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Tolerance mechanisms for breeding wheat against heat stress: A review

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ABSTRACT

Heat stress is one of the major abiotic stresses affecting the growth and yield-related characters of wheat. Using various genetic approaches we can develop heat tolerant wheat varieties in order to mitigate the effect of heat stress on wheat production. Currently different strategies have been adopted to develop thermotolerance in wheat. Development of thermotolerant wheat varieties is one of the major steps toward the improvement of wheat yield against heat stress. For this purpose, it is important to have a complete and clear concept of the morpho-physiological, biochemical and molecular mechanisms of heat tolerance in wheat. This review may provide better knowledge about heat tolerance through discussing the morphological, physiological, biochemical and molecular mechanisms of heat tolerance in wheat based on different parameters such as grain filling duration, grain yield, leaf senescence, canopy temperature depression, photosynthesis, chlorophyll content, membrane thermostability, translocation of photo-assimilates, starch synthesis, antioxidant response, protein synthesis and omics approaches.

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1. Introduction

The changes in world climate has been severely affecting the global wheat production (Qin et al., 2002). As a strategic cereal crop of several countries in the world, production of wheat has become one of the ultimate factors for food security (Curtis and Halford, 2014). Wheat provides ~ 55% and ~ 20% of the global consumption of carbohydrates and calories respectively (Enghiad et al., 2017). By 2050, considerable research attentions will be continued toward wheat in order to feed around nine billion population of the world (Godfray et al., 2010). With growing global population, it is anticipated that the demand for wheat will be increased which will require an increase of global wheat production by 2% annually (Gill et al., 2004). But, one of the major problems in wheat production is the shortening of winter period which causes temperature stress to wheat. The primary cause of increasing global mean temperature is the rise in atmospheric CO_2 that increases the frequency, intensity and duration of heat waves (Chavan et al., 2019). This increasing temperature leads to cause heat stress that has a profound effect on global wheat production (Melloy et al., 2014; Liu et al., 2017). An increase of 1 °C atmospheric temperature may reduce the wheat yield by 10% (Lesk et al., 2016). In warmer regions, grain yield of wheat are more likely to be reduced than in cooler regions (Liu et al., 2019). The annual mean temperature in a warmer region like Mediterranean basin has been supposed to be increased by 3 to 4 °C which may lead to the decrease in total wheat grain yield of about 18% to 24% in this area (Asseng et al., 2015). Rise in temperature that occurs between heading and maturity stage of crop is considered as terminal heat stress (El Hassouni et al., 2019). This terminal heat stress at reproductive phase of wheat affects the anthesis and grain filling causing a severe yield reduction (Hays et al., 2007). For flowering and grain filling of wheat, the optimum temperature ranges from 12 °C to 22 °C (Kumudini et al., 2014). Significant loss in grain yield may occur when wheat is subjected to ambient temperature more than 35 °C for a short period of time (Wolfgang et al., 2018). Based on the duration and extent of temperature, plant responses may significantly differ to heat stress (Table 1) (Ruelland and Zachowski, 2010).

Under heat stress, plants exhibit different morphological, physiological, biochemical and molecular alteration and adaptation strategies to develop heat tolerance (Fig. 1). Good germination potential, better vegetative growth, leaf rolling or leaf folding, inhibition of early leaf senescence, better plant biomass accumulation etc. can be considered as morphological adaptations of wheat against heat stress. Early maturation with smaller yield losses may also be attributed as an avoidance mechanism under heat stress. Physiological responses of wheat plant to heat stress can be divided into two distinct mechanisms; avoidance and tolerance (Adams et al., 2001).

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Table 1
Responses of plant to heat stress at different growth and developmental stages of wheat.

Temperature, Duration	Major responses to heat stress	References
34/26 °C (day/night), 16 days	Shortening of grain filling and maturity period; Drastic reduction in both fresh and dry weight, starch content and protein in grain; grain size and yield reduction	Pradhan and Prasad (2015)
35 °C, 1 h	Reduction in water soluble carbohydrate content in peduncle by 26%	Talukder et al. (2014)
37/28 °C day/night	leaf temperature increase; reduction of leaf chlorophyll content and maximum quantum yield of photosystem-II; reduction of individual grain weight and grain yield	Hurkman et al. (2009)
38 °C, 15 h	Increase of H_2O_2 content	Iqbal et al. (2015)
45 °C, 2 h	Reduction in length and dry mass of shoot and root; decrease in membrane stability index and chlorophyll content	Gupta et al. (2013a)
42 °C, 24 h	Roots and first leaves development inhibition; increase in lipid peroxidation (LP) products and reactive oxygen species (ROS) in the developing organs	Savicka and Škute (2010)
40 °C, 2 + 5 h	Photochemical efficiency (F_v/F_m) and quantum yield (F'_q/F'_m) of PSII inhibition	Haque et al. (2014)

Source: Akter and Islam (2017); Ihsan et al. (2019).

Increased root system, enhanced stomatal conductance, changing leaf orientation, increased leaf thickness and increased transpirational cooling are the avoidance mechanisms those help to escape heat stress where water stress is not a limiting factor (Fahad et al., 2017). But a different scenery of decreasing stomatal and lenticular conductance has been found as avoidance mechanism to drought stress (Goufo et al., 2017). Many changes also occur at the molecular level like alteration in gene expression and transcripts accumulation that lead to stress-related protein synthesis and act as a strategy of stress tolerance (Iba, 2002). Denaturation and aggregation of protein are the direct injuries of high temperature (Essemine et al., 2010) whereas indirect injuries include inhibition of protein synthesis, protein degradation, enzymes inactivation in chloroplast and mitochondria and loss of membrane integrity (Howarth, 2005).

Therefore, heat-tolerant wheat line selection may help to figure out how this crop respond to high temperature and how heat tolerance mechanisms can be improved in wheat (Halford, 2009). The first step towards wheat breeding program for heat stress is to identify heat stress tolerant genotypes by exploring local genotypes of wheat that are highly adapted to heats stress (Bita and Gerats, 2013). Therefore, the main objective of this review paper is to accumulate the present understanding about the effect of heat stress and heat tolerance mechanisms in wheat which may help to identify heat tolerant wheat genotypes.

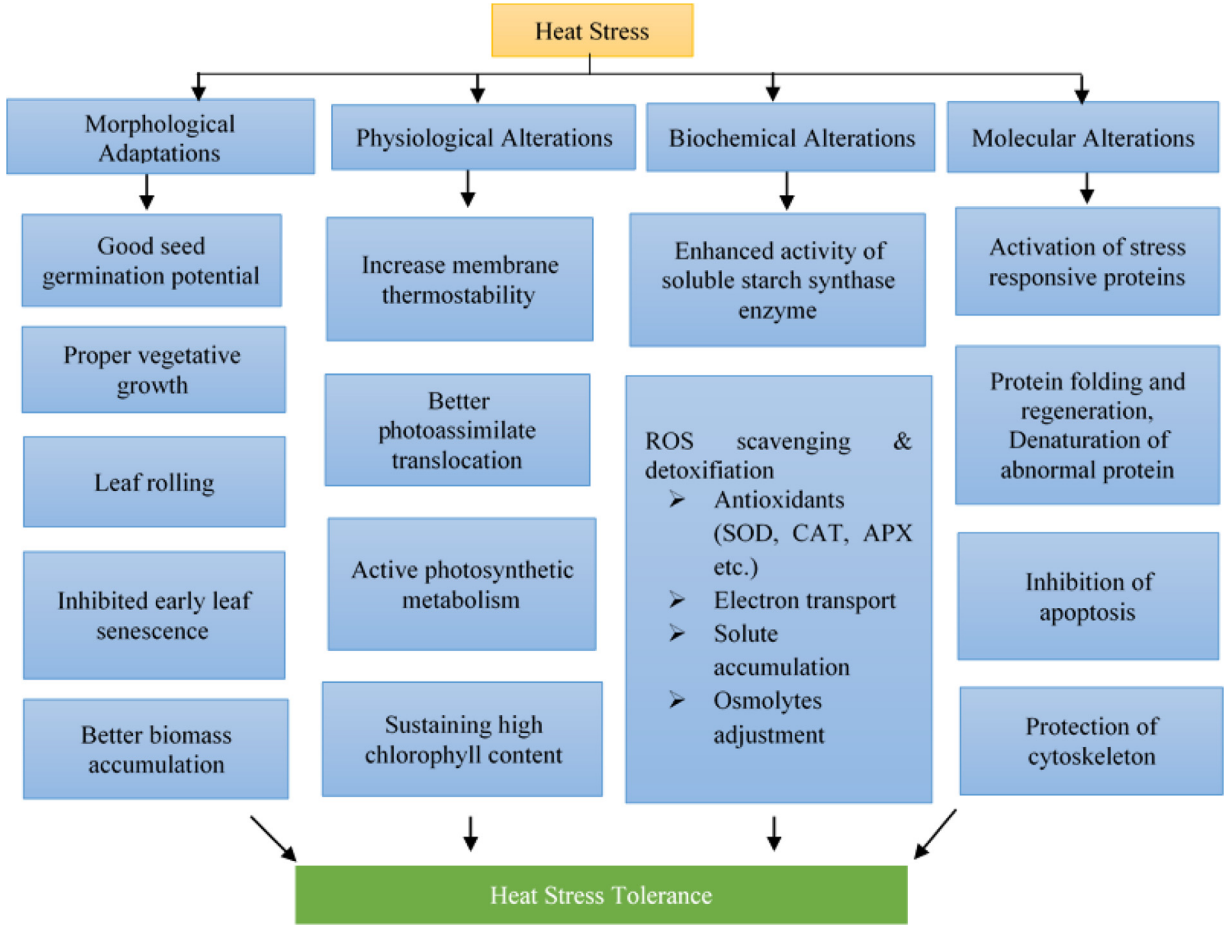


Fig. 1. Development of heat tolerance in plants; SOD= Superoxide dismutase, CAT= Catalase, APX= Ascorbate peroxidase.

2. Mechanism of heat tolerance

Before knowing about the mechanisms of heat tolerance, it is very important to have a clear concept about the critical stages of wheat that can be affected by heat stress. This knowledge may help in planning management strategies and breeding program that incorporate information about plant growth to avoid damage of crop against stress environment and to minimize crop yield loss. Different scales have been used to explain the critical stages of crop such as BBCH scale (Fig. 2).

A decimal code system is used by BBCH-scale which is divided into principal and secondary growth stages based on the cereal code system (Zadoks scale) developed by Zadoks (Table 2) (Zadoks et al., 1974). The flowering stage of wheat has been found the most sensitive stage to heat stress (Kaushal et al., 2016). Complex interaction between the sensitivity of growth phases to the stress environment and the timing of phenological stages finally influences the grain yield (Balla et al., 2019).

Table 2
Decimal growth stages scale proposed by Zadoks (Z0.0 to Z9.9).

Main stages	Description	Main stages	Description
Stage 0	Germination	Stage 5	Heading
Stage 1	Main shoot leaf production	Stage 6	Anthesis
Stage 2	Tiller production	Stage 7	Grain milk stage
Stage 3	Main shoot node production (stem elongation)	Stage 8	Grain dough stage
Stage 4	Booting	Stage 9	Ripening

Source: Zadoks et al. (1974).

3. Morphological mechanisms

3.1. Leaf senescence

Senescence of leaf is a physiological process which is responsible for chlorophyll destruction and nutrients remobilization to younger and reproductive plant parts (Vijayalakshmi et al., 2010). Premature induction of leaf senescence often occurs by heat stress which therefore causes massive yield losses through inefficient resources recycling (Talukder et al., 2014; Hosseini et al., 2016). Heat stress changes the structure of leaf and sometimes produces thinner leaves by increasing the leaf area (Poorter et al., 2009). The metabolisms of leaf particularly CO_2 assimilation decreases during leaf senescence when catabolism is enhanced by chloroplast degradation, decrease in photosynthetic capacity and deterioration of macromolecular materials (Lira et al., 2017). In many studies, it has been shown that leaf yellowing or leaf chlorosis is one of the earliest symptoms of premature leaf senescence which is caused by heat–induced chlorophyll degradation or heat inhibited chlorophyll *b*iosynthesis (Robson et al., 2013; Bergkamp et al., 2018). Particularly, the term 'stay-green,' that means the maintenance of photosynthetic capacity and leaf chlorophyll is believed as an indicator of heat tolerance (Thomas and Howarth, 2000; Sakuraba et al., 2014). This stay-green character has been technically used in breeding line selection by visual assessment since many years (Thomas and Ougham, 2014). Under eminent temperatures, stay-green genotypes should have better ability in maintaining grain filling because less assimilation of current carbon into grains is occurred by the loss of chlorophyll. It has been found that for the increment of productivity, stay-green phenotype is very effective (Pinto et al., 2016). Delayed leaf senescence in wheat helps to achieve higher seed weight and grain yield (Borrell et al., 2014). Leaf senescence can be delayed by applying 3-cyclopropyl-1-enyl-propanoic acid sodium salt (CPAS) which acts as an antagonist against ethylene, helps to improve the grain yield of wheat under heat stress (Huberman et al., 2014). Delayed leaf senescence development in wheat can also be accelerated through molecular marker assisted selection (Yang et al., 2017).

There are three major phases of leaf senescence- initiation, re-organization and terminal phase (Holland et al., 2016). The re-organization phase of leaf senescence is characterized by major alterations in cellular metabolism which is accelerated by declining cytokinins (CK), enhancing Abscisic acid (ABA) and ROS levels (Sarwat et al., 2013). ABA and CK are involved in controlling heat-induced senescence in wheat particularly plant senescence and C remobilization are enhanced by high level of ABA which accelerate grain-filling rate (Jan et al., 2019). Early genotypes having an efficient remobilization capacity of the stem carbohydrate reserves can be considered more valuable under late heat stress (Abdelrahman et al., 2020). Macronutrient mobilization enhanced within grains from senescing leaves with the increase in ABA levels under heat and drought stress (Thomas, 2013). On the other hand, CK have a potential function in controlling source to sink reallocation (Yu et al., 2015). An inverse

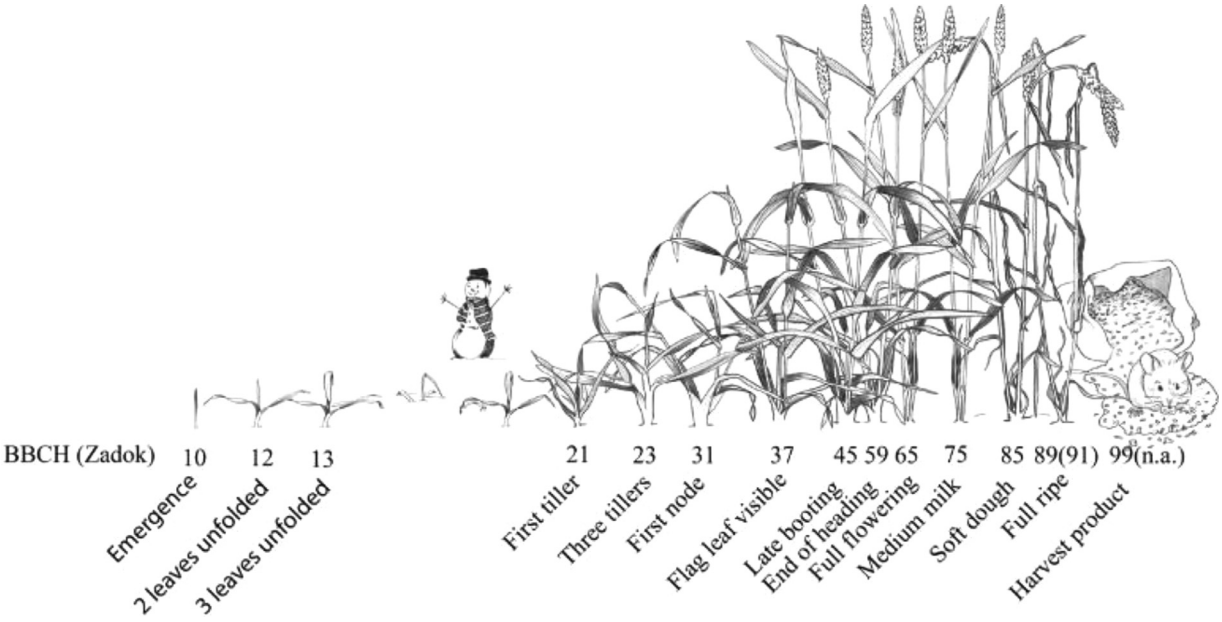


Fig. 2. Critical stages of wheat according to BBCH scale (Source: Lancashire et al., 1991).

association with photosynthetic rate and pigment content is exhibited by decreased levels of CK (Sami et al., 2016). Tolerant plants can expose augmented anti-oxidative defense with the translocation of nutrients from senescing to young leaves, until plants thrive under stress conditions and resume their normal growth (Have et al., 2017).

3.2. Grain filling duration and grain yield

Under heat stress, one of the most critical aspects for the improvement of wheat is maintaining high grain yield (Aziz et al., 2018). Wheat genotypes that may able to produce high and stable yield under heat stress can be used as a donor parent in wheat breeding program for heat tolerance (Al-Otayk, 2010). The facts those are directly involved in the decrease of wheat grain yield by heat stress are reduction in photosynthetic capacity of plant (Wahid et al., 2007), reduction of metabolic processes (Farooq et al., 2011), enhancement of oxidative damage through reactive oxidative species (ROS) production (Wang et al., 2011), reduction in the development of pollen tube, sterility of pollen (Saini et al., 2010), abortion of grain by ethylene production (Hays et al., 2007) and oxidative damage chloroplast. Crop establishment and floral fertility are adversely affected if pre-anthesis period faces heat stress (Al-Ajlouni et al., 2016).

Reproductive phase of wheat is highly sensitive to heat stress (Dwivedi et al., 2017) and in maximum wheat growing region, the grain filling period faces the highest temperature that affects the process of grain filling (Singh et al., 2011; Pradhan and Prasad, 2015). Kernel number and weight and quality of wheat grain are found to be considerably affected by heat stress (Mohammadi et al., 2012; Hutsch et al., 2019). Grain yield declines significantly due to the exposure of anthesis and grain filling period to heat stress (Stratonovitch and Semenov, 2015). There are also many other experimental evidences which show that there is a correlation between heat stress during flowering and reduction in the number and weight (Zhang et al., 2018) of grain along with significant negative effect on grain yield (Barnabas et al., 2008). Yin et al., 2009 observed a reduction in the grain filling duration by 12 days, increase in grain filling rate and reduction of seed size in wheat for each 5 °C temperature increase after 20 °C. Although he didn't find increase in grain filling rate over 30 °C temperature. Talukder et al. (2013) found 10 to 26% percent reduction in individual grain size and 11–23% reduction in grain number by exposing wheat genotypes to a short term heat stress like single-day heat event (maximum 35 °C temperature) under controlled environment (CE).

Heat stress reduces the maturity period as well as the grain filling duration of wheat up to 15% (Ahamed et al., 2010). In summer season, early maturation with lesser yield loss exhibits possible involvement in heat stress tolerance (Adams et al., 2001). So, the genotypes of wheat that mature earlier and provide a minimum yield loss comparing to control condition can be considered as truly compatible to escape heat stress injury (Menshawy, 2007).

4. Physiological mechanisms

4.1. Canopy temperature depression (CTD)

The term CTD describes the deviation of canopy temperature from ambient temperature (Deva et al., 2020). Canopy temperature depression (CTD) can be used as a good indicator of a genotype's fitness under heat stress (Urban et al., 2018). CTD plays an important role in sustaining physiological basis of grain yield of wheat after exposing to heat stress. During grain filling period, cool canopy acts as a significant physiological principle for heat stress tolerance in wheat (Munjal et al., 2003). CTD functions based on a number of environmental factors especially air temperature, relative humidity, soil water status and incident radiation (Fig. 3). CTD is best evolved at high vapor pressure deficit (VPD) conditions that is associated with warm air temperature and low relative humidity (Medina et al., 2019). Vapor pressure deficit (VPD) is a combined function of air temperature and relative humidity and changes in VPD regulates the transpiration rate of the plant (Belko et al., 2013). Heat tolerant varieties show greater stomatal conductance and a better association between VPD and leaf cooling (Kholova et al., 2012). On the other hand, in case of combined effect by heat and drought stress- proper root growth, increase in root hydraulic conductivity, reduction in stomatal conductance and leaf expansion are maintained by Abscisic acid (ABA) biosynthesis that increases thermotolerance of photosystem II (Urban et al., 2018). In response to changes in VPD, the heat tolerant wheat genotypes cool more than the heat sensitive genotype because of enhanced transpirational cooling (Deva et al., 2020). A stronger association between VPD and leaf cooling helps in maintaining higher leaf water content under heat stress conditions which allows a greater transpirational response to VPD and enhances the transpirational cooling (Omae et al., 2012). This is also facilitated by an increase in the density and diameter of vascular tissues like xylem vessels or tracheids that better continues the upward flow of water for enhancing transpirational cooling under heat stress (Qaderi et al., 2019).

Assessment of CTD has allowed the breeders to explore the yield stability of wheat as it is correlated with many adaptive physiological traits (Saxena et al., 2014). In different varieties with comparatively cooler canopy, there is a positive correlation of CTD with root traits (Man et al., 2016), leaf area index (Othmani et al., 2015), stomatal conductance (Reynolds et al., 2005), water usage (Reynolds et al., 2005), transpiration rate (Gautam et al., 2015), and grain yield (Olivares et al., 2007). Total chlorophyll content and CTD may play an important role in recognizing heat tolerant genotypes of wheat (Saxena et al., 2014). Greater CTD has been found in heat tolerant wheat genotypes as compared to sensitive genotypes which is caused by better photosynthetic enzyme activity (Wanjura et al., 1995) and greater leaf conductance (Hatfield et al., 1987). Under heat stress condition, it is estimated that around seven to nine percent gain in yield can be achieved by canopy temperature depression and remobilization of stem carbohydrates (Reynolds et al., 2007). So, high CTD is associated with the rise in yield (Fischer et al., 1998) and can be utilized as a selection criterion for the improvement of heat tolerance in wheat (Balota et al., 2007).

4.2. Photosynthesis

Photosynthesis is adversely affected by high temperature in various ways (Shah and Paulsen, 2003). According to Hemantaranjan et al. (2014) there is a link between thermotolerance increase of photosynthetic apparatus and heat stress protection mechanism. The most unstable cell components under heat stress are thylakoid membranes and Photosystem II (PSII) (Ristic et al., 2007). Thermal damage of PSII is caused by heat stress through affecting ATP synthesis and photosynthetic electron transfer (Akter et al., 2017; Jat et al., 2018). Increasing leakiness, swelling, disruption of PSII-mediated electron transfer, physical separation of the chlorophyll light harvesting complex II from the PSII core complex and damaged chloroplast structure (Brestic et al., 2016; Chen et al., 2017) are occurred in thylakoid membranes under high temperature (Ristic et al., 2008). This heat stress-induced injuries cause alterations of photochemical reactions in thylakoid membranes leading to a significant reduction in the ratio of variable fluorescence to maximum fluorescence (Fv / Fm) (Wahid et al., 2007). Heat stress causes oxidative stress in plants that leads to oxygen evolving complex (OEC) dissociation in PSII, which also inhibits transportation of electron from OEC to the acceptor side of PSII (Allakhverdiev et al., 2008). Heat stress disrupts OEC of PSII in the stroma of chloroplast as well as causes dysfunction in the carbon assimilation metabolism of Calvin cycle. There are many evidences supporting that primary reduction

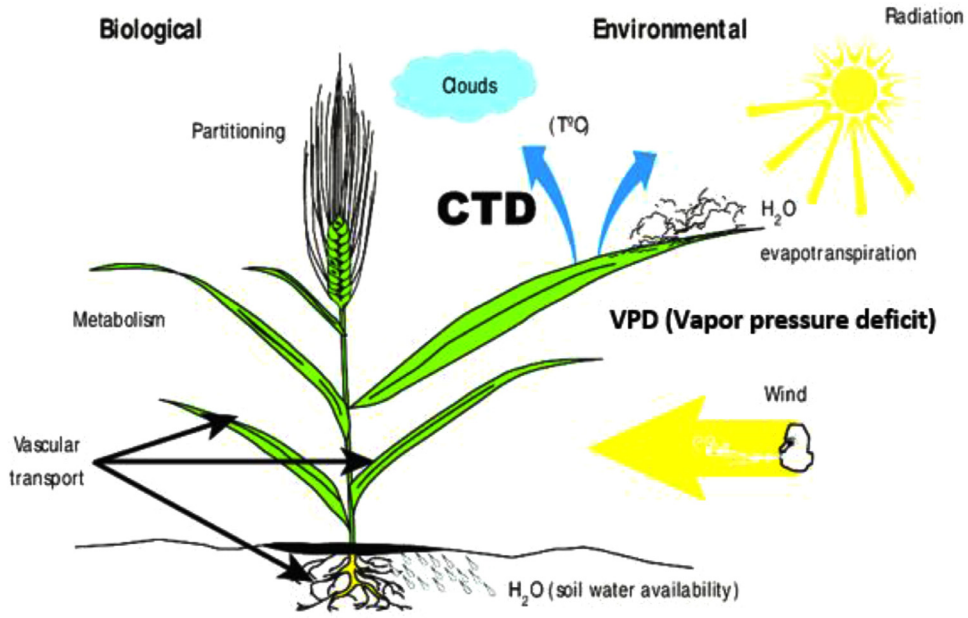


Fig. 3. Factors those affect canopy temperature depression under heat stress (Source: Reynolds et al., 2001b).

in photosynthesis occurred by the reduced activity of Rubisco in RuBP (Ribulose-1, 5-bisphosphate) carboxylation (addition of CO_2 with RuBP) due to the failure in RCA (Rubiscoactivase) enzyme activation (Fig. 3) (Perdomo et al., 2017). RCA activates Rubisco and helps in RuBP carboxylation which is essential for running the Calvin cycle under normal condition. High temperature stimulates the Rubisco activity inhibitor synthesis like XuBP (xylulose-1, 5-bisphosphate) that binds at the catalytic site of Rubisco and block this site. (Parry et al., 2008). Rubisco activase enzyme removes the tightly bound inhibitors from the catalytic site of Rubisco. Under heat stress, a stable RCA structure and maintenance of Rubisco activity can ensure the regular running of Calvin cycle (Wang et al., 2010; Chen et al., 2015). During day time when the stomata closure is a limiting factor, it is necessary to possess thermostable RCA in order to support the metabolic flux of Calvin-Benson-Bassham cycle under heat stress (Shivhare and Mueller, 2017).

Loss of organic matter and product of photosynthesis leads to reactive oxygen species (ROS) production and oxidative damage (Fig. 4) (Mathur et al., 2014). The production and accumulation of ROS is triggered by heat stress (Almeselmani et al., 2009). In Photosystem II, ROS produced by lipid peroxidation causes damage to D1 protein (Pospisil et al., 2017). A family of serine-type ATP-independent proteases is involved in the deterioration of Photosystem II reaction center protein D1 (Jarvi et al., 2015; Cheregi et al., 2016). Photo inhibition of PSII under heat stress can be mitigated by maintaining ROS at limited level (Martins et al., 2016). Therefore, it is important to protect the plant from heat stress by the detoxification of ROS through antioxidant defense systems (Suzuki and Mittler, 2006). Heat tolerant plants tend to synthesize various ROS scavenging and detoxification systems to create protection against the damaging effects of ROS (Apel and Hirt, 2004). Thermotolerance can be induced by maintaining enhanced membrane thermostability and low level of ROS accumulation (Hameed et al., 2012) by improving antioxidant capacity (Chakraborty and Pradhan, 2011). Impairment in the photosynthetic apparatus was found to be more severe in heat-sensitive cultivars comparing to heat-tolerant cultivars because of high level of ROS and malondialdehyde (MDA) accumulation (Zou et al., 2017).

Besides antioxidant defense systems, plants use some other mechanisms to protect the photosystems such as cyclic electron flow (CEF), alternative oxidase (AOX) pathway, oxidative electron transport and mitochondrial reactions of photorespiration (Sunil et al., 2019). CEF, AOX and photorespiration activities are crucial among these mechanisms (Hodges et al., 2016). Photorespiration can dissolve excess ROS both directly and indirectly (Voss et al., 2013). The photorespiration reactions can serve as direct sinks for ATP, NADPH and reduced ferredoxin those are generated photosynthetically (Araujo et al., 2014). In direct way, the peroxisomal catalase scavenge H_2O_2 and CEF optimization, promotion of AOX pathway and CO_2 release from glycine decarboxylation for intracellular recycling are the indirect ways to protect photosystem (Ziotti et al., 2019). Additionally, photorespiratory metabolism generates glycine as a source for glutathione which acts as a major antioxidant in plant cells (Hodges et al., 2016).

4.3. Chlorophyll content

Chlorophyll content is a stay-green trait and associated with heat tolerance in wheat (Feng et al., 2014; Cao et al., 2015). Wheat biomass and yield are also regulated by chlorophyll content under heat stress (Tattaris et al., 2016). High chlorophyll content can be utilized as a selection criterion for heat stress tolerance in wheat (Ramya et al., 2015; Munjal and Dhanda, 2016). High chlorophyll content under heat stress conveys low degree of photo inhibition, as a result it is considered as a desirable trait for heat tolerance in wheat (Talebi, 2011; Choudhary et al., 2020). Chlorophyll content can be involved in the mechanism of heat tolerance by being associated with transpiration efficiency (Reynolds and Trethowan, 2007). At high light intensity and high temperature when water stress is absent, increased stomatal conductance induces the transpiration rate as well as light absorption by chlorophyll in order to keep the transpirational cooling and photosynthetic activity stable respectively (Morales et al., 2020). A significant positive relationship has been found between leaf chlorophyll content and transpiration efficiency in heat tolerant genotypes (Sheshshayee et al., 2006). Yield is associated with photosynthesis rate and leaf chlorophyll content during grain filling period (Reynolds and Trethowan, 2007). The loss of chlorophyll in leaves occurs due to rapid breakdown of chlorophyll under heat stress (Jespersen et al., 2016). Breakdown of chlorophyll occurs when photosynthetic mechanisms undergo complete destruction under heat stress. Declining in chlorophyll content causes a

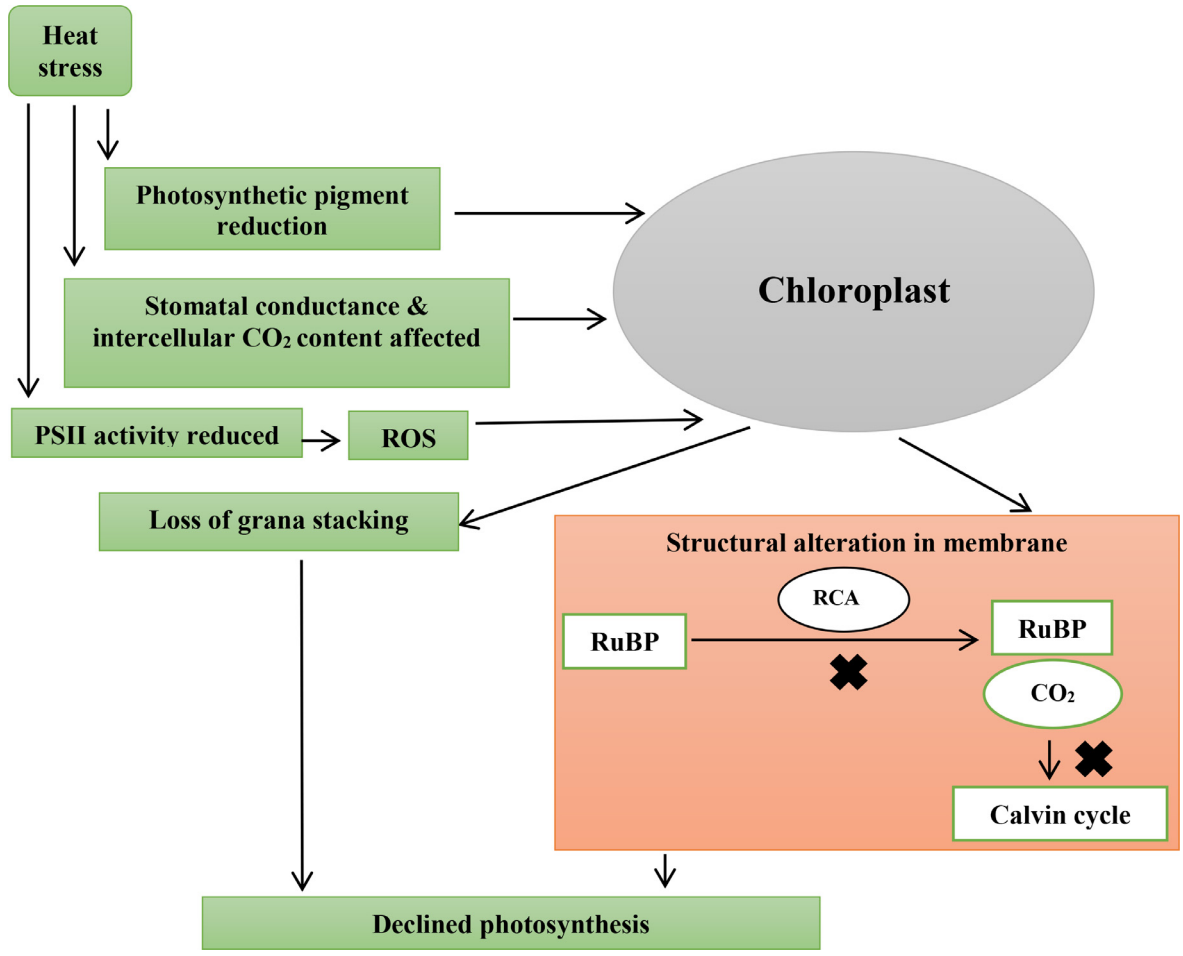


Fig. 4. Photosynthetic response in wheat under heat stress (Source: Wang et al., 2018; Salvucci and Crafts, 2004).

typical symptom in wheat called chlorosis (Rossi et al., 2017). Numerous enzymes that involve in the chlorophyll *b*iosynthesis mechanism are degraded under high-temperature resulting the inhibition of chlorophyll *b*iosynthesis (Reda and Mandoura, 2011).

High temperature firstly affects plastid particularly chloroplast that causes the impairment and reduction of chlorophyll *b*iosynthesis (Dutta et al., 2009; Li et al., 2010; Reda and Mandoura, 2011). It has been shown in previous studies that chloroplast plays a significant role in the activation of signaling of the cellular stimuli under heat stress (Yuan et al., 2015). Chloroplasts helps to induce the expression of nuclear heat-response genes. Heat stress response in the nuclear is required translation of chloroplast protein to stimulate retrograde signaling (Yang and Guo, 2014). Retrograde signaling can be defined as a communication pathway where the nuclear transcriptional activities are regulated in part by signals that are derived from plastids and mitochondria. According to previous studies, in retrograde signaling- two categories can be largely classified including developmental control of organelle biogenesis, and operational control to acclimate to environmental stresses (Sun and Guo, 2016). Chloroplasts act as a specialized sensor of intra- and extracellular stimuli and combines a variety of intracellular signals and pathways for sustaining homeostasis both at cellular and organismal levels (Pogson et al., 2008). A thorough studies aiming on the initiation of transcriptional changes in the nucleus and signaling cascades in the chloroplast may help to understand the chloroplast-nuclear signaling as a response to environmental stimuli (Schmidt et al., 2019). Various genes and proteins are stimulated and regulated to help and protect chloroplast for normal functioning and improving heat tolerance of plants (Hu et al., 2020).

4.4. Photoassimilate translocation

The transport and transfer processes of plant are greatly affected by the symplastic and apoplastic translocation of assimilate under high temperatures (Taiz and Zeiger, 2006). Three major elements of the plant system namely source (flag leaf blade), sink (spike), and transport pathway (peduncle) were examined to clarify about the agents responsible for reducing grain filling under high temperatures in wheat (Thakur et al., 2010). Around 90 to 95% of carbon needed for grain filling is achieved from current carbon assimilation under ideal conditions (Kobata et al., 1992). However under heat stress, changes were found in the pre-anthesis stored reserves and current assimilation contribution (Wang et al., 2011). Heat stress reduces the translocation of assimilates from the photosynthetic source provoking the remobilization of variant source like stem reserves for grain filling (Aslam et al., 2013). Under heat stress, the need of stem reserves is highly increased from the range of 6 to 100% based on the heat-incited decrement in photosynthesis (Blum, 1998). An effective heat tolerance mechanism in wheat is enhancing the mobilization of stem reserves (Bala and Sikder, 2017). Water soluble carbohydrates (WSC) reserves are reduced in wheat stem and remobilization of these carbohydrates plays a significant role in improving grain yield against heat stress (Gupta et al., 2011). During wheat grain filling WSC can be a major source of carbon as both the photosynthesis and respiration are reduced by heat stress (Wang et al., 2012). When the temperature rises above 30 °C, the translocation of assimilate from flag leaf to grain is reduced remarkably whereas there is no impact of temperature (1 to 50 °C) on assimilates translocation from the stem. This phenomenon concludes that, although the rate of the transportation of

assimilate from vegetative parts to grain in wheat is reduced by heat stress, the impact on assimilate translocation by heat stress is indirect (Plaut et al., 2004). Therefore, it can be suggested that leaves, stem or other plant parts reserves can be used as an efficient contrivance by increasing their solidarity to improve grain filling and yield in wheat under heat stress.

4.5. Membrane thermostability

Membrane thermostability (MTS) is a significant physiological mechanism for heat tolerance which helps plants to adapt in high ambient temperatures (Barma et al., 2011). The tertiary and quaternary structures of membrane proteins are altered by heat stress. This type of alteration enhances the loss of electrolytes, as a result decreasing membrane thermostability. The kinetic energy is accelerated by heat stress and it makes the molecules movable along membranes by detaching the chemical bonds into molecules of biological membranes. Thus, the lipid bilayers of the membranes become more fluid due to proteins denaturation or unsaturated fatty acids increase (Savchenko et al., 2002; Higashi and Saito, 2019). The efflux of released electrolytes into surrounding solution from the affected cells or leaf tissue can be used to measure cell membrane damage caused by heat stress (AHN and Zimmerman, 2006; Choudhary et al., 2020). The membrane thermostability (MTS) can be evaluated using this formula: $MTS = (1 - T1/T2) \times 100$, here $T1$ is reading of conductivity after heat treatment and $T2$ is reading of conductivity after autoclaving (Ibrahim and Quick, 2001).

The increase in solute leakage is suggested as an indicator of decrease in cell membrane thermostability that can be used as an indirect measure of heat-stress tolerance in wheat (Ram et al., 2014; Bala and Sikder, 2017). Membrane systems which remain functional during heat stress lead to the adaptation of plants to high temperature (Blum, 1988). Thus, the tolerance to heat stress is determined by the efficiency of plant in maintaining the integrity and function of membrane (Almeselmani et al., 2011). After exposing plant to prehardening treatment, it is recommended to assess cell membrane stability for estimating cellular thermotolerance of plants (Ibrahim and Quick, 2001). If grain filling occurred under stress conditions, then the wheat lines with high membrane thermostability attend better yield as compared to the lines with low membrane thermal stability (Khatoon et al., 2016). In wheat, cell membrane thermostability provides as a fair index of genetic variation and shows a liable relationship to the performance of plant under heat stress and may consider as an important selection criterion for heat tolerance (Behle et al., 1993).

5. Biochemical mechanisms

5.1. Starch synthesis

In wheat, 55–75% of total grain dry weight is occupied by a major component which is starch (Gillies et al., 2012). During grain filling period, two types (A and B type) of starch granules are derived in wheat grain (Zheng et al., 2014). Wheat starch contains amylase and amylopectin which are being synthesized in the amyloplast (Li et al., 2018). Starch is more vulnerable to heat stress comparing to protein (Farooq et al., 2011) because the amylopectin of starch readily decreases under high temperature which leads to a reduction in starch content (Liu et al., 2011). Starch synthesis is remarkably disturbed by reduction in the activities of sucrose phosphate synthase (Chaitanya et al., 2001), ADP glucose pyrophosphorylase and invertase (Vu et al., 2001). A study has shown that the impact of heat stress on the starch quality of bread wheat could be extreme (Labuschagne et al., 2009). The starch content of wheat grain reduces at a critical level under heat stress that results into the reduction of kernel weight and diameter (Poudel and Poudel, 2020). Heat stress significantly affects the starch content during grain development of wheat resulting in poor grain quality, grain size and yield (Chinnusamy and Khanna-Chopra, 2003). The duration needed for starch biosynthesis and grain filling is reduced if the temperatures increase over 18–22 °C (Spiertz et al., 2006). There are three enzymes that limit starch biosynthesis in wheat namely soluble starch synthase (SSS), sucrose synthase and granule bound starch synthase (Hawker and Jenner, 1993). Starch synthesis rate is determined by sucrose synthase (Hawker and Jenner, 1993), on the other hand the amylose biosynthesis is controlled by granule-bound starch synthase (Morell et al., 2001). Starch synthesis is regulated by SSS (soluble starch synthase) which is mostly sensitive to heat stress (Keeling et al., 1993). SSS activity is deteriorated in wheat by heat stress which causes declining in grain growth and starch accumulation (Prakash et al., 2004). Recent observations suggest that the soluble starch synthase enzyme can be an important indicator for the improvement of heat stress tolerance as high temperature tolerance for grain growth in wheat is closely associated with the catalytic efficiency of this enzyme (Tian et al., 2018).

5.2. Antioxidant response

It has been indicated in several studies that under heat stress, damage to membrane is increased and level of antioxidants is decreased in wheat at the stages of seedling (Yogita et al., 2015), anthesis (Narayanan et al., 2015) and grain filling period (Balla et al., 2013). Plants are able to survive under heat stress if they can be protected from heat-induced oxidative stress. ROS singlet oxygen, superoxide radicals and hydrogen peroxide reactions are among usual events in cell under heat stress. To avoid cell damage by these reactions, plants initiate antioxidants defense system (Suzuki et al., 2014). Different types of antioxidants from variable pathways are accumulated in plants under heat stress (Bokszczanin and Fragkostefanakis, 2013). There are mainly two types of defense system of antioxidants found in wheat enzymatic and non-enzymatic (Sattar et al., 2020). Catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione-S-transferase (GST), superoxide dismutase (SOD), guaiacol peroxidase (GPX) and glutathione reductase (GR) are the enzymatic antioxidant system (Noctor and Foyer, 1998) whereas ascorbate (AsA), glutathione (GHS) and tocopherols are non-enzymatic antioxidant systems. SOD is one of the major antioxidants that helps to convert superoxide into H_2O_2. On the other hand, detoxification of ROS is governed by APX, GPX and CAT (Buttar et al., 2020). To detoxify H_2O_2, APX requires AsA and reduced glutathione (GSH) that are produced via AsA-glutathione cycle to convert H_2O_2 into H_2O with the help of AsA oxidation into monodehydroascorbate (MDHA) which again dismutate to dehydroascorbate (DHA) (Fig. 5) (Asthir, 2015). Catalase, ascorbate peroxidase, and superoxide dismutase activities extenuated at 50 °C but before reaching at this temperature, these enzymes activities are initially increased (Chakrabortty and Pradhan, 2011) whereas peroxidase (POX) and glutathione reductase activities are decreased at a temperatures range from 20 to 50 °C. In tolerant wheat varieties total antioxidant activity was highest at 35–40 °C and in the case of susceptible varieties highest antioxidant activities was shown at 30 °C (Chakrabortty and Pradhan, 2011). Activities of these enzymes are also varied with the growth stages and growing season of wheat (Chakraborty and Pradhan, 2011). Enzymatic antioxidants were considerably increased at the reproductive phase of heat tolerant genotypes of wheat when subjected to heat stress (Balla et al., 2009). Catalase and superoxide dismutase activities have the competence to attain thermotolerance in wheat (Almeselmani et al., 2009) as well as a strong correlation with heat stress at the reproductive phase (Zhao et al., 2007). Heat stress tolerance wheat varieties demonstrate enhanced GST, APX

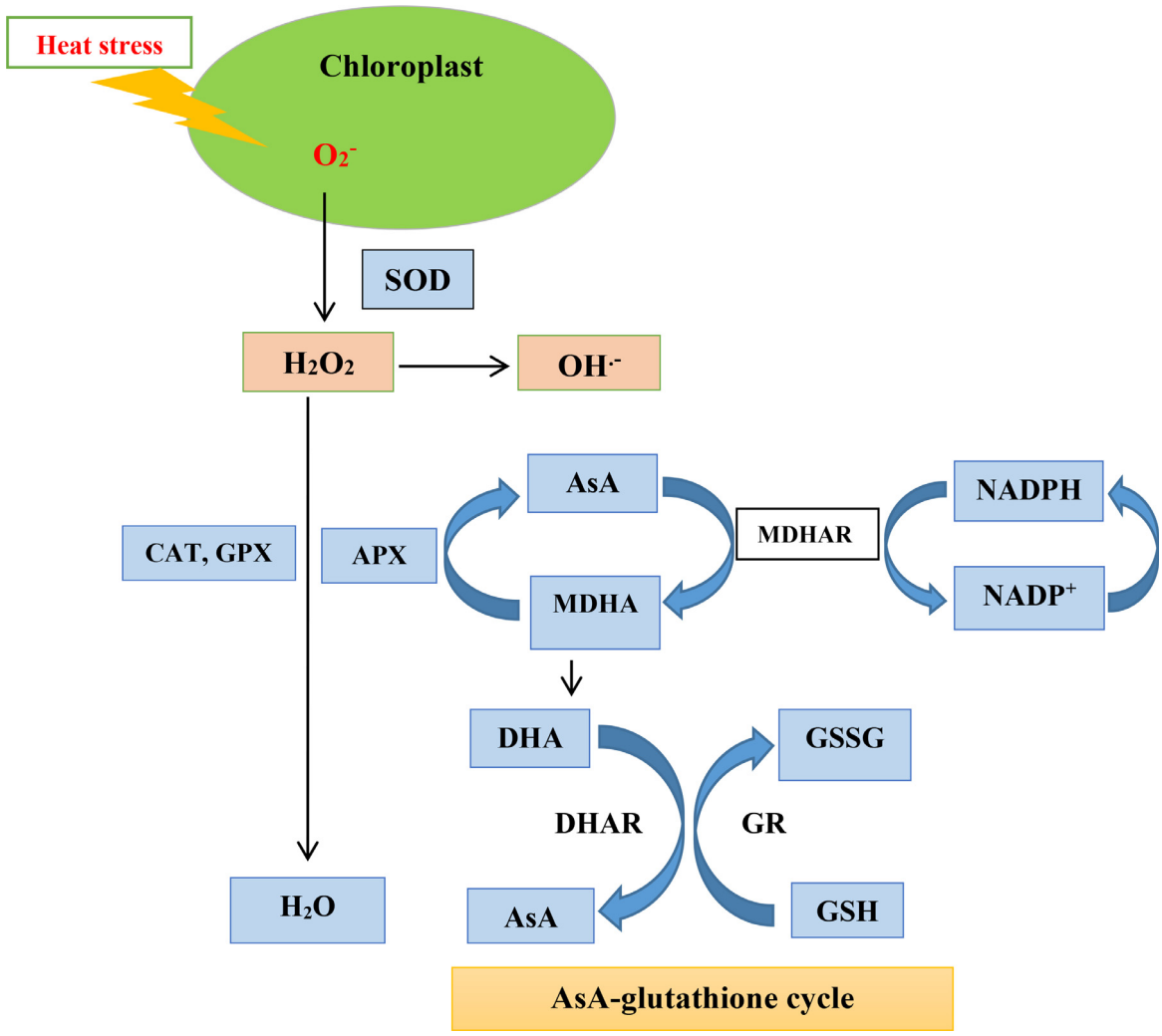


Fig. 5. Antioxidants defense system in wheat under heat stress (Source: Wang et al., 2018); Superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), ascorbate (AsA), monodehydroascorbate reductase (MDHAR), monodehydroascorbate (MDHA), dehydroascorbate reductase (DHAR), dehydroascorbate (DHA), glutathione reductase (GR), glutathione (GSH), glutathione disulfide (GSSG). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and CAT activities and protection against heat stress injuries (Ahmad and Prasad, 2011).

6. Molecular mechanism

6.1. Protein synthesis

Plant develops some defense mechanisms under heat stress such as expression of particular genes that only express under stress condition (Feder, 2006). These genes may be either Heat-Shock Proteins (HSPs) or Stress-Induced Proteins or Stress Proteins (Lindquist and Craig, 1988). Heat-Shock Proteins are a group of protein synthesized in wheat coleoptiles when exposed to heat stress (Blumenthal et al., 1990). To understand the role of HSPs in adaptation under heat stress, membranes associations must be considered because under heat stress about two third of the chloroplast HSPs are transferred to thylakoid membranes (Bernfur et al., 2017). In general, HSPs act as molecular chaperones and play a vital role in regulating the accumulation, folding, localization and degradation of proteins in plants (Gupta et al., 2010). At vegetative stage of wheat, proteins in ER (endoplasmic reticulum) and cytosol found to become unfolded via ROS (reactive oxygen species) regulatory mechanisms under heat stress (Sun and Guo, 2016; Kataoka et al., 2017). However, HSPs as chaperones inhibit other proteins from aggregating irreversibly by taking part in refolding of those proteins (Morrow and Tanguay, 2012) which hinders apoptosis or cell death (Fig. 6) (Altenbach et al., 2003). Under heat stress, heat shock genes are activated in wheat plant during grain filling period, generating more HSPs in the mature grains (Blumenthal et al., al.,1991) and producing weaker dough (Zhang et al., 2018). In many studies it has been suggested that plants develop thermotolerance by overexpression of HSPs (Grover et al., 2013). Various types of HSPs are developed in different tissues of wheat plant based on type and duration of heat stress (Xu et al., 2011). HSPs can be divided into five classes: HSP100, HSP90, HSP70, HSP60 and HSP20 (Swindell et al., 2007). An increase in ABA (abscisic acid) content in the embryo of wheat is accompanied with HSPs development during the period of grain filling and maturation (Xue et al., 2014).

Heat inducible genes regulation is contributed by heat shock factors (HSFs) as a process of acclimation in heat stress (Yabuta, 2016). The chloroplast protein synthesis elongation factor, EF-Tu (elongation factor thermo unstable) may avail to heat tolerance in wheat as it acts as a molecular chaperone and has the ability to protect chloroplast protein from thermal aggregation (Ristic et al., 2007). In a study by Djukic et al., 2019, 25% higher accumulation of chloroplast EF-Tu found under high temperature (38 °C) comparing to accumulation at

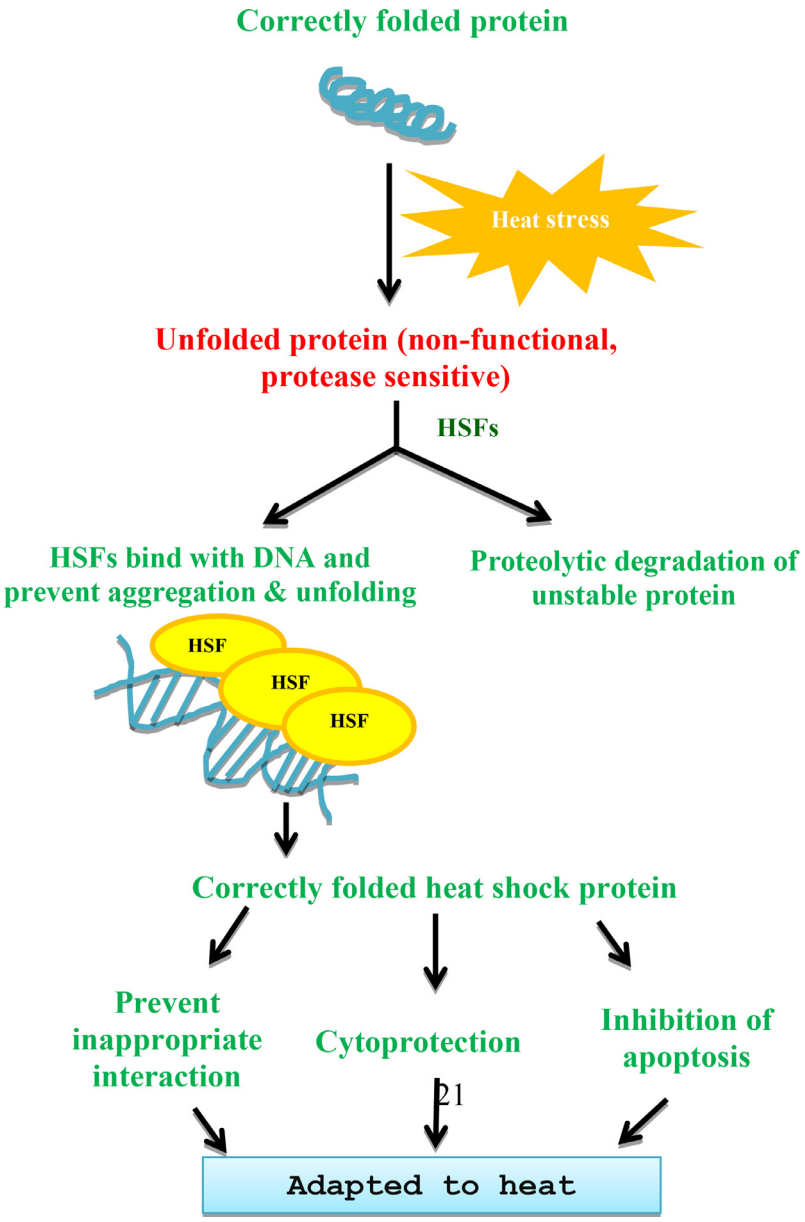


Fig. 6. Heat shock protein synthesis in wheat plant under heat stress (Source: Whitley et al., 1999).

a moderate temperature (23 °C) in a winter wheat cultivar named Zvezdana and this cultivar was better able to decrease protein aggregation under heat stress comparing to other cultivars. The accumulation of EF-Tu in mature plants induces by high temperature and the plants where EF-Tu are highly accumulated show more resistance to heat stress indicating the fact that EF-Tu may play a vital role in adapting plants to heat stress (Ristic et al., 2008).

6.2. Omics approaches

The large-scale studies of cellular processes and their genetic control over the entire genetic, structural and functional components are called omics. Genomics, transcriptomics, metabolomics and proteomics are the major components of omics (Fig. 7). Several heat stress tolerance genes containing genomic DNA is the initial site of all molecular approaches associated with heat stress tolerance in wheat plant (Deshmukh et al., 2014). Studies of genomic screen and genome expression have been used to identify the role of genes in heat tolerance of wheat (Yeh et al., 2012). Transcriptomes (Transcriptomics) are produced from mRNAs (transcript products) of heat tolerance genes and proteomes (proteomics) are produced when mRNAs of such genes are translated into functional proteins (responsible for heat stress tolerance). Plants reveal some post-transcriptional gene expression by small non-protein coding RNAs (also called microRNAs). Study of microRNAs and micromics helps in better understanding of the heat tolerance mechanisms in wheat (Chinnusamy et al., 2007).

Metabolomics are another omics approaches that can be utilized for phenotyping of genetically modified plants and considerable similarity testing, gene function determination and observing responses to biotic and abiotic stresses (Abdelrahman et al., 2020). Metabolomics studies can provide an indication of alteration in plant metabolites under heat stress (Roessner and Bowne, 2009). The ability of wheat grains to accumulate available assimilates that is related to metabolic activities of sink organs, plays an important role in controlling wheat grain yields under heat stress (Girousse et al., 2018; Hutsch et al., 2019). Under heat

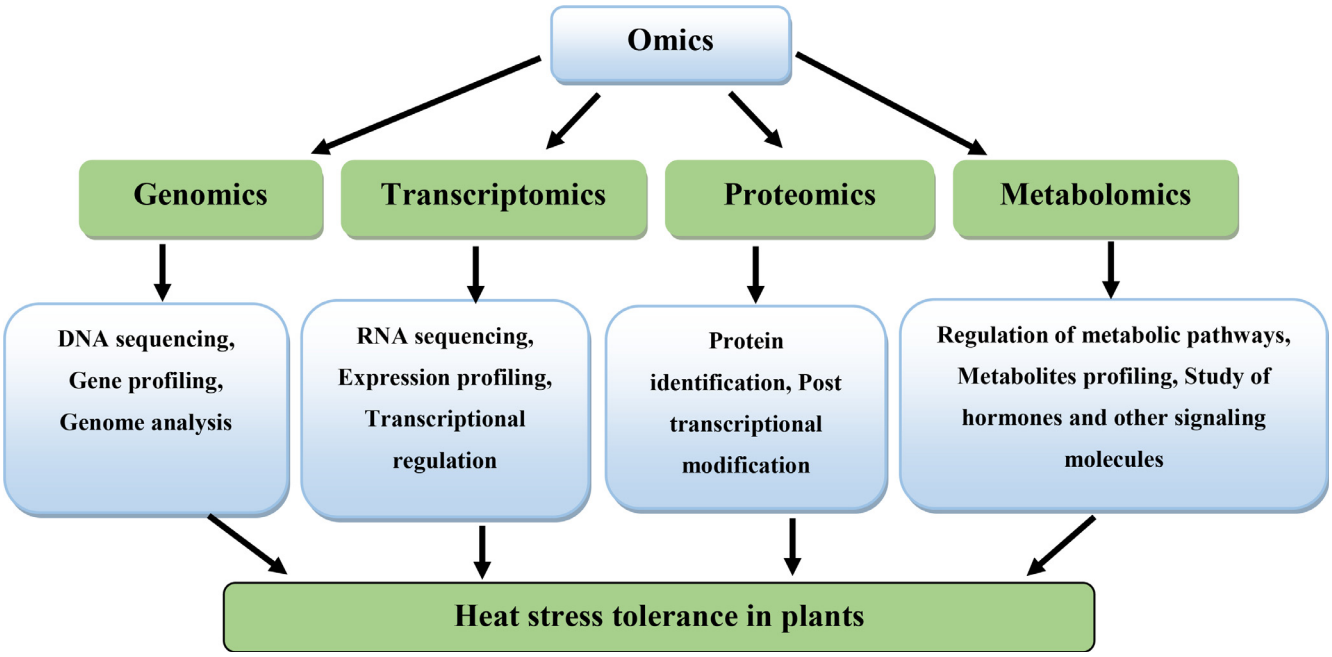


Fig. 7. Omics approaches for heat tolerance in wheat (Source: Hasanuzzaman et al., 2013).

stress, primary metabolites such as carbohydrates accumulation increases the protein stability and firmness of cell membrane bilayer structure (Sairam and Tyagi, 2004). Thus, approaches that accelerate the increase in soluble carbohydrates and the capacity of fatty acids synthesis that protect cell from damage can be suggested as a efficient protective mechanism against heat stress (Sardans et al., 2020).

7. Breeding for heat tolerance in wheat

7.1. Conventional breeding

In general, breeding programs are conducted within the region similar to where the crop is being grown. Therefore, selection of breeding lines for heat tolerance should be done under hot conditions (Mickelbart et al., 2015). In order to identifying superior genetic stock for progress in heat tolerance, it is a common approach to evaluate wheat genotypes for yield stability under heat stress throughout different locations (Mishra et al., 2014). Screening of genetic resources must be practiced to identify donor genotypes for heat tolerance. Recurrent selection has effectively exercised to improve grain filling rate and grain size in BC1F6 plants of wheat under heat stress using ancestor Triricum tauschii as a donor parent (Gororo et al., 2002). In southern Australia, selected F_2-derivedlines of backcross derivatives obtained from synthetic hexaploid wheats (T. turgidum / T. tauschii) were evaluated under heat stress condition. In F_6 generation, re-selection was carried out and further evaluation was done for high grain yield, yield components and grain growth characters under heat stress and T. tauschii found with exceptional capacity to improve wheat yield (Gororo et al., 2002).

7.2. Advanced breeding

Marker-assisted recurrent selection and genome-wide selection are among advanced breeding strategies that have been used to develop heat stress tolerant varieties. Adaptation to heat stress can be obtained through inter-specific genome diversity which is used as a source of heat tolerance genes. As heat tolerance is a polygenically controlled trait, identification of quantitative trait loci (QTL) helps to achieve the understanding of thermo-tolerance in wheat (Wahid et al., 2007). Different Quantitative trait loci (QTL) has been identified for different traits of wheat associated with drought or heat stress; combined dry and hot conditions (Table 3).

Low-density simple sequence repeat (SSR) markers and/or amplified fragment length polymorphism (AFLP) markers have been used in mapping Most of these reported QTL (Lu et al., 2020). GWAS (Genome-wide association studies), QTL mapping and GS (Genomic selection) have provided the basis for the development of different molecular markers like SNP (single nucleotide polymorphism), SSR (simple sequence repeat), NGS (next generation sequencing) etc. (Sonah et al., 2012; Cabral et al., 2018). QTL or GWAS can be combined with GS to maximize the breeding values which represent an estimate of the genomic merit correlated with all minor or major effects throughout the entire genome (Bassi et al., 2016). Genome wide analysis has been proved as a valuable method to identify heat stress responsive genes with the complexity of the underlying heat tolerance mechanisms (Wang et al., 2015). Recent advances in wheat gene transformation technology and transgenic study has accelerated the evolution in functional analysis of heat-responsive genes in wheat (Clavijo et al., 2017). The functions of some genes has been characterized by overexpression of these genes involved in sensing and responding to heat stress in wheat (Zang et al., 2017) (Table 4).

Beside these, a new breeding method named ‘speed breeding’ has been developed (Watson et al., 2018) to shorten the generation time which can be utilized to speed up the breeding program for heat tolerance in wheat. This speed breeding method can be used to get up to six generations of both bread wheat (Triticum aestivum) and durum wheat (Triticum durum) every year (Watson et al., 2018). In recent times, genome editing tools and resources like CRISPR-Cas9, TILLING etc. (Liang et al., 2017) are being used to improve wheat for heat tolerance. In spite of having such advances, the slow generation time may continue to impose a barrier toward developing heat tolerant wheat variety (Watson et al., 2018). Therefore, combination of these advance tools with speed breeding may provide the scientists an effective inducement to perform improvement research for heat tolerance in wheat.

Table 3
QTL found in wheat associated with drought or heat stress; combined dry and hot conditions.

Trait	Chromosome	References
Heat stress		
Grain yield	1A, 1BL, 1D, 2BS, 3A, 3BS, 3BL, 3D, 4A, 4B, 4DL, 5A, 5B, 6A, 6B, 6D, 7AS, 7AL, 7BS, 7BL	Merchuk-Ovnat et al. (2016); Ogbonnaya et al. (2017)
Rate of senescence	2A, 6A, 6B	Vijayalakshmi et al. (2010)
Thousand grain weight	1A, 2A, 2B, 2D, 3A, 3BS, 3D, 4A, 4B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7D	Tahmasebi et al. (2016)
Days to maturity	1B, 1D, 2A, 2B, 3B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B, 7DS	Ogbonnaya et al. (2017)
Canopy temperature depression	7BL	Paliwal et al. (2012)
Chlorophyll content	1A, 1B, 1D, 2B, 3A, 3BS, 4A, 4D, 5A, 5B, 6A, 6D, 7A, 7B, 7D	Tahmasebi et al. (2016)
F_v/F_m chlorophyll fluorescence	7A	Vijayalakshmi et al. (2010)
Grain filling duration	1B, 1D, 2A, 2B, 2D, 3BS, 5A, 6A, 6B, 6D	Shirdelmoghanloo et al. (2016); Ogbonnaya et al. (2017)
Number of grains	1A, 2A, 3B, 4A, 5B	Pinto et al. (2010)
Drought stress		
Grain yield	2D, 3D, 3DL, 4AL, 4BS, 4DL, 5A, 5B, 5DL, 6B, 6D, 7AL, 7BL, 7D	Kadam et al. (2012); Tahmasebi et al. (2016)
Thousand grain weight	1B, 1D, 2A, 2B, 3A, 3D, 4A, 4D, 5A, 6A, 6D, 7A, 7B	Xu et al. (2017)
Flag leaf rolling	4B, 5A	Tahmasebi et al. (2016)
Root length	2D, 4B, 5D, 6B	Kadam et al. (2012)
Stomatal conductance	5A	Xu et al. (2017)
Chlorophyll content	1B, 2B, 5B, 7A, 7B	Tahmasebi et al. (2016); Xu et al. (2017)
Transpiration rate	3Al, 4BL, 6D	Parent et al. (2015); Xu et al. (2017)
Water use efficiency	2AL, 4D	Parent et al. (2015); Xu et al. (2017)
Combined dry and hot conditions		
Grain yield	1AL, 1B, 1D, 2A, 2BL, 3A, 3B, 4AL, 4B, 5A, 6A, 6B, 7A, 7B, 7D	Merchuk-Ovnat et al. (2016); Tahmasebi et al. (2016)
Thousand grain weight	1D, 2B, 3A, 3B, 4A, 6A, 7A, 7B, 7D	Bennett et al. (2012); Tahmasebi et al. (2016)
Biomass	2BS, 4AL, 4B, 5A, 7AS	Tahmasebi et al. (2016)
Canopy temperature depression	1A, 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, 7B	Diab et al. (2008)
Chlorophyll content	1A, 1B, 3A, 4A, 4B, 4D, 5A, 5B, 6A, 6B, 7A	Bennett et al. (2012)
Grain filling duration	4AL	Kirigwi et al. (2007)
Days to maturity	1A, 1D,5A, 7B, 7D	Tahmasebi et al. (2016)
Stomatal density	4AS, 5AS, 7AL	Shahinnia et al. (2016)

Source: Farooq et al., 2011; Tricker et al. (2018).

Table 4
Genes identified to function in heat tolerance through transgenic studies.

Gene	Trans- host	Source	Function	References
TaHsfA6f	T. aestivum	T. aestivum	Transgenic plants overexpressing TaHsfA6f showed improved thermotolerance	Xue et al. (2015)
TaHsfC2a	T. aestivum	T. aestivum	Improved thermotolerance	Hu et al. (2018)
TaFER-5B	T. aestivum	T. aestivum	Transgenic plants exhibited enhanced thermotolerance	Zang et al. (2017)
TaGASR1	T. aestivum	T. aestivum	Enhanced tolerance to oxidative stress	Zhang et al. (2017)
Sucrose transporter gene HvSUT1	T. aestivum	Hordeum vulgare	Sucrose transport enhancement and a superior performance for many yield-related traits	Weichert et al. (2017)
EF-Tu	T. aestivum	Zea mays	Improved thermotolerance	Fu et al. (2008)
TamiR159	Oryza sativa	T. aestivum	TamiR159 overexpressing plants were more sensitive to heat stress relative to the wild type	Wang et al. (2012)
TaMBF1c	Oryza sativa	T. aestivum	Overexpress TaMBF1c showed higher thermotolerance than control plants at both seedling and reproductive stages	Qin et al. (2015)

Source: Ni et al. (2018); Janni et al. (2020).

8. Conclusion

Heat stress is one of the major concerns for wheat production in the world. To develop thermotolerant and high yielding wheat varieties, we first should systematically understand different metabolic and developmental mechanisms of plant associated with heat stress. This review paper briefly explains different aspects of heat stress and various morpho-physiological, biochemical and molecular basis of heat tolerance which is required for the improvement of wheat yield under the upcoming warmer environment. It is well established that molecular study may confirm increasing economic crop yield, but full potential yield expression of wheat under heat stress must be estimated at field level. Different agronomic options along with biochemical and molecular approaches required to combine for exploring the actual effect of heat stress at field level. Finally, collaborative efforts from plant physiologist, molecular biologist and breeder would contribute to the success of developing heat tolerant wheat varieties.

Declaration of Competing Interest

The author(s) declare(s) that there is no conflict of interest regarding the publication of this paper.

Consent for publication

All co-authors has consent for submission of manuscript.

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References

Abdelrahman, M., Burritt, D.J., Gupta, A., Tsujimoto, H., Tran, L.S.P., 2020. Heat stress effects on source–sink relationships and metabolome dynamics in wheat. Journal of Experimental Botany 71 (2), 543–554.

Adams, S.R., Cockshull, K.E., Cave, C.R.J., 2001. Effect of temperature on the growth and development of tomato fruits. Annals of Botany 88 (5), 869–877.

Ahamed, K.U., Nahar, K., Fujita, M., 2010. Sowing date mediated heat stress affects the leaf growth and dry matter partitioning in some spring wheat (Triticum aestivum L.) cultivars. The Institute of Integrative Omics and Applied Biotechnology Journal 1 (3), 1–9.

Ahmad, P., Prasad, M.N.V, 2011. Environmental Adaptations and Stress Tolerance of Plants in the Era of Climate Change. Springer Science & Business Media.

AHN, Y.J., Zimmerman, J.L., 2006. Introduction of the carrot HSP17. 7 into potato (Solanum tuberosum L.) enhances cellular membrane stability and tuberization in vitro. Plant, Cell & Environment 29 (1), 95–104.

Akter, N., Islam, M.R., 2017. Heat stress effects and management in wheat. A review. Agronomy for Sustainable Development 37 (5), 37.

Al-Ajlouni, Z.I., Al-Abdallat, A.M., Al-Ghzawi, A.L.A., Ayad, J.Y., Abu Elenein, J.M., Al-Quraan, N.A., Baenziger, P.S, 2016. Impact of pre-anthesis water deficit on yield and yield components in barley (Hordeum vulgare L.) plants grown under controlled conditions. Agronomy 6 (2), 33.

Allakhverdiev, S.I., Kreslavski, V.D., Klimov, V.V., Los, D.A., Carpentier, R., Mohanty, P., 2008. Heat stress: an overview of molecular responses in photosynthesis. Photosynthesis Research 98 (1-3), 541–550.

Almeselmani, M., Abdullah, F., Hareri, F., Naaesan, M., Ammar, M.A., ZuherKanbar, O., Saud, A.A., 2011. Effect of drought on different physiological characters and yield component in different varieties of Syrian durum wheat. Journal of Agricultural Science 3 (3), 127.

Almeselmani, M., Deshmukh, P., Sairam, R., 2009. High temperature stress tolerance in wheat genotypes: role of antioxidant defence enzymes. Acta Agronomica Hungarica 57 (1), 1–14.

Al-Otayk, S.M., 2010. Performance of yield and stability of wheat genotypes under high stress environments of the central region of Saudi Arabia. Meteorology, Environment and Arid Land Agriculture Sciences 21 (1).

Altenbach, S.B., DuPont, F.M., Kothari, K.M., Chan, R., Johnson, E.L., Lieu, D., 2003. Temperature, water and fertilizer influence the timing of key events during grain development in a US spring wheat. Journal of Cereal Science 37 (1), 9–20.

Apel, K., Hirt, H., 2004. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annual Review of Plant Biology 55, 373–399.

Araujo, W.L., Nunes-Nesi, A., Fernie, A.R., 2014. On the role of plant mitochondrial metabolism and its impact on photosynthesis in both optimal and sub-optimal growth conditions. Photosynthesis research 119 (1-2), 141–156.

Aslam, M., Sanghi, A.H., Javed, S., Khalid, L., 2013. Effect of sowing time on yield and yield components of wheat sown in standing cotton. Journal of Agricultural Research 51, 133–140.

Asseng, S., Ewert, F., Martre, P., Rötter, R.P., Lobell, D.B., Cammarano, D., Kimball, B.A., Ottman, M.J., Wall, G.W., White, J.W., et al., 2015. Rising temperatures reduce global wheat production. Nature Climate Change 5 (2), 143–147.

Asthir, B., 2015. Protective mechanisms of heat tolerance in crop plants. Journal of Plant Interactions 10 (1), 202–210.

Aziz, A., Mahmood, T., Mahmood, Z., Shazadi, K., Mujeeb-Kazi, A., Rasheed, A., 2018. Genotypic Variation and genotype× environment interaction for yield-related traits in synthetic hexaploid wheats under a range of optimal and heat-stressed environments. Crop Science 58 (1), 295–303.

Bala, P., Sikder, S., 2017. Evaluation of heat tolerance of wheat genotypes through membrane thermostability test. MAYFEB Journal of Agricultural Science 2, 1–6.

Balla, K., Bencze, S., Janda, T., Veisz, O., 2009. Analysis of heat stress tolerance in winter wheat. Acta Agronomica Hungarica 57 (4), 437–444.

Balla, K., Karsai, I., Bencze, S., Kiss, T., Veisz, O., 2013. Effect of heat stress on the physiological processes of wheat. Acta Agronomica Hungarica 61 (1), 1–12.

Balla, K., Karsai, I., Bónis, P., Kiss, T., Berki, Z., Horváth, Á., Mayer, M., Bencze, S., Veisz, O., 2019. Heat stress responses in a large set of winter wheat cultivars (Triticum aestivum L.) depend on the timing and duration of stress. PloS One 14 (9), e0222639.

Balota, M., Payne, W.A., Evett, S.R., Lazar, M.D., 2007. Canopy temperature depression sampling to assess grain yield and genotypic differentiation in winter wheat. Crop Science 47 (4), 1518–1529.

Barma, N.C.D., Islam, M.A., Hakim, M.A., Sarker, D.K.R, 2011. Genetic variability and selection response to heat tolerance through membrane thermostability in spring wheat (Triticum aestivum L). Bangladesh Journal of Plant Breeding and Genetics 23 (2), 15–22.

Barnabas, B., Jager, K., Feher, A., 2008. The effect of drought and heat stress on reproductive processes in cereals. Plant, Cell & Environment 31 (1), 11–38.

Bassi, F.M., Bentley, A.R., Charmet, G., Ortiz, R., Crossa, J., 2016. Breeding schemes for the implementation of genomic selection in wheat (Triticum spp.). Plant Science 242, 23–36.

Belko, N., Zaman-Allah, M., Diop, N.N., Cisse, N., Zombre, G., Ehlers, J.D., Vadez, V., 2013. Restriction of transpiration rate under high vapour pressure deficit and non-limiting water conditions is important for terminal drought tolerance in cowpea. Plant Biology 15 (2), 304–316.

Bennett, D., Reynolds, M., Mullan, D., Izanloo, A., Kuchel, H., Langridge, P., Schnurbusch, T., 2012. Detection of two major grain yield QTL in bread wheat (Triticum aestivum L.) under heat, drought and high yield potential environments. Theoretical and Applied Genetics 125 (7), 1473–1485.

Bergkamp, B., Impa, S.M., Asebedo, A.R., Fritz, A.K., Jagadish, S.K., 2018. Prominent winter wheat varieties response to post-flowering heat stress under controlled chambers and field based heat tents. Field Crops Research 222, 143–152.

Bernfur, K., Rutsdottir, G., Emanuelsson, C., 2017. The chloroplast-localized small heat shock protein Hsp21 associates with the thylakoid membranes in heat-stressed plants. Protein Science 26 (9), 1773–1784.

Bita, C., Gerats, T., 2013. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Frontiers in Plant Science 4, 273.

Blum, A., 1988. Plant Breeding For Stress environments. CRC press Inc., Boca Raton, Florida, p. 223.

Blum, A., 1998. Improving wheat grain filling under stress by stem reserve mobilisation. Euphytica 100 (1–3), 77–83.

Blumenthal, C.S., Batey, I.L., Bekes, F., Wrigley, C.W., Barlow, E.W.R., 1991. Seasonal changes in wheat-grain quality associated with high temperatures during grain filling. Australian Journal of Agricultural Research 42 (1), 21–30.

Blumenthal, C., Bekes, F., Wrigley, C.W., Barlow, E.W.R., 1990. The acquisition and maintenance of thermotolerance in Australian wheats. Functional Plant Biology 17 (1), 37–47.

Bokszczanin, K.L., Fragkostefanakis, S., 2013. Perspectives on deciphering mechanisms underlying plant heat stress response and thermotolerance. Frontiers in Plant Science 4, 315.

Borrell, A.K., Oosterom, E.J., Mullet, J.E., George-Jaeggli, B., Jordan, D.R., Klein, P.E., Hammer, G.L., 2014. Stay-green alleles individually enhance grain yield in sorghum under drought by modifying canopy development and water uptake patterns. New Phytologist 203 (3), 817–830.

Brestic, M., Zivcak, M., Kunderlikova, K., Allakhverdiev, S.I., 2016. High temperature specifically affects the photoprotective responses of chlorophyll b-deficient wheat mutant lines. Photosynthesis Research 130 (1-3), 251–266.

Buttar, Z.A., Wu, S.N., Arnao, M.B., Wang, C., Ullah, I., Wang, C., 2020. Melatonin Suppressed the Heat Stress-Induced Damage in Wheat Seedlings by Modulating the Antioxidant Machinery. Plants 9 (7), 809.

Cabral, A.L., Jordan, M.C., Larson, G., Somers, D.J., Humphreys, D.G., McCartney, C.A., 2018. Relationship between QTL for grain shape, grain weight, test weight, milling yield, and plant height in the spring wheat cross RL4452/'AC Domain. PloS One 13 (1), e0190681.

Cao, X., Mondal, S., Cheng, D., Wang, C., Liu, A., Song, J., Li, H., Zhao, Z., Liu, J., 2015. Evaluation of agronomic and physiological traits associated with high temperature stress tolerance in the winter wheat cultivars. Acta Physiologiae Plantarum 37 (4), 90.

Chaitanya, K.V., Sundar, D., Reddy, A.R., 2001. Mulberry leaf metabolism under high temperature stress. Biologia Plantarum 44 (3), 379–384.

Chakraborty, U., Pradhan, D., 2011. High temperature-induced oxidative stress in Lens culinaris, role of antioxidants and amelioration of stress by chemical pre-treatments. Journal of Plant Interactions 6 (1), 43–52.

Chavan, S.G., Duursma, R.A., Tausz, M., Ghannoum, O., 2019. Elevated CO2 alleviates the negative impact of heat stress on wheat physiology but not on grain yield. Journal of experimental botany 70 (21), 6447–6459.

Chen, Y., Wang, X.M., Zhou, L., He, Y., Wang, D., Qi, Y.H., Jiang, D.A., 2015. Rubiscoactivase is also a multiple responder to abiotic stresses in rice. PloS One 10 (10), e0140934.

Chen, Y.E., Su, Y.Q., Zhang, C.M., Ma, J., Mao, H.T., Yang, Z.H., Yuan, M., Zhang, Z.W., Yuan, S., Zhang, H.Y., 2017. Comparison of photosynthetic characteristics and antioxidant systems in different wheat strains. Journal of Plant Growth Regulation 1–13.

Cheregi, O., Wagner, R., Funk, C., 2016. Insights into the cyanobacterial Deg/HtrA proteases. Frontiers in Plant Science 7, 694.

Chinnusamy, V., Khanna-Chopra, R., 2003. Effect of heat stress on grain starch content in diploid, tetraploid and hexaploid wheat species. Journal of Agronomy and Crop Science 189 (4), 242–249.

Chinnusamy, V., Zhu, J., Zhou, T., Zhu, J.K., 2007. Small RNAs: big role in abiotic stress tolerance of plants. Advances in Molecular Breeding Toward Drought and Salt Tolerant Crops. Springer, Dordrecht, pp. 223–260.

Choudhary, M., Yadav, M., Saran, R., 2020. Advanced screening and breeding approaches for heat tolerance in wheat. Journal of Pharmacognosy and Phytochemistry 9 (2), 1047–1052.

Clavijo, B.J., Venturini, L., Schudoma, C., Accinelli, G.G., Kaithakottil, G., Wright, J., Borrill, P., Kettleborough, G., Heavens, D., Chapman, H., Lipscombe, J., 2017. An improved assembly and annotation of the allohexaploid wheat genome identifies complete families of agronomic genes and provides genomic evidence for chromosomal translocations. Genome Research 27 (5), 885–896.

Deshmukh, R., Sonah, H., Patil, G., Chen, W., Prince, S., Mutava, R., Vuong, T., Valliyodan, B., Nguyen, H.T., 2014. Integrating omic approaches for abiotic stress tolerance in soybean. Frontiers in Plant science 5, 244.

Deva, C.R., Urban, M.O., Challinor, A.J., Falloon, P., Svitákova, L., 2020. Enhanced leaf cooling is a pathway to heat tolerance in common bean. Frontiers in Plant Science 11, 19.

Diab, A.A., Kantety, R.V., Ozturk, N.Z., Benscher, D., Nachit, M.M., Sorrells, M.E., 2008. Drought-inducible Genes and Differentially Expressed Sequence Tags Associated With Components of Drought Tolerance in Durum Wheat. Scientific Research and Essays.

Djukic, N., Knezevic, D., Pantelic, D., Zivancev, D., Torbica, A., Markovic, S., 2019. Expression of protein synthesis elongation factors in winter wheat and oat in response to heat stress. Journal of plant physiology 240, 153015.

Dutta, S., Mohanty, S., Tripathy, B.C., 2009. Role of temperature stress on chloroplast biogenesis and protein import in pea. Plant Physiology 150 (2), 1050–1061.

Dwivedi, R., Prasad, S., Jaiswal, B., Kumar, A., Tiwari, A., Patel, S., Pandey, G., 2017. Evaluation of wheat genotypes (Triticum aestivum L.) at grain filling stage for heat tolerance. International Journal of Pure Applied Bioscience 5 (2), 971–975.
El Hassouni, K., Belkadi, B., Filali-Maltouf, A., Tidiane-Sall, A., Al-Abdallat, A., Nachit, M., Bassi, F.M., 2019. Loci controlling adaptation to heat stress occurring at the reproductive stage in durum wheat. Agronomy 9 (8), 414.
Enghiad, A., Ufer, D., Countryman, A.M., Thilmany, D.D., 2017. An overview of global wheat market fundamentals in an era of climate concerns. International Journal of Agronomy 2017.
Essemine, J., Ammar, S., Bouzid, S., 2010. Impact of heat stress on germination and growth in higher plants: physiological, biochemical and molecular repercussions and mechanisms of defence. Journal of Biological Sciences 10 (6), 565–572.
Fahad, S., Bajwa, A.A., Nazir, U., Anjum, S.A., Farooq, A., Zohaib, A., Sadia, S., Nasim, W., Adkins, S., Saud, S., Sadia, S., Nasim, W., Adkins, S., Saud, S., Ihsan, M.Z., 2017. Crop production under drought and heat stress: plant responses and management options. Frontiers in plant science 8, 1147.
Farooq, M., Bramley, H., Palta, J.A., Siddique, K.H., 2011. Heat stress in wheat during reproductive and grain-filling phases. Critical Reviews in Plant Sciences 30 (6), 491–507.
Feder, M.E., 2006. Integrative biology of stress: molecular actors, the ecological theater, and the evolutionary play. In: Proceedings of the International Symposium on Environmental Factors, Cellular Stress and Evolution, Varanasi, India. Vol. 2006.
Feng, B., Liu, P., Li, G., Dong, S.T., Wang, F.H., Kong, L.A., Zhang, J.W., 2014. Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. Journal of Agronomy and Crop Science 200 (2), 143–155.
Fischer, R.A., Rees, D., Sayre, K.D., Lu, Z.M., Condon, A.G., Saavedra, A.L., 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. Crop Science 38 (6), 1467–1475.
Fu, J., Momčilović, I., Clemente, T.E., Nersesian, N., Trick, H.N., Ristic, Z., 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 Molecular Biology 68 (3), 277–288.
Gautam, A., Prasad, S.S., Jajoo, A., Ambati, D., 2015. Canopy temperature as a selection parameter for grain yield and its components in durum wheat under terminal heat stress in late sown conditions. Agricultural Research 4 (3), 238–244.
Gill, B., Appels, R., Botha-Oberholster, A., Buell, C., Bennetzen, J., Chalhoub, B., et al., 2004. A workshop report on wheat genome sequencing: international genome research on wheat consortium. Genetics 168 (2), 1087–1096.
Gillies, S.A., Futardo, A., Henry, R.J., 2012. Gene expression in the developing aleurone and starchy endosperm of wheat. Plant Biotechnology Journal 10 (6), 668–679.
Girousse, C., Roche, J., Guerin, C., Le Gouis, J., Balzegue, S., Mouzeyar, S., Bouzidi, M.F., 2018. Coexpression network and phenotypic analysis identify metabolic pathways associated with the effect of warming on grain yield components in wheat. PLoS One 13 (6), e0199434.
Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. Science 327, 812–818.
Gororo, N.N., Eagles, H.A., Eastwood, R.F., Nicolas, M.E., Flood, R.G., 2002. Use of Triticum tauschii to improve yield of wheat in low-yielding environments. Euphytica 123 (2), 241–254.
Goufo, P., Moutinho-Pereira, J.M., Jorge, T.F., Correia, C.M., Oliveira, M.R., Rosa, E.A.S., et al., 2017. Cowpea (Vigna unguiculata L. Walp.) metabolomics: osmoprotection as a physiological strategy for drought stress resistance and improved yield. Frontiers in Plant Science 8, 586.
Grover, A., Mittal, D., Negi, M., Lavania, D., 2013. Generating high temperature tolerant transgenic plants: achievements and challenges. Plant Science 205, 38–47.
Gupta, A.K., Kaur, K., Kaur, N., 2011. Stem reserve mobilization and sink activity in wheat under drought conditions. American Journal of Plant Sciences 2 (1), 70.
Gupta, N.K., Agarwal, S., Agarwal, V.P., Nathawat, N.S., Gupta, S., Singh, G., 2013. Effect of short-term heat stress on growth, physiology and antioxidative defence system in wheat seedlings. Acta Physiologiae Plantarum 35 (6), 1837–1842.
Gupta, S.C., Sharma, A., Mishra, M., Mishra, R.K., Chowdhuri, D.K., 2010. Heat shock proteins in toxicology: how close and how far? Life Sciences 86 (11-12), 377–384.
Halford, N.G., 2009. New insights on the effects of heat stress on crops. Journal of Experimental Botany 60 (15), 4215–4216.
Hameed, A., Goher, M., Iqbal, N., 2012. Heat stress-induced cell death, changes in antioxidants, lipid peroxidation, and protease activity in wheat leaves. Journal of Plant Growth Regulation 31 (3), 283–291.
Haque, M.S., Kjaer, K.H., Rosenqvist, E., Sharma, D.K., Ottosen, C.O., 2014. Heat stress and recovery of photosystem II efficiency in wheat (Triticum aestivum L.) cultivars acclimated to different growth temperatures. Environmental and Experimental Botany 99, 1–8.
Hasanuzzaman, M., Nahar, K., Alam, M.M., Roychowdhury, R., Fujita, M., 2013. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. International Journal of Molecular Sciences 14 (5), 9643–9684.
Hatfield, J.L., Quisenberry, J.E., Dilbeck, R.E., 1987. Use of canopy temperatures of identify water conservation in cotton germplasm 1. Crop Science 27 (2), 269–273.
Have, M., Marmagne, A., Chardon, F., Masclaux-Daubresse, C., 2017. Nitrogen remobilization during leaf senescence: lessons from Arabidopsis to crops. Journal of Experimental Botany 68 (10), 2513–2529.
Hawker, J.S., Jenner, C.F., 1993. High temperature affects the activity of enzymes in the committed pathway of starch synthesis in developing wheat endosperm. Functional Plant Biology 20 (2), 197–209.
Hays, D.B., Do, J.H., Mason, R.E., Morgan, G., Finlayson, S.A., 2007. Heat stress induced ethylene production in developing wheat grains induces kernel abortion and increased maturation in a susceptible cultivar. Plant Science 172 (6), 1113–1123.
Hemantaranjan, A., NishantBhanu, A., Singh, M.N., Yadav, D.K., Patel, P.K., 2014. Heat stress responses and thermotolerance. Advances in Plants and Agriculture Research 1 (3) 00012.
Higashi, Y., Saito, K., 2019. Lipidomic studies of membrane glycerolipids in plant leaves under heat stress. Progress in Lipid Research 75, 100990.
Hodges, M., Dellero, Y., Keech, O., Betti, M., Raghavendra, A.S., Sage, R., Zhu, X.G., Allen, D.K., Weber, A.P., 2016. Perspectives for a better understanding of the metabolic integration of photorespiration within a complex plant primary metabolism network. Journal of Experimental Botany 67 (10), 3015–3026.
Holland, V., Koller, S., Lukas, S., Brüggemann, W., 2016. Drought-and frost-induced accumulation of soluble carbohydrates during accelerated senescence in Quercus pubescens. Trees 30 (1), 215–226.
Hosseini, S.A., Hajirezaei, M.R., Seiler, C., Sreenivasulu, N., von Wiren, N., 2016. A potential role of flag leaf potassium in conferring tolerance to drought-induced leaf senescence in barley. Frontiers in Plant Science 7, 206.
Howarth, C.J., 2005. Genetic improvements of tolerance to high temperature. Abiotic Stresses: Plant Resistance through Breeding And Molecular Approaches. Howarth Press, New York, USA. 1920.
Hu, S., Ding, Y., Zhu, C., 2020. Sensitivity and responses of chloroplasts to heat stress in plants. Frontiers in Plant Science 11, 375.
Hu, X.J., Chen, D., Lynne Mclntyre, C., Fernanda Dreccer, M., Zhang, Z.B., Drenth, J., Kalaipandian, S., Chang, H., Xue, G.P., 2018. Heat shock factor C2a serves as a proactive mechanism for heat protection in developing grains in wheat via an ABA-mediated regulatory pathway. Plant, cell & environment 41 (1), 79–98.
Huberman, M., Riov, J., Goldschmidt, E.E., Apelbaum, A., Goren, R., 2014. The novel ethylene antagonist, 3-cyclopropyl-1-enyl-propanoic acid sodium salt (CPAS), increases grain yield in wheat by delaying leaf senescence. Plant Growth Regulation 73 (3), 249–255.
Hurkman, W.J., Vensel, W.H., Tanaka, C.K., Whitehand, L., Altenbach, S.B., 2009. Effect of high temperature on albumin and globulin accumulation in the endosperm proteome of the developing wheat grain. Journal of Cereal Science 49 (1), 12–23.
Hutsch, B.W., Jahn, D., Schubert, S., 2019. Grain yield of wheat (Triticum aestivum L.) under long-term heat stress is sink-limited with stronger inhibition of kernel setting than grain filling. Journal of Agronomy and Crop Science 205 (1), 22–32.
Iba, K., 2002. Acclimative response to temperature stress in higher plants: approaches of gene engineering for temperature tolerance. Annual Review of Plant Biology 53 (1), 225–245.
Ibrahim, A.M., Quick, J.S., 2001. Heritability of heat tolerance in winter and spring wheat. Crop Science 41 (5), 1401–1405.
Ihsan, M.Z., Daur, I., Alghabari, F., Alzamanan, S., Rizwan, S., Ahmad, M., Waqas, M., Shafqat, W., 2019. Heat stress and plant development: role of sulphur metabolites and management strategies. Acta Agriculturae Scandinavica, Section B—Soil & Plant Science 69 (4), 332–342.
Iqbal, M., Hussain, I., Liaqat, H., Ashraf, M.A., Rasheed, R., Rehman, A.U., 2015. Exogenously applied selenium reduces oxidative stress and induces heat tolerance in spring wheat. Plant Physiology and Biochemistry 94, 95–103.
Jan, S., Abbas, N., Ashraf, M., Ahmad, P., 2019. Roles of potential plant hormones and transcription factors in controlling leaf senescence and drought tolerance. Protoplasma 256 (2), 313–329.
Janni, M., Gullì, M., Maestri, E., Marmiroli, M., Valliyodan, B., Nguyen, H.T., Marmiroli, N., 2020. Molecular and genetic bases of heat stress responses in crop plants and breeding for increased resilience and productivity. Journal of Experimental Botany.
Jarvi, S., Suorsa, M., Aro, E.M., 2015. Photosystem II repair in plant chloroplasts—Regulation, assisting proteins and shared components with photosystem II biogenesis. Biochimica et Biophysica Acta (BBA)-Bioenergetics 1847 (9), 900–909.
Jat, R.K., Singh, P., Jat, M.L., Dia, M., Sidhu, H.S., Jat, S.L., Bijarniya, D., Jat, H.S., Parihar, C.M., Kumar, U., Ridaura, S.L., 2018. Heat stress and yield stability of wheat genotypes under different sowing dates across agro-ecosystems in India. Field Crops Research 218, 33–50.
Jespersen, D., Zhang, J., Huang, B., 2016. Chlorophyll loss associated with heat-induced senescence in bentgrass. Plant Science 249, 1–12.
Kadam, S., Singh, K., Shukla, S., Goel, S., Vikram, P., Pawar, V., Gaikwad, K., Khanna-Chopra, R., Singh, N., 2012. Genomic associations for drought tolerance on the short arm of wheat chromosome 4B. Functional & integrative genomics 12 (3), 447–464.
Kataoka, R., Takahashi, M., Suzuki, N., 2017. Coordination between bZIP28 and HSFA2 in the regulation of heat response signals in Arabidopsis. Plant Signaling & Behavior 12 (11), e1376159.
Kaushal, N., Bhandari, K., Siddique, K.H., Nayyar, H., 2016. Food crops face rising temperatures: an overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. Cogent Food & Agriculture 2 (1), 1134380.
Keeling, P.L., Bacon, P.J., Holt, D.C., 1993. Elevated temperature reduces starch deposition in wheat endosperm by reducing the activity of soluble starch synthase. Planta 191 (3), 342–348.
Khatoon, S., Majid, S.A., Bibi, A., Javed, G., Ulfat, A., 2016. Yield stability evaluation of wheat (Triticum aestivum L.) cultivated on different environments of district Poonch (AJK) Pakistan based upon water-related parameters. International Journal of Agronomy and Agricultural Research 11–21.
Kirigwi, F.M., Van Ginkel, M., Brown-Guedira, G., Gill, B.S., Paulsen, G.M., Fritz, A.K., 2007. Markers associated with a QTL for grain yield in wheat under drought. Molecular Breeding 20 (4), 401–413.

Kobata, T., Palta, J.A., Turner, N.C., 1992. Rate of development of postanthesis water deficits and grain filling of spring wheat. Crop Science 32 (5), 1238–1242.
Kumudini, S., Andrade, F.H., Boote, K.J., Brown, G.A., Dzotsi, K.A., Edmeades, G.O., Gocken, T., Goodwin, M., Halter, A.L., Hammer, G.L., Hatfield, J.L., 2014. Predicting maize phenology: intercomparison of functions for developmental response to temperature. Agronomy Journal 106 (6), 2087–2097.
Labuschagne, M.T., Elago, O., Koen, E., 2009. The influence of temperature extremes on some quality and starch characteristics in bread, biscuit and durum wheat. Journal of Cereal Science 49 (2), 184–189.
Lancashire, P.D., Bleiholder, H., Boom, T.V.D., Langelüddeke, P., Stauss, R., WEBER, E., Witzenberger, A, 1991. A uniform decimal code for growth stages of crops and weeds. Annals of applied Biology 119 (3), 561–601.
Lesk, C., Rowhani, P., Ramankutty, N., 2016. Influence of extreme weather disasters on global crop production. Nature 529 (7584), 84.
Li, R., Hou, L., Zhang, A., Lu, Y., Song, W., Tadesse, W., Wang, X., Liu, M., Zheng, W., Xu, S., 2018. Heat stress in filling stage confers distinct effect on starch granules formation in different thermotolerant wheat accessions. Pakistan Journal of Botany 50 (3), 913–920.
Li, S., Zhou, X., Chen, L., Huang, W., Yu, D., 2010. Functional characterization of Arabidopsis thaliana WRKY39 in heat stress. Molecules and cells 29 (5), 475–483.
Liang, Z., Chen, K., Li, T., Zhang, Y., Wang, Y., Zhao, Q., Liu, J., Zhang, H., Liu, C., Ran, Y., Gao, C., 2017. Efficient DNA-free genome editing of bread wheat using CRISPR/Cas9 ribonucleoprotein complexes. Nature Communications 8, 14261.
Lindquist, S., Craig, E.A., 1988. The heat-shock proteins. Annual Review of Genetics 22 (1), 631–677.
Lira, B.S., Gramegna, G., Trench, B.A., Alves, F.R., Silva, E.M., Silva, G.F., Thirumalaikumar, V.P., Lupi, A.C., Demarco, D., Purgatto, E., Nogueira, F.T., 2017. Manipulation of a senescence-associated gene improves fleshy fruit yield. Plant Physiology 175 (1), 77–91.
Liu, S., Waqas, M.A., Wang, S-h, Xiong X-y, Wan, Y-f, 2017. Effects of increased levels of atmospheric CO_2 and high temperatures on rice growth and quality. PLoS One 12 (11), e0187724.
Liu, B., Martre, P., Ewert, F., Porter, J.R., Challinor, A.J., Müller, C., Ruane, A.C., Waha, K., Thorburn, P.J., Aggarwal, P.K., Ahmed, M., 2019. Global wheat production with 1.5 and 2.0°C above pre-industrial warming. Global Change Biology 25 (4), 1428–1444 .
Liu, P., Guo, W., Jiang, Z., Pu, H., Feng, C., Zhu, X., Peng, Y., Kuang, A., Little, C.R., 2011. Effects of high temperature after anthesis on starch granules in grains of wheat (Triticum aestivum L.). The Journal of Agricultural Science 149 (2), 159–169.
Lu, L., Liu, H., Wu, Y., Yan, G., 2020. Development and Characterization of Near-Isogenic Lines Revealing Candidate Genes for a Major 7AL QTL Responsible for Heat Tolerance in Wheat. Frontiers in Plant Science 11, 1316.
Man, J., Shi, Y., Yu, Z., Zhang, Y., 2016. Root growth, soil water variation, and grain yield response of winter wheat to supplemental irrigation. Plant Production Science 19 (2), 193–205.
Martins, M.Q., Rodrigues, W.P., Fortunato, A.S., Leitão, A.E., Rodrigues, A.P., Pais, I.P., Martins, L.D., Silva, M.J., Reboredo, F.H., Partelli, F.L., Campostrini, E., 2016. Protective response mechanisms to heat stress in interaction with high [CO_2] conditions in Coffea spp. Frontiers in Plant Science 7, 947.
Mathur, S., Agrawal, D., Jajoo, A., 2014. Photosynthesis: response to high temperature stress. Journal of Photochemistry and Photobiology B: Biology 137, 116–126.
Medina, S., Vicente, R., Nieto-Taladriz, M.T., Aparicio, N., Chairi, F., Vergara-Diaz, O., Araus, J.L., 2019. The plant-transpiration response to vapor pressure deficit (VPD) in Durum Wheat is associated with differential yield performance and specific expression of genes involved in primary metabolism and water transport. Frontiers in plant science 9,. https://doi.org/10.3389/fpls.2018.01994 1994.
Melloy, P., Aitken, E., Luck, J., Chakraborty, S., Obanor, F., 2014. The influence of increasing temperature and CO_2 on Fusarium crown rot susceptibility of wheat genotypes at key growth stages. European Journal of Plant Pathology 140 (1), 19–37.
Menshawy, A.M.M, 2007. Evaluation of some early bread wheat genotypes under different sowing dates: 1. Earliness characters. Egyptian Journal of Plant Breeding 11 (1), 25–40.
Merchuk-Ovnat, L., Fahima, T., Krugman, T., Saranga, Y., 2016. Ancestral QTL alleles from wild emmer wheat improve grain yield, biomass and photosynthesis across enviroinments in modern wheat. Plant Science 251, 23–34.
Mickelbart, M.V., Hasegawa, P.M., Bailey-Serres, J., 2015. Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. Nature Reviews Genetics 16 (4), 237.
Mishra, S.C., Singh, S.K., Patil, R., Bhusal, N., Malik, A., Sareen, S., Shukla, R.S., Mishra, P.C., Chatrath, R., Gupta, R.K., Tomar, S.S., 2014. Breeding for heat tolerance in Wheat. Genetics 2 (2), 1.
Mohammadi, M., Karimizadeh, R., Shefazeadeh, M.K., 2012. Grain yield performance of bread wheat germplasm under heat and drought field conditions. Annals of Biological Research 3, 3149–3155.
Morales, F., Ancín, M., Fakhet, D., González-Torralba, J., Gámez, A.L., Seminario, A., Soba, D., Ben Mariem, S., Garriga, M., Aranjuelo, I., 2020. Photosynthetic Metabolism under Stressful Growth Conditions as a Bases for Crop Breeding and Yield Improvement. Plants 9 (1), 88.
Morell, M.K., Rahman, S., Regina, A., Appels, R., Li, Z., 2001. Wheat starch biosynthesis. Euphytica, 119, 55–58.
Morrow, G., Tanguay, R.M., 2012. Small heat shock protein expression and functions during development. International Journal of Biochemistry and Cell Biology 44, 1613–1621.
Munjal, R., Dhanda, S.S., 2016. Assessment of drought resistance in Indian wheat cultivars for morpho-physiological traits. Ekin Journal of Crop Breeding and Genetics 2 (1), 74–81.
Munjal, R., Rana, R.K., 2003. Evaluation of physiological traits in wheat (Triticum aestivum L.) for terminal high temperature tolerance. In: Proceedings of the Tenth International Wheat Genetics Symposium, Poestum, Italy2, pp. 804–805.
Narayanan, S., Prasad, P.V.V., Fritz, A.K., Boyle, D.L., Gill, B.S, 2015. Impact of high nighttime and high daytime temperature stress on winter wheat. Journal of Agronomy and Crop Science 201 (3), 206–218.
Noctor, G., Foyer, C.H., 1998. Ascorbate and glutathione: keeping active oxygen under control. Annual Review of Plant Biology 49 (1), 249–279.
Ogbonnaya, F.C., Rasheed, A., Okechukwu, E.C., Jighly, A., Makdis, F., Wuletaw, T., Hagras, A., Uguru, M.I., Agbo, C.U., 2017. Genome-wide association study for agronomic and physiological traits in spring wheat evaluated in a range of heat prone environments. Theoretical and Applied Genetics 130 (9), 1819–1835.
Olivares-Villegas, J.J., Reynolds, M.P., McDonald, G.K., 2007. Drought-adaptive attributes in the Seri/Babaxhexaploid wheat population. Functional Plant Biology 34 (3), 189–203.
Omae, H., Kumar, A., Kashiwaba, K., Shono, M., 2012. Adaptation to high temperature and water deficit in the common bean (Phaseolus vulgaris L.) during the reproductive period. J Bot.
Othmani, A., Rezgui, M., Cherif, S., Mouelhi, M., Melki, M., 2015. Effects of water regimes on root and shoot growth parameters and agronomic traits of Tunisian durum wheat (Triticum durum Desf.). Journal of New Science Agriculture and Biotechnology 18, 695–702.
Paliwal, R., Röder, M.S., Kumar, U., Srivastava, J.P., Joshi, A.K., 2012. QTL mapping of terminal heat tolerance in hexaploid wheat (T. aestivum L.). Theoretical and Applied Genetics 125 (3), 561–575.
Parent, B., Shahinnia, F., Maphosa, L., Berger, B., Rabie, H., Chalmers, K., Kovalchuk, A., Langridge, P., Fleury, D., 2015. Combining field performance with controlled environment plant imaging to identify the genetic control of growth and transpiration underlying yield response to water-deficit stress in wheat. Journal of Experimental Botany 66 (18), 5481–5492.
Parry, M.A., Keys, A.J., Madgwick, P.J., Carmo-Silva, A.E., Andralojc, P.J., 2008. Rubisco regulation: a role for inhibitors. Journal of Experimental Botany 59 (7), 1569–1580.
Perdomo, J.A., Capó-Bauçà, S., Carmo-Silva, E., Galmés, J., 2017. Rubisco and rubiscoactivase play an important role in the biochemical limitations of photosynthesis in rice, wheat, and maize under high temperature and water deficit. Frontiers in Plant Science 8, 490.
Pinto, R.S., Lopes, M.S., Collins, N.C., Reynolds, M.P., 2016. Modelling and genetic dissection of staygreen under heat stress. Theoretical and Applied Genetics 129 (11), 2055–2074.
Pinto, R.S., Reynolds, M.P., Mathews, K.L., McIntyre, C.L., Olivares-Villegas, J.J., Chapman, S.C., 2010. Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. Theoretical and Applied Genetics 121 (6), 1001–1021.
Plaut, Z., Butow, B.J., Blumenthal, C.S., Wrigley, C.W., 2004. Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. Field Crops Research 86 (2-3), 185–198.
Pogson, B.J., Woo, N.S., Förster, B., Small, I.D., 2008. Plastid signalling to the nucleus and beyond. Trends in Plant Science 13 (11), 602–609. https://doi.org/10.1016/j.tplants.2008.08.008Poorter.
Pospisil, P., Yamamoto, Y., 2017. Damage to photosystem II by lipid peroxidation products. Biochimica et Biophysica Acta (BBA)-General Subjects 1861 (2), 457–466.
Poudel, P.B., Poudel, M.R., 2020. Heat stress effects and tolerance in wheat: a review. Journal of Biology and Today's World 9 (3), 1–6.
Pradhan, G.P., Prasad, P.V., 2015. Evaluation of wheat chromosome translocation lines for high temperature stress tolerance at grain filling stage. PLoS One 10 (2), e0116620.
Prakash, P., Sharma-Natu, P., & Ghildiyal, M.C. (2004). Effect of different temperature on starch synthase activity in excised grains of wheat cultivars.
Qaderi, M.M., Martel, A.B., Dixon, S.L., 2019. Environmental factors influence plant vascular system and water regulation. Plants 8 (3), 65.
Qin, D.H., Ding, Y.H., Wang, S.W., 2002. A study of environment change and its impacts in western China. Earth Science Frontiers 9 (2), 321–328.
Qin, D., Wang, F., Geng, X., Zhang, L., Yao, Y., Ni, Z., Peng, H., Sun, Q., 2015. Overexpression of heat stress-responsive TaMBF1c, a wheat (Triticum aestivum L.) Multiprotein Bridging Factor, confers heat tolerance in both yeast and rice. Plant molecular biology 87 (1-2), 31–45.
Singh, R.M., Agrawal, R.K, 2014. Genetic analysis for terminal heat stress in bread Wheat (Triticum aestivum L. em. thell). The Bioscan 9 (2), 771–776.
Ramya, P., Jain, N., Singh, G.P., Singh, P.K., Prabhu, K.V., 2015. Population structure, molecular and physiological characterization of elite wheat varieties used as parents in drought and heat stress breeding in India. Indian Journal of Genetics and Plant Breeding 75, 250–252.
Reda, F., Mandoura, H.M., 2011. Response of enzymes activities, photosynthetic pigments, proline to low or high temperature stressed wheat plant (Triticum Aestivum l.) in the presence or absence of exogenous proline or cysteine. International Journal of Academic Research 3 (4).
Reynolds, M.P., Trethowan, R.M., 2007. Physiological interventions in breeding for adaptation to abiotic stress. Frontis 127–144.
Reynolds, M.P., Mujeeb-Kazi, A., Sawkins, M., 2005. Prospects for utilising plant-adaptive mechanisms to improve wheat and other crops in drought-and salinity-prone environments. Annals of Applied Biology 146 (2), 239–259.
Reynolds, M.P., Nagarajan, S., Razzaque, M.A., Ageeb, O.A.A., 2001. Heat Tolerance. Application of Physiology in wheat breeding, Mexico, DF, CIMMYT.
Ristic, Z., Bukovnik, U., Prasad, P.V., 2007. Correlation between heat stability of thylakoid membranes and loss of chlorophyll in winter wheat under heat stress. Crop Science 47 (5), 2067–2073.

Ristic, Z., Bukovnik, U., Momčilović, I., Fu, J., Prasad, P.V., 2008. Heat-induced accumulation of chloroplast protein synthesis elongation factor, EF-Tu, in winter wheat. Journal of Plant Physiology 165 (2), 192–202.
Robson, P.R., Farrar, K., Gay, A.P., Jensen, E.F., Clifton-Brown, J.C., Donnison, I.S., 2013. Variation in canopy duration in the perennial biofuel crop Miscanthus reveals complex associations with yield. Journal of Experimental Botany 64 (8), 2373–2383.
Roessner, U., Bowne, J., 2009. What is metabolomics all about? Biotechniques 46 (5), 363–365 What is metabolomics all about?. Biotechniques, 46(5), 363-365.
Rossi, S., Burgess, P., Jespersen, D., Huang, B., 2017. Heat-induced leaf senescence associated with Chlorophyll metabolism in Bentgrass lines differing in heat tolerance. Crop Science 57 (supplement1) S-169.
Ruelland, E., Zachowski, A., 2010. How plants sense temperature. Environmental and Experimental Botany 69 (3), 225–232.
Saini, H.S., Sedgley, M., Aspinall, D., 2010. Effect of Heat stress during floral development on pollen tube growth and ovary anatomy in wheat (Triticum aestivum L.). Australian Journal of Plant Physiology 10, 137–144.
Sairam, R.K., Tyagi, A., 2004. Physiology and molecular biology of salinity stress tolerance in plants. Current Science 407–421.
Sakuraba, Y., Jeong, J., Kang, M.Y., Kim, J., Paek, N.C., Choi, G., 2014. Phytochrome-interacting transcription factors PIF4 and PIF5 induce leaf senescence in Arabidopsis. Nature Communications 5 (1), 1–13.
Sami, F., Yusuf, M., Faizan, M., Faraz, A., Hayat, S., 2016. Role of sugars under abiotic stress. Plant Physiology and Biochemistry 109, 54–61.
Sardans, J., Gargallo-Garriga, A., Urban, O., Klem, K., Walker, T.W., Holub, P., Janssens, I.A., Peñuelas, J., 2020. Ecometabolomics for a better understanding of plant responses and acclimation to abiotic factors linked to global change. Metabolites 10 (6), 239.
Sarwat, M., Naqvi, A.R., Ahmad, P., Ashraf, M., Akram, N.A., 2013. Phytohormones and microRNAs as sensors and regulators of leaf senescence: assigning macro roles to small molecules. Biotechnology advances 31 (8), 1153–1171.
Sattar, A., Sher, A., Ijaz, M., Ul-Allah, S., Rizwan, M.S., Hussain, M., Jabran, K., Cheema, M.A., 2020. Terminal drought and heat stress alter physiological and biochemical attributes in flag leaf of bread wheat. Plos One 15 (5), e0232974.
Savchenko, G.E., Klyuchareva, E.A., Abramchik, L.M., Serdyuchenko, E.V., 2002. Effect of periodic heat shock on the inner membrane system of etioplasts. Russian Journal of Plant Physiology 49 (3), 349–359.
Savicka, M., Škute, N., 2010. Effects of high temperature on malondialdehyde content, superoxide production and growth changes in wheat seedlings (Triticum aestivum L.). Ekologija 56 (1), 26–33.
Saxena, D.C., Prasad, S.S., Chatrath, R., Mishra, S.C., Watt, M., Prashar, R., Wason, A., Gautam, A., Malviya, P., 2014. Evaluation of root characteristics, canopy temperature depression and stay green trait in relation to grain yield in wheat under early and late sown conditions. Indian Journal of Plant Physiology 19 (1), 43–47.
Schmidt, J., Tricker, P.J., Eckermann, P., Kalambettu, P., Garcia, M., Fleury, D.L., 2019. Novel alleles for combined drought and heat stress tolerance in wheat. Frontiers in Plant Science 10, 1800.
Shah, N.H., Paulsen, G.M., 2003. Interaction of drought and high temperature on photosynthesis and grain-filling of wheat. Plant and Soil 257 (1), 219–226.
Shahinnia, F., Le Roy, J., Laborde, B., Sznajder, B., Kalambettu, P., Mahjourimajd, S., Tilbrook, J., Fleury, D., 2016. Genetic association of stomatal traits and yield in wheat grown in low rainfall environments. BMC Plant Biology 16 (1), 150.
Sheshshayee, M.S., Bindumadhava, H., Rachaputi, N.R., Prasad, T.G., Udayakumar, M., Wright, G.C., Nigam, S.N., 2006. Leaf chlorophyll concentration relates to transpiration efficiency in peanut. Annals of Applied Biology 148 (1), 7–15.
Shirdelmoghanloo, H., Taylor, J.D., Lohraseb, I., Rabie, H., Brien, C., Timmins, A., Martin, P., Mather, D.E., Emebiri, L., Collins, N.C., 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 Biology 16 (1), 100.
Shivhare, D., Mueller-Cajar, O., 2017. Characterization of thermostable CAM Rubiscoactivase reveals a Rubisco interacting surface loop. Plant Physiology 00554.
Singh, K., Sharma, S.N., Sharma, Y., 2011. Effect of high temperature on yield attributing traits in bread wheat. Bangladesh Journal of Agricultural Research 36 (3), 415–426.
Sonah, H., Deshmukh, R.K., Chand, S., Srinivasprasad, M., Rao, G.J., Upreti, H.C., et al., 2012. Molecular mapping of quantitative trait loci for flag leaf length and other agronomic traits in rice (Oryza sativa). Cereal Research Communication 40, 362–372.
Spiertz, J.H.J., Hamer, R.J., Xu, H., Primo-Martin, C., Don, C., Van Der Putten, P.E.L, 2006. Heat stress in wheat (Triticum aestivum L.): effects on grain growth and quality traits. European Journal of Agronomy 25 (2), 89–95.
Stratonovitch, P., Semenov, M.A., 2015. Heat tolerance around flowering in wheat identified as a key trait for increased yield potential in Europe under climate change. Journal of Experimental Botany 66 (12), 3599–3609.
Sun, A.Z., Guo, F.Q., 2016. Chloroplast retrograde regulation of heat stress responses in plants. Frontiers in Plant Science 7, 398.
Sunil, B., Saini, D., Bapatla, R.B., Aswani, V., Raghavendra, A.S., 2019. Photorespiration is complemented by cyclic electron flow and the alternative oxidase pathway to optimize photosynthesis and protect against abiotic stress. Photosynthesis research 139 (1-3), 67–79.
Suzuki, N., Mittler, R., 2006. Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction. Physiologia plantarum 126 (1), 45–51.
Suzuki, N., Rivero, R.M., Shulaev, V., Blumwald, E., Mittler, R., 2014. Abiotic and biotic stress combinations. New Phytologist 203 (1), 32–43.
Swindell, W.R., Huebner, M., Weber, A.P., 2007. Transcriptional profiling of Arabidopsis heat shock proteins and transcription factors reveals extensive overlap between heat and non-heat stress response pathways. BMC genomics 8 (1), 125.
Tahmasebi, S., Heidari, B., Pakniyat, H., McIntyre, C.L., 2016. Mapping QTLs associated with agronomic and physiological traits under terminal drought and heat stress conditions in wheat (Triticum aestivum L.). Genome 60 (1), 26–45.
Taiz, L., Zeiger, E., 2006. Water and plant cells, Plant Physiology. 4th edn. Sinauer Associates Inc, p. 672.
Talebi, R., 2011. Evaluation of chlorophyll content and canopy temperature as indicators for drought tolerance in durum wheat (Triticum durum Desf.). Australian Journal of Basic Applied Science 5, 1457–1462.
Talukder, A.S.M.H.M., McDonald, G.K., Gill, G.S, 2013. Effect of short-term heat stress prior to flowering and at early grain set on the utilization of water-soluble carbohydrate by wheat genotypes. Field Crops Research 147, 1–11.
Talukder, A.S.M.H.M., McDonald, G.K., Gill, G.S, 2014. Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat. Field Crops Research 160, 54–63.
Tattaris, M., Reynolds, M.P., Chapman, S.C., 2016. A direct comparison of remote sensing approaches for high-throughput phenotyping in plant breeding. Frontiers in Plant Science 7, 1131.
Thakur, P., Kumar, S., Malik, J.A., Berger, J.D., Nayyar, H., 2010. Cold stress effects on reproductive development in grain crops: an overview. Environmental and Experimental Botany 67 (3), 429–443.
Thomas, H., 2013. Senescence, ageing and death of the whole plant. New Phytologist 197 (3), 696–711.
Thomas, H., Howarth, C.J., 2000. Five ways to stay green. Journal of Experimental Botany 51 (suppl_1), 329–337.
Thomas, H., Ougham, H., 2014. The stay-green trait. Journal of Experimental Botany 65, 3889–3900.
Tian, B., Talukder, S.K., Fu, J., Fritz, A.K., Trick, H.N., 2018. Expression of a rice soluble starch synthase gene in transgenic wheat improves the grain yield under heat stress conditions. In Vitro Cellular & Developmental Biology-Plant 54 (3), 216–227.
Tricker, P.J., ElHabti, A., Schmidt, J., Fleury, D., 2018. The physiological and genetic basis of combined drought and heat tolerance in wheat. Journal of experimental botany 69 (13), 3195–3210.
Urban, O., Hlaváčová, M., Klem, K., Novotná, K., Rapantová, B., Smutná, P., Horáková, V., Hlavinka, P., Škarpa, P., Trnka, M., 2018. Combined effects of drought and high temperature on photosynthetic characteristics in four winter wheat genotypes. Field Crops Research 223, 137–149.
Vijayalakshmi, K., Fritz, A.K., Paulsen, G.M., Bai, G., Pandravada, S., Gill, B.S., 2010. Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. Molecular Breeding 26 (2), 163–175.
Voss, I., Sunil, B., Scheibe, R., Raghavendra, A.S., 2013. Emerging concept for the role of photorespiration as an important part of abiotic stress response. Plant biology 15 (4), 713–722.
Vu, J.C., Gesch, R.W., Pennanen, A.H., Hartwell Jr, L.A., Boote, K.J., Bowes, G, 2001. Soybean photosynthesis, Rubisco, and carbohydrate enzymes function at supraoptimal temperatures in elevated CO2. Journal of Plant Physiology 158 (3), 295–307.
Wahid, A., Gelani, S., Ashraf, M., Foolad, M.R., 2007. Heat tolerance in plants: an overview. Environmental and Experimental Botany 61 (3), 199–223.
Wang, G.P., Hui, Z., Li, F., Zhao, M.R., Zhang, J., Wang, W., 2010. Improvement of heat and drought photosynthetic tolerance in wheat by overaccumulation of glycinebetaine. Plant Biotechnology Reports 4 (3), 213–222.
Wang, Q.L., Chen, J.H., He, N.Y., Guo, F.Q., 2018. Metabolic reprogramming in chloroplasts under heat stress in plants. International Journal of Molecular Sciences 19 (3), 849.
Wang, X., Cai, J., Jiang, D., Liu, F., Dai, T., Cao, W., 2011. Pre-anthesis high-temperature acclimation alleviates damage to the flag leaf caused by post-anthesis heat stress in wheat. Journal of Plant Physiology 168 (6), 585–593.
Wang, X., Cai, J., Liu, F., Jin, M., Yu, H., Jiang, D., Wollenweber, B., Dai, T., Cao, W., 2012. Pre-anthesis high temperature acclimation alleviates the negative effects of post-anthesis heat stress on stem stored carbohydrates remobilization and grain starch accumulation in wheat. Journal of Cereal Science 55 (3), 331–336.
Wang, X., Dinler, B.S., Vignjevic, M., Jacobsen, S., Wollenweber, B., 2015. Physiological and proteome studies of responses to heat stress during grain filling in contrasting wheat cultivars. Plant Science 230, 33–50.
Wanjura, D.F., Upchurch, D.R., Mahan, J.R., 1995. Control of irrigation scheduling using temperature-time thresholds. Transactions of the ASAE 38 (2), 403–409.
Watson, A., Ghosh, S., Williams, M.J., Cuddy, W.S., Simmonds, J., Rey, M.D., Hatta, M.A.M., Hinchliffe, A., Steed, A., Reynolds, D., Adamski, N.M, 2018. Speed breeding is a powerful tool to accelerate crop research and breeding. Nature Plants 4 (1), 23.
Weichert, H., Högy, P., Mora-Ramirez, I., Fuchs, J., Eggert, K., Koehler, P., Weschke, W., Fangmeier, A., Weber, H., 2017. Grain yield and quality responses of wheat expressing a barley sucrose transporter to combined climate change factors. Journal of experimental botany 68 (20), 5511–5525.
Whitley, D., Goldberg, S.P., Jordan, W.D., 1999. Heat shock proteins: a review of the molecular chaperones. Journal of Vascular Surgery 29 (4), 748–751.
Xu, Y.F., Li, S.S., Li, L.H., Ma, F.F., Fu, X.Y., Shi, Z.L., Xu, H.X., Ma, P.T., An, D.G., 2017. QTL mapping for yield and photosynthetic related traits under different water regimes in wheat. Molecular breeding 37 (3), 34.
Xu, Y., Zhan, C., Huang, B., 2011. Heat shock proteins in association with heat tolerance in grasses. International Journal of Proteomics 2011, 529648. https://doi.org/10.1155/2011/529648.
Xue, G.P., Sadat, S., Drenth, J., McIntyre, C.L., 2014. The heat shock factor family from Triticum aestivum in response to heat and other major abiotic stresses and their

role in regulation of heat shock protein genes. Journal of Experimental Botany 65 (2), 539–557.
Xue, G.P., Drenth, J., McIntyre, C.L., 2015. TaHsfA6f is a transcriptional activator that regulates a suite of heat stress protection genes in wheat (Triticum aestivum L.) including previously unknown Hsf targets. Journal of Experimental Botany 66 (3), 1025–1039.
Yabuta, Y., 2016. Functions of heat shock transcription factors involved in response to photooxidative stresses in Arabidopsis. Bioscience, Biotechnology and Biochemistry 80 (7), 1254–1263.
Yang, X.F., Guo, F.Q., 2014. Research advances in mechanisms of plant leaf senescence under heat stress. Plant Physiology Journal 50 (9), 1285–1292.
Yang, Z., Li, X., Zhang, N., Wang, X., Zhang, Y., Ding, Y., Kuai, B., Huang, X., 2017. Mapping and validation of the quantitative trait loci for leaf stay-green-associated parameters in maize. Plant Breeding 136 (2), 188–196.
Yeh, C.H., Kaplinsky, N.J., Hu, C., Charng, Y.Y., 2012. Some like it hot, some like it warm: phenotyping to explore thermotolerance diversity. Plant Science 195, 10–23.
Yin, X., Guo, W., Spiertz, J.H., 2009. A quantitative approach to characterize sink–source relationships during grain filling in contrasting wheat genotypes. Field Crops Research 114 (1), 119–126.
Yogita, K., Madan, S., Rani, B., Reena, K., Munjal, R., 2015. Trehalose mitigates heat stress-induced damages in wheat seedlings. Journal of Wheat Research 7 (1).
Yu, S.M., Lo, S.F., Ho, T.H.D., 2015. Source–sink communication: regulated by hormone, nutrient, and stress cross-signaling. Trends in Plant Science 20 (12), 844–857.
Yuan, C.H.E.N., Cothren, J.T., De-hua, C.H.E.N., Ibrahim, A.M., Lombardini, L, 2015. Ethylene inhibiting compound 1-MCP delays leaf senescence in cotton plants under abiotic stress conditions. Journal of Integrative Agriculture 14 (7), 1321–1331.
Zadoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. Weed Research 14 (6), 415–421.
Zang, X., Geng, X., Wang, F., Liu, Z., Zhang, L., Zhao, Y., Tian, X., Ni, Z., Yao, Y., Xin, M., Hu, Z., 2017. Overexpression of wheat ferritin gene TaFER-5B enhances tolerance to heat stress and other abiotic stresses associated with the ROS scavenging. BMC Plant Biology 17 (1), 1–13.
Zhang, L., Geng, X., Zhang, H., Zhou, C., Zhao, A., Wang, F., Zhao, Y., Tian, X., Hu, Z., Xin, M., Yao, Y., 2017. Isolation and characterization of heat-responsive gene TaGASR1 from wheat (Triticum aestivum L.). Journal of Plant Biology 60 (1), 57–65.
Zhang, Y., Lou, H., Guo, D., Zhang, R., Su, M., Hou, Z., Zhou, H., Liang, R., Xie, C., You, M., Li, B., 2018. Identifying changes in the wheat kernel proteome under heat stress using iTRAQ. The Crop Journal 6 (6), 600–610.
Zhao, H., Dai, T., Jing, Q., Jiang, D., Cao, W., 2007. Leaf senescence and grain filling affected by post-anthesis high temperatures in two different wheat cultivars. Plant Growth Regulation 51 (2), 149–158.
Zheng, K., Jiang, Q.T., Zhang, X.W., Lan, X.J., Dai, S.F., Wei, Y.M., Laroche, A., Lu, Z.X., Zheng, Y.L., 2014. Differences in starch composition and physiochemical properties are influenced by granule types in wheat and its relatives. Pakistan Journal of Botany 46 (6), 2239–2248.
Ziotti, A.B., Silva, B.P., Neto, M.C.L., 2019. Photorespiration is crucial for salinity acclimation in castor bean. Environmental and Experimental Botany 167, 103845.
Zou, M., Yuan, L., Zhu, S., Liu, S., Ge, J., Wang, C., 2017. Effects of heat stress on photosynthetic characteristics and chloroplast ultrastructure of a heat-sensitive and heat-tolerant cultivar of wucai (Brassica campestris L.). Acta Physiologiae Plantarum 39 (1), 30.