2008.06.014

IPCC (2013) Climate change 2013: the physical science basis. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, New York, pp 1535. https://doi.org/10.1017/CBO9781107415324.

Ivanov AG, Velitchkova MY, Allakhverdiev SI, Huner NPA (2017) Heat stress-induced effects of photosystem I: an overview of structural and functional responses. Photosynth Res 133:17–30. https://doi.org/10.1007/s11120-017-0383-x

Jaganathan D, Ramasamy K, Sellamuthu G et al (2018) CRISPR for crop improvement: an update review. Front Plant Sci. https://doi.org/10.3389/fpls.2018.00985

Jamil M, Ali A, Gul A et al (2019) Genome-wide association studies of seven agronomic traits under two sowing conditions in bread wheat. BMC Plant Biol 19:149. https://doi.org/10.1186/s12870-019-1754-6

Janda T, Khalil R, Tajti J et al (2019) Responses of young wheat plants to moderate heat stress. Acta Physiol Plant 41:1–8. https://doi.org/10.1007/s11738-019-2930-x

Janni M, Gullì M, Maestri E et al (2020) Molecular and genetic bases of heat stress responses in crop plants and breeding for increased resilience and productivity. J Exp Bot 71:3780–3802

Khan MIR, Iqbal N, Masood A et al (2013) Salicylic acid alleviates adverse effects of heat stress on photosynthesis through changes in proline production and ethylene formation. Plant Signal Behav. https://doi.org/10.4161/psb.26374

Klimenko SB, Peshkova AA, Dorofeev NV (2006) Nitrate reductase activity during heat shock in winter wheat. J Stress Physiol Biochem 2:50–55

Kong L, Liu Y, Wang X, Chang C (2020) Insight into the role of epigenetic processes in abiotic and biotic stress response in wheat and barley. Int J Mol Sci 21:1480. https://doi.org/10.3390/ijms21041480

Kosová K, Vítámvás P, Prášil IT, Renaut J (2011) Plant proteome changes under abiotic stress—contribution of proteomics studies to understanding plant stress response. J Proteom 74:1301–1322

Kothari A, Lachowiec J (2021) Roles of brassinosteroids in mitigating heat stress damage in cereal crops. Int J Mol Sci 22:1–15. https://doi.org/10.3390/ijms22052706

Kumar RR, Goswami S, Sharma SK et al (2012) Protection against heat stress in wheat involves change in cell membrane stability, antioxidant enzymes, osmolyte, H_2O_2 and transcript of heat shock protein. Int J Plant Physiol Biochem 4:83–91. https://doi.org/10.5897/ijppb12.008

Kumar RR, Pathak H, Sharma SK et al (2015) Novel and conserved heat-responsive microRNAs in wheat (*Triticum aestivum* L.). Funct Integr Genom 15:323–348. https://doi.org/10.1007/s10142-014-0421-0

Kumar RR, Singh K, Ahuja S et al (2019a) Quantitative proteomic analysis reveals novel stress-associated active proteins (SAAPs) and pathways involved in modulating tolerance of wheat under terminal heat. Funct Integr Genom 19:329–348. https://doi.org/10.1007/s10142-018-0648-2

Kumar RR, Tasleem M, Jain M et al (2019b) Nitric oxide triggered defense network in wheat: augmenting tolerance and grain-quality related traits under heat-induced oxidative damage. Environ Exp Bot 158:189–204. https://doi.org/10.1016/j.envexpbot.2018.11.016

Kumar RR, Dubey K, Arora K et al (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. Biotechnol Rep 29:e00597. https://doi.org/10.1016/j.btre.2021.e00597

Kumari A, Hemantaranjan A (2019) Mitigating effects of 24-epibrassinolide on heat stress damage by shifting biochemical and antioxidant defense mechanisms in wheat (*Triticum aestivum* L.) at pre-flowering stage and post-flowering stage. J Pharmacogn Phytochem 8:1157–1161

Law RD, Crafts-Brandner SJ (1999) Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase. Plant Physiol 120:173–181. https://doi.org/10.1104/pp.120.1.173

Li X, Lawas LMF, Malo R et al (2015) Metabolic and transcriptomic signatures of rice floral organs reveal sugar starvation as a factor in reproductive failure under heat and drought stress. Plant Cell Environ 38:2171–2192. https://doi.org/10.1111/pce.12545

Li L, Mao X, Wang J et al (2019) Genetic dissection of drought and heat-responsive agronomic traits in wheat. Plant Cell Environ 42:2540–2553. https://doi.org/10.1111/pce.13577

Liu Z, Xin M, Qin J et al (2015) Temporal transcriptome profiling reveals expression partitioning of homeologous genes contributing to heat and drought acclimation in wheat (*Triticum aestivum* L.). BMC Plant Biol 15:152. https://doi.org/10.1186/s12870-015-0511-8

Liu B, Asseng S, Wang A et al (2017) Modelling the effects of post-heading heat stress on biomass growth of winter wheat. Agric Meteorol 247:476–490. https://doi.org/10.1016/j.agrformet.2017.08.018

Liu C, Sukumaran S, Claverie E et al (2019) Genetic dissection of heat and drought stress QTLs in phenology-controlled synthetic-derived recombinant inbred lines in spring wheat. Mol Breed. https://doi.org/10.1007/s11032-019-0938-y

Lu Y, Li R, Wang R et al (2017) Comparative proteomic analysis of flag leaves reveals new insight into wheat heat adaptation. Front Plant Sci. https://doi.org/10.3389/fpls.2017.01086

Macabuhay A, Houshmandfar A, Nuttall J et al (2018) Can elevated CO_2 buffer the effects of heat waves on wheat in a dryland cropping system? Environ Exp Bot 155:578–588. https://doi.org/10.1016/j.envexpbot.2018.07.029

Machado S, Paulsen GM (2001) Combined effects of drought and high temperature on water relations of wheat and sorghum. Plant Soil 233:179–187

Mangelsen E, Kilian J, Harter K et al (2011) Transcriptome analysis of high-temperature stress in developing barley caryopses: early stress responses and effects on storage compound biosynthesis. Mol Plant 4:97–115. https://doi.org/10.1093/mp/ssq058

Martínez-Ballesta MC, López-Pérez L, Muries B et al (2009) Climate change and plant water balance: the role of aquaporins–a review. Climate change, intercropping pest control and beneficial microorganisms. . Springer, pp 71–89

Mathur S, Agrawal D, Jajoo A (2014) Photosynthesis: response to high temperature stress. J Photochem Photobiol B Biol 137:116–126. https://doi.org/10.1016/j.jphotobiol.2014.01.010

Maulana F, Ayalew H, Anderson JD et al (2018) Genome-wide association mapping of seedling heat tolerance in winter wheat. Front Plant Sci. https://doi.org/10.3389/fpls.2018.01272

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 Physiol Biochem 132:213–221. https://doi.org/10.1016/j.plaphy.2018.09.002

Mohammadi M, Karimizadeh RA, Naghavi MR et al (2009) Selection of bread wheat genotypes against heat and drought tolerance based on chlorophyll content and stem reserves. J Agric Soc Sci 5:119–122

Nahar K, Ahamed KU, Fujita M (2010) Phenological variation and its relation with yield in several wheat (*Triticum aestivum* L.) cultivars under normal and late sowing mediated heat stress condition. Not Sci Biol 2:51–56

Narayanan S, Prasad PVV, Welti R (2016) Wheat leaf lipids during heat stress: II. Lipids experiencing coordinated metabolism are detected by analysis of lipid co-occurrence. Plant Cell Environ 39:608–617. https://doi.org/10.1111/pce.12648

Narayanan S, Prasad PVV, Welti R (2018) Alterations in wheat pollen lipidome during high day and night temperature stress. Plant Cell Environ 41:1749–1761. https://doi.org/10.1111/pce.13156

Neuwald AF, Aravind L, Spouge JL, Koonin EV (1999) Assembly, operation, and disassembly of protein complexes AAA+: a class of chaperone-like atpases associated with the assembly, operation, and disassembly of protein complexes. Genome Res 9:27–43. https://doi.org/10.1101/gr.9.1.27

Nishiyama Y, Allakhverdiev SI, Murata N (2011) Protein synthesis is the primary target of reactive oxygen species in the photoinhibition of photosystem II. Physiol Plant 142:35–46

Niu Y, Xiang Y (2018) An overview of biomembrane functions in plant responses to high-temperature stress. Front Plant Sci 9:915

Ohama N, Sato H, Shinozaki K, Yamaguchi-Shinozaki K (2017) Transcriptional regulatory network of plant heat stress response. Trends Plant Sci 22:53–65. https://doi.org/10.1016/j.tplants.2016.08.015

Paliwal R, Röder MS, Kumar U et al (2012) QTL mapping of terminal heat tolerance in hexaploid wheat (*Triticum aestivum* L.). Theor Appl Genet 125:561–575. https://doi.org/10.1007/s00122-012-1853-3

Parry MAJ, Reynolds M, Salvucci ME et al (2011) Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. J Exp Bot 62:453–467. https://doi.org/10.1093/jxb/erq304

Patel D, Franklin KA (2009) Temperature-regulation of plant architecture. Plant Signal Behav 4:577–579

Perdomo JA, Capó-Bauçà S, Carmo-Silva E, Galmés J (2017) Rubisco and rubisco activase play an important role in the biochemical limitations of photosynthesis in rice, wheat, and maize under high temperature and water deficit. Front Plant Sci 8:490. https://doi.org/10.3389/fpls.2017.00490

Portis AR (2003) Rubisco activase—Rubisco's catalytic chaperone. Photosynth Res 75:11–27

Poudel PB, Poudel MR (2020) Heat stress effects and tolerance in wheat: a review. J Biol Today's World 9:1–6

Prasad PVV, Boote KJ, Vu JCV, Allen LH (2004) The carbohydrate metabolism enzymes sucrose-P synthase and ADG-pyrophosphorylase in phaseolus bean leaves are up-regulated at elevated growth carbon dioxide and temperature. Plant Sci 166:1565–1573. https://doi.org/10.1016/j.plantsci.2004.02.009

Prasad PVV, Pisipati SR, Momčilović I, Ristic Z (2011) Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. J Agron Crop Sci 197:430–441. https://doi.org/10.1111/j.1439-037X.2011.00477.x

Qin D, Wu H, Peng H et al (2008) Heat stress-responsive transcriptome analysis in heat susceptible and tolerant wheat (*Triticum aestivum* L.) by using Wheat Genome Array. BMC Genomics. https://doi.org/10.1186/1471-2164-9-432

Ragupathy R, Ravichandran S, Mahdi MSR et al (2016) Deep sequencing of wheat sRNA transcriptome reveals distinct temporal expression pattern of miRNAs in response to heat, light and UV. Sci Rep 6:1–15. https://doi.org/10.1038/srep39373

Rai KK, Pandey N, Rai SP (2019) Salicylic acid and nitric oxide signaling in plant heat stress. Physiol Plant 168:ppl.12958. https://doi.org/10.1111/ppl.12958

Rangan P, Furtado A, Henry R (2020) Transcriptome profiling of wheat genotypes under heat stress during grain-filling. J Cereal Sci. https://doi.org/10.1016/j.jcs.2019.102895

Ravichandran S, Ragupathy R, Edwards T et al (2019) Microrna-guided regulation of heat stress response in wheat. BMC Genom 20:1–16. https://doi.org/10.1186/s12864-019-5799-6

Rennenberg H, Loreto F, Polle A et al (2006) Physiological responses of forest trees to heat and drought. Plant Biol 8:556–571

Rezaei EE, Siebert S, Manderscheid R et al (2018) Quantifying the response of wheat yields to heat stress: the role of the experimental setup. F Crop Res 217:93–103

Rochaix J-D (2011) Assembly of the photosynthetic apparatus. Plant Physiol 155:1493–1500. https://doi.org/10.1104/pp.110.169839

Roy S, Arora A, Chinnusamy V, Singh VP (2017) Endogenous reduced ascorbate: an indicator of plant water deficit stress in wheat. Indian J Plant Physiol 22:365–368. https://doi.org/10.1007/s40502-017-0308-x

Rumeau D, Peltier G, Cournac L (2007) Chlororespiration and cyclic electron flow around PSI during photosynthesis and plant stress response. Plant Cell Environ 30:1041–1051. https://doi.org/10.1111/j.1365-3040.2007.01675.x

Sairam RK, Srivastava GC, Saxena DC (2000) Increased antioxidant activity under elevated temperatures: a mechanism of heat stress tolerance in wheat genotypes. Biol Plant 43:245–251

Salvucci ME, Crafts-Brandner SJ (2004) Mechanism for deactivation of Rubisco under moderate heat stress. Physiol Plant 122:513–519. https://doi.org/10.1111/j.1399-3054.2004.00419.x

Sattar A, Sher A, Ijaz M et al (2020) Terminal drought and heat stress alter physiological and biochemical attributes in flag leaf of bread wheat. PLoS One 15:e0232974. https://doi.org/10.1371/journal.pone.0232974

Scafaro AP, De Vleesschauwer D, Bautsoens N et al (2019) A single point mutation in the C-terminal extension of wheat Rubisco activase dramatically reduces ADP inhibition via enhanced ATP binding affinity. J Biol Chem 294:17931–17940. https://doi.org/10.1074/jbc.RA119.010684

Sehgal A, Sita K, Siddique KHM et al (2018) Drought or/and heat-stress effects on seed filling in food crops: impacts on functional biochemistry, seed yields, and nutritional quality. Front Plant Sci 9:1–19. https://doi.org/10.3389/fpls.2018.01705

Shah MH, Paulsen GM (2005) Injury to photosynthesis and productivity from interaction between high temperature and drought during maturation of wheat. Asian J Plant Sci 4:67–74

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot 2012:1–26. https://doi.org/10.1155/2012/217037

Sharma DK, Torp AM, Rosenqvist E et al (2017) QTLs and potential candidate genes for heat stress tolerance identified from the mapping populations specifically segregating for Fv/Fm in wheat. Front Plant Sci. https://doi.org/10.3389/fpls.2017.01668

Shirdelmoghanloo H, Taylor JD, Lohraseb I et al (2016) A QTL on the short arm of wheat (*Triticum aestivum* L) chromosome 3B affects the stability of grain weight in plants exposed to a brief heat shock early in grain filling. BMC Plant Biol. https://doi.org/10.1186/s12870-016-0784-6

Sing S (2009) Variation in physiological traits for thermotolerance in wheat. Indian J Plant Physiol 14:407–412

Spilde LA (1989) Influence of seed size and test weight on several agronomic traits of barley and hard red spring wheat. J Prod Agric 2:169. https://doi.org/10.2134/jpa1989.0169

Spreitzer RJ, Salvucci ME (2002) Rubisco: structure, regulatory interactions, and possibilities for a better enzyme. Annu Rev Plant Biol 53:449–475

Stocker TF, Qin D, Plattner GK et al (2014) Climate change 2013—the physical science basis. Cambridge University Press, Cambridge

Stone PJ, Nicolas ME, Stone P, Nicolas M (1994) Wheat cultivars vary widely in their responses of grain yield and quality to short periods of post-anthesis heat stress. Aust J Plant Physiol 21:887–900. https://doi.org/10.1071/PP9940887

Tadesse W, Suleiman S, Tahir I et al (2019) Heat-tolerant QTLs associated with grain yield and its components in spring bread wheat under heat-stressed environments of Sudan and Egypt. Crop Sci 59:199–211. https://doi.org/10.2135/cropsci2018.06.0389

Talukder ASMHM, McDonald GK, reGill GS, (2014a) Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat. F Crop Res 160:54–63. https://doi.org/10.1016/j.fcr.2014.01.013

Talukder SK, Babar MA, Vijayalakshmi K et al (2014b) Mapping QTL for the traits associated with heat tolerance in wheat (*Triticum aestivum* L.). BMC Genet. https://doi.org/10.1186/s12863-014-0097-4

Tewari AK, Tripathy BC (1998) Temperature-stress-induced impairment of chlorophyll biosynthetic reactions in cucumber and wheat. Plant Physiol 117:851–858

Thomason K, Babar MA, Erickson JE et al (2018) Comparative physiological and metabolomics analysis of wheat (*Triticum aestivum* L.) following post-anthesis heat stress. PLoS One. https://doi.org/10.1371/journal.pone.0197919

Tian X, Wang F, Zhao Y et al (2020) Heat shock transcription factor A1b regulates heat tolerance in wheat and Arabidopsis through OPR3 and jasmonate signalling pathway. Plant Biotechnol J 18:1109. https://doi.org/10.1111/PBI.13268

Tiwari RK, Lal MK, Kumar R et al (2020a) Mechanistic insights on melatonin mediated drought stress mitigation in plants. Physiol Plant. https://doi.org/10.1111/ppl.13307

Tiwari RK, Lal MK, Naga KC et al (2020b) Emerging roles of melatonin in mitigating abiotic and biotic stresses of horticultural crops. Sci Hortic (Amst) 272:109592. https://doi.org/10.1016/j.scienta.2020.109592

ur Rehman A, Habib I, Ahmad N, et al (2009) Screening wheat germplasm for heat tolerance at terminal growth stage. Plant Omics 2:9–19

Upreti KK, Sharma M (2016) Role of plant growth regulators in abiotic stress tolerance 2. Springer. https://doi.org/10.1007/978-81-322-2725-0_2

Valluru R, Davies WJ, Reynolds MP, Dodd IC (2016) Foliar abscisic acid-to-ethylene accumulation and response regulate shoot growth sensitivity to mild drought in wheat. Front Plant Sci 7:461. https://doi.org/10.3389/fpls.2016.00461

Vijayalakshmi K, Fritz AK, Paulsen GM et al (2010) Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. Mol Breed 26:163–175. https://doi.org/10.1007/s11032-009-9366-8

Viswanathan C, Khanna-Chopra R (2001) Effect of heat stress on grain growth, starch synthesis and protein synthesis in grains of wheat (*Triticum aestivum* L.) varieties differing in grain weight stability. J Agron Crop Sci 186:1–7. https://doi.org/10.1046/j.1439-037x.2001.00432.x

Wachter RM, Henderson JN (2015) Photosynthesis: rubisco rescue. Nat Plants 1:1–2

Wahid A (2007) Physiological implications of metabolite biosynthesis for net assimilation and heat-stress tolerance of sugarcane (*Saccharum officinarum*) sprouts. J Plant Res 120:219–228. https://doi.org/10.1007/s10265-006-0040-5

Wang X, Dinler BS, Vignjevic M et al (2015) Physiological and proteome studies of responses to heat stress during grain filling in contrasting wheat cultivars. Plant Sci 230:33–50. https://doi.org/10.1016/j.plantsci.2014.10.009

Wang QL, Chen JH, He NY, Guo FQ (2018a) Metabolic reprogramming in chloroplasts under heat stress in plants. Int J Mol Sci 19(3):849

Wang X, Xu Y, Hu Z, Xu C (2018b) Genomic selection methods for crop improvement: current status and prospects. Crop J 6:330–340. https://doi.org/10.1016/j.cj.2018.03.001

Wei Y, Hu W, Wang Q et al (2017) Identification, transcriptional and functional analysis of heat-shock protein 90s in banana (*Musa acuminata* L.) highlight their novel role in melatonin-mediated plant response to Fusarium wilt. J Pineal Res. https://doi.org/10.1111/jpi.12367

Weis E (1981) Reversible heat-inactivation of the Calvin cycle: a possible mechanism of the temperature regulation of photosynthesis. Planta 151:33–39. https://doi.org/10.1007/BF00384234

Wu B, Qiao J, Wang X et al (2021) Factors affecting the rapid changes of protein under short-term heat stress. BMC Genom 22:1–11. https://doi.org/10.1186/s12864-021-07560-y

Xin M, Wang Y, Yao Y et al (2010) Diverse set of microRNAs are responsive to powdery mildew infection and heat stress in wheat (*Triticum aestivum* L). BMC Plant Biol 10:123. https://doi.org/10.1186/1471-2229-10-123

Yan K, Chen P, Shao H et al (2013) Dissection of photosynthetic electron transport process in sweet sorghum under heat stress. PLoS One 8:e62100. https://doi.org/10.1371/journal.pone.0062100

Yousuf PY, Abd_Allah EF, Nauman M, et al (2017) Responsive Proteins in Wheat Cultivars with Contrasting Nitrogen Efficiencies under the Combined Stress of High Temperature and Low Nitrogen. Genes (Basel) 8:356. doi: https://doi.org/10.3390/genes8120356

Zhang X, Zhou Q, Wang X et al (2016) Physiological and transcriptional analyses of induced post-anthesis thermo-tolerance by heat-shock pretreatment on germinating seeds of winter wheat. Environ Exp Bot 131:181–189. https://doi.org/10.1016/J.ENVEXPBOT.2016.08.002

Zhang X, Högy P, Wu X, Schmid I, Wang X, Schulze WX, Jiang D, Fangmeier A (2018) Physiological and proteomic evidence for the interactive effects of post-anthesis heat stress and elevated CO_2 on wheat. Proteomics. https://doi.org/10.1002/pmic.201800262

Zhao H, Dai T, Jing Q et al (2007) Leaf senescence and grain filling affected by post-anthesis high temperatures in two different wheat cultivars. Plant Growth Regul 51:149–158

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