REVIEW

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PHYSIOLOGICAL AND MOLECULAR ASPECTS OF HEAT TOLERANCE IN WHEAT

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SUMMARY

Abiotic stresses are major constraints to crop production and food security. The situation is critical due to rapid changes in climatic conditions. Heat stress for wheat is one of the most important stresses having a severe impact on plant growth and productivity. Various studies have indicated that average maximum temperature higher than 32 °C during the reproductive phase negatively influenced wheat grain yield and average yield loss of up to 30% was reported. To screen or to develop a heat tolerant variety, it is very important to understand the physiological and molecular changes occurring inside the plant under heat stress. Terminal heat stress led to reduction in grain filling duration, thousand grain weight, grain number per head, and final yield. Furthermore, the elevated temperature-driven interruption in the transport of photosynthate from green foliage (source) to anther tissues (sink) leads to high pollen mortality and thereby decreases grain yield. This review provides a current update about heat induced physiological and molecular changes in wheat and the traits suitable for breeding of heat tolerant wheat genotypes. Previous studies conducted in the past have proven that wheat growth and yield were negatively influenced by abnormal temperatures due to physiological disruption. During recent years, many QTLs with significant effect on heat tolerance were identified. Further, heat stress has multilayered impact and, therefore, is very complex to understand completely. A better understanding of plant responses to heat stress has pragmatic implications for wheat breeding.

Keywords: Heat stress, molecular traits, physiological traits, wheat

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INTRODUCTION

The production of food grains in recent decades is not keeping pace with growing population demand, leading to inflation and a risk to food and nutritional security in India and other developing countries. Furthermore, urbanization has forced agriculture into more harsh situations and marginal lands. The projected 70 % increase in global food requirements by the end of 2050 necessitates improvement in agricultural productivity with lower use of land and water (Fischer, 2014). Climate change could also strongly affect wheat production, which accounts for 21% of food production and 200 million hectares (ha) of farmland worldwide (Ortiz *et al*., 2008). The productivity of agriculturally important crops may be severely reduced when they experience short episodes of high temperatures during the reproductive period. Heat stress has been recognized as the major threat to global food security (IPCC, 2007). Cropping areas of the Eastern and central part of the Asia, including the northern part of the Indian subcontinent and North America have been identified as the extremely threatened by heat stress (Teixeira *et al*., 2013).

Wheat is one of the major staple food crops and is the cheapest source of carbohydrate and protein in most parts of the world. It is grown on approximately 30% of the world's cereal area and around 220 million ha of global wheat cultivation area suffer from high temperature stress (Cossani and Reynolds, 2012). South Asia, which comprises of India, Bangladesh, Nepal and Pakistan, are the most populous regions of the world with a population of around 1.5 billion (Witcombe and Virk, 2001). Together with rice, wheat is the primary food crop of this region and, therefore, is of vital significance for food security of these developing nations (Joshi, 2007). South Asia has around 36 million ha (or approximately 16% of the global wheat area) under wheat cultivation, contributing to around 15% of the world's wheat production (FAO, 2007). The present wheat production in South Asia is around 98 million tons but the projected demand till 2020 has been estimated to be around 137 million tons. The demand of wheat is rising but there is no additional increase in land for wheat cultivation chiefly by reason of growing urbanization and diversification (Anonymous, 2007).

In most parts of the world, global climate change due to rising ambient temperature is considered as one of the most negative actors for agricultural productivity. Global temperature is expected to be increased by 3 to 5 ^{0}C by the end of this century (IPCC, 2014). Temperature accelerates the developmental process in plants leading to the induction of earlier senescence and shortening of the growth cycle (Bita and Gerats, 2013).Terminal heat stress is a key abiotic stress severely affecting wheat growth and yield (Joshi 2007; Dwivedi *et al*., 2015). A major part of wheat cultivation in South East Asia including India has been found to be under threat of high temperature stress (Joshi, 2007). Heat stress is more prevalent in Eastern Indo-Gangetic Plains (EIGP), central and peninsular India, and Bangladesh and is more moderate in the north western parts of the EIGP. Delayed sowing of wheat due to the late harvesting of rice is one of the main reasons for terminal heat stress in the eastern part of India (Dwivedi *et al.,* 2017a). Wheat is grown under subtropical environment in India during mild winters, which warms up toward the grain filling stage of the crop. The North-West Plain Zone (NWPZ) contributes about 80% of the total wheat production. Forced crop maturity and yield reduction of wheat in the NWPZ is due to high temperature in the months of February and March, which causes stressful conditions for growth. Climate change does not only increase the mean temperature during the growth season but also intensifies the frequency of extreme heat events (Teixeira *et al*., 2013). Teixeira *et al*. (2013) emphasized the need to develop strategies and policies regarding agriculture to mitigate the impact of heat stress on the global food supply, particularly in sub-tropical agricultural areas which bear extensive crop yield losses due to extreme temperature events.

Heat waves occur more frequently with global warming (Tebaldi *et al*., 2006; IPCC, 2007). Production of major agriculture crops can be drastically reduced due to high temperature peaks even when they occur just for few hours (Prasad *et al*., 2008). The damage due to heat stress is particularly high when elevated temperatures occur concurrently with the critical crop developmental stages, particularly the reproductive period. Because of this, the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) has acknowledged heat stress as an important threat to global food supply (IPCC, 2007). Early reports of heat stress on wheat, indicated a threshold temperature of 31 °C for the expected reduction in grain number during the period around anthesis (EyshiRezaei *et al*., 2015) but other studies showed 30 °C (Liu *et al.,* 2016) or 27 °C (Tashiro and Wardlaw, 1989) as heat stress threshold temperature in wheat. Asseng *et al*. (2015) tested 30 wheat crop models with artificial heating where mean temperatures in the growing season ranged from 15 to 32°C. There was a 1 to 28% decrease in wheat yield across 30 sites around the world from 1981 to 2010 with a 2 °C increase in temperature and the variation increased between 6 to 55 % when the temperature increased to 4 °C. Asseng *et al.* (2015) also projected global wheat production to decline by 6% for each 1 °C of further temperature increase.

Lower yields are obtained in dry and semi-dry environments as a result of continual rise in temperature that coincide with the anthesis and grain filling periods of crops (Moral *et al*., 2003, Dwivedi *et al.,* 2015). Due to global warming and changes in climate patterns, it is vital to mitigate the effects of heat stress and identify potential ways of improving heat tolerance for the success of wheat production under heat stress environments. Deryng *et al*. (2014) considered selection of cultivars and managing sowing windows as adaptive measures under extreme heat stress conditions. Some other adaptation measures are surface cooling by irrigation (Lobell *et al*., 2008), antioxidants defense (Suzuki *et al.,* 2011; Caverzan *et al*., 2016), and osmoprotectants (Farooq *et al*., 2011; Kaushal *et al*., 2016). However, development of heat-tolerant wheat varieties and improved pre-breeding materials for any future breeding program is vital in meeting food security (Ortiz *et al.,* 2008). Proteomic and transcriptomic studies are significant to identify environmental stress responsive genes and proteins that affect yield and quality of wheat. The problem of heat stress is likely to be even worse in the near future under global climate change scenarios, which has become one of the utmost challenges that humanity will face to feed the growing population. Hence, development and identification of terminal heat stress tolerance wheat germplasm may be a noble strategy to resolve the imminent crucial problem caused by global warming. Besides, it is crucial to develop genotypes that are early in maturity so as to escape the terminal heat stress (Joshi, 2007).

MORPHO-PHYSIOLOGICAL TRAITS INFLUENCED BY HIGH TEMPERATURE

Late sowing of wheat in India, particularly in the EIGP, is a quite common practice due to the late harvesting of long-duration rice varieties. Heat stress has been described as a complex phenomenon affecting plant growth and physiology, ultimately resulting in poor yield and grain quality (Mondal *et al*., 2013). Heat stress has also been reported to modify plant water relations (Hasanuzzaman *et al*., 2012, 2013), thereby reducing photosynthetic performance (Almeselmani *et al*. 2012). It also alters the metabolic activities in plants leading to the production of reactive oxygen species (Farooq *et al*., 2011; Wang *et al*., 2011). Furthermore, heat stress has also been found to alter hormonal levels in plants, promoting ethylene production (Hays *et al*., 2007; Krasensky and Jonak, 2012). Elevated temperature also hampers the reproductive development in plants, leading to impaired pollen tube formation and pollen mortality (Oshino *et al*., 2011). High temperature also induces considerable variations in the gas exchange processes and membrane thermo stability. Disturbance of protection system under high temperature stress caused an alteration in normal carbon metabolic process, which in turn negatively regulated starch granule deposition in the developing endosperm. Studies also show that rises in temperature causes metabolic changes in the wheat senescence (Farooq *et al*., 2011). Furthermore, heat stress also led to the inhibition of chlorophyll biosynthesis which triggers the senescence programme (Gupta *et al*., 2000). Heat stress during the terminal phase of the crop also inhibits starch biosynthesis which in turn reduces the normal grain size (Kushwaha *et al*., 2011). Deshmukh *et al*. (1991) suggested the estimation of membrane stability in terms of ion leakage to act as an index for screening wheat genotypes against heat. Apart from these, production of active oxygen species (AOS) was suggested as another criteria to measure the impact of heat stress (Liu and Huang, 2000). However, plants have developed a chain of scavenging mechanisms that convert highly AOS to H_2O under heat stress conditions (Larkindale and Huang, 2004). The protection mechanism at the cellular and sub- cellular levels is manifested via various anti-oxidants like superoxide dismutase, ascorbate peroxidase, glutathione reductase, and catalase while metabolites like glutathione, ascorbic acid, α-tocopherol, and carotenoids were produced regularly inside the plant system.(Sairam *et al*., 2000, Bansal and Srivatstava, 2012).

Morpho-anatomical and phenological responses

High temperature alters plant morphology and phenology in terms of leaf area, plant height, and pattern of plant development. Previous studies showed that long-term impact of high temperature stress on growing seeds caused poor germination and vigor; in turn affecting emergence and seedling establishment. The harmful effect of heat stress has also been observed in terms of scorching of leaves and twigs, leaf senescence, lesser canopy growth and poor yield (Vollenweider, 2005). One of the severe effects of high temperature is the premature death of plants (Hall, 1992). Moreover, little information is available regarding the anatomical changes of the plant system under high temperatures. Reduction in cell size, partial closure of stomata for restriction of water loss, and increased number of xylem vessels in root and shoot have been observed at whole plant level in response to heat stress (Anonymous, 2004). At the sub-cellular level, significant alterations occur in the chloroplast structure that causes variation in the normal photosynthetic process. Heat stress negatively regulates the stacking of the grana and structural organization of thylakoids (Karim, 1997). The collective effect of the heat stress-induced morpho-physiological alterations may lead to poor canopy formation and decreased productivity. Further depiction of variations in terms of plant phenology due to high temperature stress provides a clue for the better understanding of the interaction between the plant and its surrounding atmosphere. Different stages of plant growth vary in their sensitivity to rising temperatures; however, it is species and genotypic specific (Howarth, 2005). Moreover, the reproductive stage is highly vulnerable to heat stress. During reproduction, a spell of heat stress lead to the pollen sterility and abortion of the open flower, and this may vary between species (Guilioni, 1997; Young, 2004).

Physiological responses under heat stress

Physiological responses of wheat to terminal heat stress have been found to be well determined by genotype resistance or susceptibility (Almeselmani, 2006). Increase in temperature due to late sowing significantly decreases leaf ascorbic acid content and relative water content (RWC) in wheat after anthesis (Sairam *et al*., 2000).

Waters relations and heat stress

Plant water status is one of the important parameters under changing temperatures as it is severely impeded by heat stress (Machado and Paulsen, 2001). Simoes-Araujo *et al*. (2003) showed that high temperature stress leads to reduced water availability under field conditions. In general, during daytime, high rate of transpiration in plants creates water insufficiency, causing a lower water potential and leading to disturbances of many physiological processes (Tsukaguchi, 2003). Relative water content (RWC) of wheat cultivars were studied in leaves under normal and late sowing conditions during the dry seasons and the results showed a reduction in RWC across the cultivars as compared to the normal sown condition (Dwivedi *et al*., 2017b). It was observed that, high temperature strongly affects water relations when water is limiting. Thus, increasing the level of thermo-tolerance in wheat might improve its potential to acclimate to both high temperature and drought (Machado and Paulsen, 2001).

Accumulation of compatible osmolytes under heat stress

A major adaptive mechanism to extreme temperatures is the accumulation of certain low-molecular weight organic compounds called osmolytes like sugars, polyols, proline, glycine betaine, and tertiary sulphonium (Sakamoto, 2002, Sairam and Tyagi, 2004). Accumulation of such osmolytes provides tolerance to the plant under high temperature stress. One important osmolyte Glycinebetaine (GB) plays a significant role in plants under salinity or high temperature (Sakamoto, 2002). Another compatible solute proline also acts as an osmo-protectant and has been widely reported in various plants in response to abiotic stresses (Kavi Kishore *et al*., 2005). Glycine betaine and proline act as a buffering agent thus buffer cellular redox potential under high temperature stress (Wahid and Close, 2007).

Photosynthetic characteristics under heat stress

Plant growth is usually determined by various gas exchange traits and both are severely impeded by heat stress. Therefore, modifications in these physiological activities regulate the thermal tolerance. Wise *et al.* (2004) reported that photochemical reactions in the thylakoid lamellae and carbon metabolism in the stroma of the chloroplast are the main sites of heat injury. Chlorophyll fluorescence has been shown to be correlated with thermo-tolerance (Yamada 1996). Under high temperatures, the photo system II activity is greatly reduced as it is highly thermo-sensitive (Camejo *et al*., 2005). Heat stress alters the enzymatic activities involved in carbon metabolism. Rubisco, the chief enzyme of Calvin cycle is severely down-regulated under heat stress that alters the RuBP regeneration rate through disrupted electron transport chain and inactivated oxygen evolving enzymes of PSII (Salvucci, 2004). Moreover, the concentration of photosynthetic pigments (Todorov *et al.,* 2003), different soluble proteins, and rubisco binding proteins (RBP) decreases due to heat shock. Heat stress also affects the large and small sub units of rubisco in darkness; however, it induces them in light, indicating their functions as chaperones and heat shock proteins (HSP) (Kepova *et al*., 2005). Further, the starch or sucrose synthesis greatly influenced by heat stress as noticed from decreased activities of sucrose phosphate synthase (Chaitanya *et al*., 2001), ADP glucose pyrophosphorylase, and invertase (Vu *et al*., 2001). A familiar impact of increasing temperature in plants is the damage caused by heat-induced imbalance in photosynthesis and respiration. Heat stress causes decrease in the photosynthesis rate contrasting with significant increase in the dark and photo-respiration rates. Moreover, the photosynthetic CO_2 assimilation rate in developing leaves has been found to be less influenced by high temperature than the completely developed leaves.

Senescence of leaves due to physiological changes in cool season cereal species due to decreased chlorophyll content may be the effect of heat stress. Further, it is important to understand how terminal heat stress particularly impairs chlorophyll biosynthesis (Almeselmani *et al*., 2011).Heat stress-induced degradation of chlorophyll and thereby reduced photosynthetic rate in plants may be due to the over accumulation of ROS Alternatively, reduction in photosynthetic rate can also be explained through restrictions in stomatal and non-stomatal conductance under high temperature stress (Misson *et al.,* 2010). According to Shao *et al*. (2008), limitation in non-stomatal conductance may be induced by the ROS-induced membrane injury as depicted from the membrane stability index. Reduced transpiration under heat stress may be due to the unavailability of enough water caused by lower conductance.

Assimilate partitioning inside plant system under heat stress

About 30–50% of global yield variability was explained by climate related factors (Ray *et al*., 2015; Frieler *et al*., 2017; Zampieri *et al*., 2017). Liu *et al*. (2016) estimated that 1 °C global temperature increase might cause reduction in global wheat yield by 4.1% to 6.4% depending on the method used for yield projection. Increased mean temperatures mainly results in a shortening of the length of the growing season by acceleration of the development rate (Asseng *et al*., 2015).Heat stress severely decreases the grain yield in plants by hampering the source-sink movement. Assimilate partitioning in the plant system take place via two major modes i.e. symplastic and apoplastic pathways and these plays significant roles in transfer and partitioning of assimilate under heat stress (Taiz and Zeiger, 2006; Yang *et al*., 2002). Wardlaw (1974) reported that three main reasons for lower grain filling rate in wheat under heat stress are source (flag leaf blade), sink (ear), and transport pathway (peduncle).The transport and portioning of assimilates (phloem loading) is optimum up to 30 ^{0}C; however, the movement through the shoot is independent of temperature. In the case of wheat, the transport and mobilization of assimilates are highly temperature-dependent. This suggests that improved mobilization efficiency from the source to the sink act as a key strategy for better grain filling and yield in wheat under high temperature stress. However, limited knowledge is available on assimilate partitioning under heat stress; thus in depth studies are required to improve production efficiency of the crop.

Cell membrane thermo-stability and heat stress

The role of cellular membranes under different stresses is critical for photosynthetic and respiration mechanisms (Blum 1988). Plant cells maintain the membrane fluidity under heat stress through denaturation of proteins or increased amount of unsaturated fatty acids (Savchenko *et al*., 2002). Heat stress induces the membrane permeability, leading to increased electrolyte leakage. Heat stress tolerance in plants has been found to be associated with decreased cell membrane thermo-stability (CMT) and has been well established in wheat (Blum *et al*., 2001).

Hormonal changes inside plant system under heat stress

Plants are usually capable of sensing and acclimatizing themselves to the unfavorable environmental conditions. Plants' tolerance towards the changing climatic conditions is significantly governed by their specific and genotypic variation. Regulation of major phyto-hormones play important role in this background. It was observed that the hormonal homeostasis, stability, content, biosynthesis and compartmentalization are altered under heat stress (Maestri *et al*., 2002). Different environmental stresses including high temperature resulted in increased levels of ABA. ABA helps in adaptation of plants to desiccation by modulating the regulation of numerous abiotic genes (Xiong *et al*., 2002). Maestri (2002) reported that the induction of ABA is an important component of thermo-tolerance. Other studies also suggest that ABA-mediated induction of several HSPs (e.g., HSP70) may be a probable mechanism for conferring thermo-tolerance (Pareek *et al*., 1998).

Among plant hormones, salicylic acid (SA) is also involved in high temperature responses evoked by plants.SA has been reported to stabilize the heat shock transcription factors (trimers) and assists them to bind the heat shock elements with the promoter of heat shock related genes. Ca^{2+} homeostasis and antioxidant systems have been reported to be involved in SA-induced long term thermo-tolerance (Wang, 2006). In dwarf wheat varieties, heat stress-induced reduction in cytokinin content has been found to be accountable for decreased grain filling and dry weight (Banowetz, 1999). The possible functions of other phytohormones in plant heat-tolerance are yet to be revealed.

BIOCHEMICAL AND MOLECULAR TRAITS INFLUENCED BY HEAT STRESS

Oxidative stress and antioxidants potential of plant system under heat stress

Oxidative stress also known as secondary stress arises as a consequence of different kinds of abiotic stresses, including heat stress. Under heat stress, various kinds of active oxygen species (AOS) like singlet oxygen ($^1O_2$), superoxide radical (O^{2-}), hydroxyl radical (OH^-), and hydrogen peroxide (H_2O_2) are produced in the plant system, which causes cellular injury (Liu and Huang 2000). Reactive oxygen species causes cell injury by hindering the semi-permeability of cellular and sub-cellular membrane through membrane lipid peroxidation, which is usually measured in terms of malondialdehyde (MDA) or 2-thiobarbituric acid reactive substances (TBARS) content (Xu *et al*., 2006). For scavenging ROS, the plant produces various anti-oxidants like catalase (CAT), super oxide dismutase (SOD), and ascorperoxidase (APX). Superoxide dismutase (SOD) mediated detoxification of O_2^-results in H_2O_2production, which is further scavenged by CAT and APX. Further research regarding the involvement of signaling molecules for improving the antioxidant system under heat stress is required.

Role of stress proteins under heat stress

The plant synthesizes various stress proteins in response to abiotic stresses which perform a vital role in the survival mechanism of plants (Wahid *et al*., 2007). Further, HSPs are entirely involved in high temperature response; certain other proteins also play significant roles in this background. It has been found that with sudden or steady raise in temperature, plants experience the increased production of HSPs (Nakamoto and Hiyama, 1999). HSP-triggered thermo-tolerance by induction coincides with the organism being under stress and extremely rapid and intensive biosynthesis of HSPs. Particular HSPs have been identified in response to rising temperatures in different crop species. There is substantial evidence that attainment of heat-tolerance is directly related to the synthesis and accumulation of HSPs (Bowen *et al*., 2002).

Molecular research of heat stress in wheat

Despite advances in our understanding of genes of major effect conferring disease resistance in wheat (Krattinger *et al*., 2009), the genetic basis of heat adaptation is poorly understood. Currently, no "heat tolerance" genes have been cloned. Heat stress tolerance in plants has been found to be linked to different quantitative trait loci (QTLs) (Blum, 1988). QTLs in wheat have been detected by using various traits indicating heat tolerance, including GFD, CTD and yield (Paliwal *et al*., 2012; Mason *et al*., 2010; Bennett *et al*., 2012). Mason *et al*. (2010) performed studies involving QTL analysis for the heat susceptibility index (HSI) of yield and yield related traits. Mapping of QTL associated with heat tolerance traits may help in developing wheat cultivars with enhanced thermo-tolerance using marker-assisted selection (MAS) (Paliwal *et al*., 2012) (Table 1). Many QTLs have been identified in relation to heat stress (Table 2) however they need to thoroughly validate to confirm usefulness before selection in actual breeding programs.

Ca^{2+} and HSPs under heat stress

Seed germination, one of the critical stages in a plant's life cycle is severely hindered by heat stress. Thermo-tolerance of the adult plant is associated with the seed germination in wheat (Blum and Sinmen, 1994). The developing seedling uses the carbohydrates stored in the endosperm of cotyledons. Starch, the main storage reserve in the wheat endosperm is hydrolyzed by α- and β-amylases to glucose, maltose, and low molecular weight oligo- and di-saccharides. High temperature decreases starch mobilization caused by reduced activities of α- and β-amylases (Bhatia and Asthir, 2014). During seed germination, sucrose synthase, amylases, and invertases play critical roles in carbohydrate metabolism in wheat. Differential amylase activity has been found to determine thermo-tolerance in wheat (Alka *et al*., 1995). Calcium has been revealed to enhance thermo-tolerance in plants by regulating carbohydrate metabolism (Berenguer *et al*., 2004; Bhattacharjee, 2008). Elevated Ca^{2+}concentration regulate seedling growth under heat stress by stimulating the activities of sucrose

Table 1. List of QTL associated with heat tolerance (Adopted from Ni *et al*., 2018).

Chromosome	QTL	Trait	Reference
1A	*QHskm.tam-1A*	HSIfor kernel weight	Mason *et al.,* 2010
		Ethyleneproduction in spikes	Valluru *et al*., 2017
1B	*QCch.cgb-1B*	HTI for chlorophyll content	Li *et al*., 2012
	QWax.tam08-1B QWax.tam09-1B	Flag leaf cuticular waxes	Mondal *et al*.,2015
	QHtscc.ksu-1B	Chlorophyll content	Talukder *et al*., 2014
1D	*QHttmd.ksu-1D*	Thylakoid membrane damage	Talukder *et al*., 2014
2A	*QHskm.tam-2A*	HSI for kernel weight	Mason *et al*., 2010
2B	*QHthsitgw.bhu-2B*	TGW	Paliwal *et al*., 2012
	QHknm.tam-2B	HSI for kernel number	Mason *et al*., 2010
	QHtpmd.ksu-2B	Plasma membrane damage	Talukder *et al*., 2014
		Spike dry weight	Valluru *et al*., 2017
2D	*Q.Irwc.cgb-2D*	LeafRWC	Li *et al*., 2013
	Q.Icc.cgb-2D	Chlorophyll content	Li *et al*., 2013
	QTdl.tam09-2D	TD of flag leaves	Mondal *et al*., 2015
3A	*QCfph.cgb-3A*	HTI for chlorophyll fluorescence	Li *et al*., 2013
3B	*Q.Yld.aww-3B-2*	Grain yield	Bennett *et al*., 2012
	qDHY.3BL	Yield, TGW	Thomelin *et al*., 2016
	Q.Yld.aww-3B-1	Grain yield	Bennett *et al*., 2012
	QHknm.tam-3B	HSI for kernel number, HSI for kernel weight	Mason *et al*., 2010
		Ethylene production in spike	Valluru *et al*., 2017
	QTdl.tam09-3B	TD of flag leaves	Mondal *et al*., 2015
	QTds.tam09-3B	TD of main spike	Mondal *et al*., 2015
	QCch.cgb-3B	HTI for chlorophyll content	Li *et al*., 2013
3D	*Q.Yld.aww-3D*	Grain yield	Bennett *et al*., 2012
	QWax.tam09-3D	Flag leaf cuticular waxes	Mondal *et al*., 2015
	Q.Itgw.cgb-3D	TGW	Li *et al*., 2013
4B	*Q.Icc.cgb-4B.1*	Chlorophyll content	Li *et al*., 2013
		Spike dry weight	Valluru *et al*., 2017
4D	*Q.Yld.aww-4D*	Grain yield	Bennett *et al*., 2012
5A	*QTds.tam09-5A*	TD of main spike	Mondal *et al*., 2015
	QWax.tam09-5A	Flag leaf cuticular waxes	Mondal *et al*., 2015
5B		Ethylene production in spike, Spike dry weight	Valluru *et al*., 2017
	QTds.tam09-5B	TD of main spike	Mondal *et al*., 2015
	Q.Icc.cgb-5B.1	Chlorophyll content	Li *et al*., 2013
	Q.Icfps.cgb-5B	Chlorophyll fluorescence	Li *et al*., 2013
6A	*QHttmd.ksu-6A*	Thylakoid membrane damage	Talukder *et al*., 2014
	Q.Itgw.cgb-6A	TGW	Li *et al*., 2013

Table 1. List of QTL associated with heat tolerance (Adopted from Ni *et al*., 2018)(cont'd).

Chromosome	QTL	Trait	Reference
	QRdwh.cgb-6A	HTI for root DW	Li *et al*., 2013
	QSDwh.CGB-6A	HTI for shoot DW	Li *et al*., 2013
	Q.Ictd.cgb-6A.1	CTD	Li *et al*., 2013
6B		Spike DW	Valluru*et al*., 2017
7A	*Q.Yld.aww-7A-1*	Grain yield	Bennett *et al*., 2012
	QHttmd.ksu-7A	Thylakoid membrane damage	Talukder *et al*., 2014
		Spike DW	Valluru *et al*., 2017
	Q.Irwc.cgb-7A.1	Leaf RWC	Li *et al*., 2013
7B		Spike DW	Valluru *et al*., 2017
	QHthsitgw.bhu-7B	TGW	Paliwal *et al*., 2012
	QHthsiYLD.bhu-7B	Grain yield	Paliwal *et al*., 2012
	QlsYLD.bhu-7B	Grain yield	Paliwal *et al*., 2012
	QHtctd.bhu-7B	CTD	Paliwal *et al*., 2012
7D	*QHthsitgw.bhu-7D*	TGW	Paliwal *et al*., 2012
	Qls-dm.bhu-7D	Days to maturity	Paliwal *et al*., 2012

Table 2. Relatively heat tolerant wheat genotypes developed (Adopted from Dwivedi *et al*., 2017a).

Heat tolerant wheat varieties	WH730, GW273, NW1014, RAJ 3765, NW 1014, HUW 234, Halna, HD3120, DBW 14, HI 1563 and HD2987

andstarch-hydrolysing enzymes (Bhatia and Singh, 2000). Calcium ions (Ca^{2+}) alleviate heat-induced damages and assist the plant cells to recover from stress by forming heat shock proteins (HSPs) (Marina *et al*., 1999; Wang and Li, 1999).

Heat shock proteins play a crucial regulatory role in acquired heat tolerance. The HSPs are induced by heat stress function as molecular chaperones (Basha *et al*., 2004). They stabilize proteins by binding to unstable proteins and facilitating proper folding of non-native proteins under heat stress (Hendrick and Hartl, 1993). HSPs play an important role in protein folding, refolding, translocation, and degradation (Feder and Hofmann, 1999). Twelve cytosolic wheat small HSPs (Joshi and Nguyen, 1996) along with two mitochondrial sHSPs (Basha *et al*., 1999) and chloroplastics HSP (Chauhan *et al*., 2012) have been reported in wheat. HSP20 genes play an important role in the growth and development processes in wheat. Up-regulation of selected transcripts in wheat indicates strong correlation of plant defense under heat stress. Over-expression of small wheat chloroplastic HSP (TaHSP26) has been reported to improve thermo-tolerance (Chauhan *et al.* 2012). Wheat adaptation to heat stress is mediated by regulation of HSP genes with Heat shock factors (HSFs) (Xue *et al*., 2014). A member of HSFs- HSF3 of the wheat HSF family, has been found to be responsible for enhanced heat tolerance (Zhang *et al*., 2013).

Heat stress effect on reactive oxygen species and antioxidant activities

Energy-related metabolism in plant cells takes place in the mitochondria, chloroplasts and peroxisomes. These cellular compartments produce cytotoxic reactive oxygen species (ROS) under oxidative stress employed by heat stress (Gill and Tuteja, 2010; Caverzan *et al*., 2016). ROS is being detoxified by a specialized cellular antioxidant defence machinery. Heat stress disturbs the balance between ROS production and detoxification, causing severe damage to cellular components (Bhattacharjee, 2013). Accumulation of ROS is considered as one of the major phases in the heat stress signaling cascades. ROS-induced potential damage can be avoided by regulating the equilibrium between ROS production and detoxification at the intra cellular level. Production of hydrogen peroxide (H_2O_2) has been reported to depend on the intensity and duration of the stress. Difference in level of H_2O_2 between various cellular compartments is associated with the type of stress (Slesak *et al*., 2007).

The balance between the production and elimination of ROS is sustained by enzymatic and non-enzymatic antioxidants (Mittler, 2002; Mittler *et al*., 2004). The enzymatic anti-oxidative system comprise several antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), guaiacolperoxidise (POX) and enzymes of the ascorbate-glutathione (AsAGSH) cycle, such as ascorbate peroxidase (APX), glutathione reductase (GR) (Asada, 1999; Mittler, 2004). Non enzymatic components include the major cellular redox buffers ascorbate (AsA) and glutathione (GSH) as well as tocopherol, carotenoids and phenolic compounds (Mittler*et al*., 2004; Gratao*et al*., 2005; Scandalios, 2005). Super oxide dismutases establish a primary line of defence against ROS, by catalysing the dismutation of $O_2^{\cdot-}$(superoxide radical) to H_2O_2. These enzymes are classified according to their sub-cellular location and metal cofactor (Cu/Zn, Mn,Fe, and Ni).. Increase in the SOD transcript in response to differential heat shock treatment has been observed in wheat indicating enhanced tolerance (Kumar *et al.* 2013). Catalases catalyze the conversion of H_2O_2 into H_2O. CAT proteins are abundantly localized to peroxisomes. The CATs genes respond differentially to various stress conditions (Scandalios, 2005). Ascorbate peroxidases detoxify H_2O_2 through its reduction into H_2O and use ascorbate as a specific electron donor. APX proteins are distributed in chloroplasts, mitochondria, peroxisomes, and the cytosol. The APX genes show differential modulation by several abiotic stresses in plants (Caverzan *et al*., 2012). A mutant wheat line with reduced thylakoid APX activity has been reported to cause impaired photosynthesis (Danna *et al*., 2003). In wheat, several studies have reported alterations in the activity of SOD, APX, CAT, GR, and POX to govern heat-induced oxidative stress indicating positive activation of ROS detoxification (Sairam *et al.,* 2000). Heat tolerance in wheat has been found to be determined by higher antioxidant capacity resulting in lower oxidative damage, which has a distinctive genotypic effect.

Heat stress effect on photosystem II

Photosystem II (PSII) is a large pigment-protein complex, comprising reaction centers (RCs), the oxygen-evolving complex (OEC), and the chlorophyll a/b light-harvesting antenna complex (LHC) (Allahverdiyeva *et al*., 2013). The PSII complex is composed of many low molecular weight proteins (molecular mass below 15 kDa), involved in PSII dimerization, assembly, electron transfer, and protein phosphorylation (Shi *et al*., 2012; Pagliano *et al*., 2013). Heat stress leads to the inactivation of PSII (Oukarroum *et al*., 2012), stomatal closure (Yamori *et al*., 2006a), and deactivation of rubisco (Yamori et al. 2006b), thereby inhibiting the Calvin cycle and photosynthetic activities in plants (Crafts-Brandner and Law, 2000). Heat stress has been revealed to primarily damage RCs of PSII. Within the PSII complex, the D1 protein – the main member of PSII core - is the most sensitive tos heat stress (Li *et al.,* 2016). Heat stress-induced ROS production in the thylakoid membrane has been found to be involved in degrading the D1 protein (Yamamoto *et al*., 2008) and inactivating of PSII (Yamashita *et al*., 2008).

Heat stress and pollen development

During reproduction, a short period of heat stress can cause flower abortion (Guilioni *et al*., 1997; Young *et al*., 2004). Elevated ambient temperature negatively affects pollen development in wheat. Heat stress for prolonged duration depletes the amount of food reserves in maturing pollen grains owing to increased respiration for sustaining adaptive metabolic activity, thereby resulting in pollen mortality (Dwivedi *et al*., 2017b). Furthermore, high temperature-induced earlier microsporogenesis causes aberrations in the tapetum development and decreases hexose supply by tapetal cells reducing pollen viability (De Storme and Geelen, 2014). Aberrations during tapetum development and degeneration, including hypertrophy and prematureness, along with delayed degeneration and morphology of the tapetal endoplasmic reticulum, have been observed in wheat (Saini *et al*., 1984). Pollen and tapetum cells accumulate innumerable mitochondria and show fast respiration during development and pollen tube growth (Lee and Warmke, 1979; Selinski and Scheibe, 2014). Heat stress leads to a dramatic increase in ROS within the mitochondria, obstructing the ROS scavenging mechanism. Hydrogen peroxide level within pollen has been observed to increase dramatically in wheat under heat stress (42 ^{o}C) accompanied by the antioxidant activity (Kumar *et al*., 2014). The APX has been found to be upregulated in developing wheat pollen in response to heat stress (Chaturvedi *et al.,* 2015; Frank *et al*., 2009) (Table 3).

CRITERIA FOR SCREENING HEAT TOLERANT WHEAT GENOTYPES

Various criteria have been reported by many researchers to identify heat tolerant wheat genotypes (Table 2 and 4). Traits like heat susceptibility index (HSI) (Mason *et al*., 2010), membrane thermo-stability (Reynolds *et al*., 1994) canopy temperature depression (Reynolds *et al*., 1994) chlorophyll content, the normalized difference

Table 3. Different molecular strategies of heat stress mitigation in plants.

Molecular strategies	References
Elevated Ca^{2+} concentration	Marina *et al.* (1999); Wang and Li (1999); Bhatia and Asthir (2014)
HSFs and HSPs upregulations	Blumenthal *et al.*(1994), Joshi and Nguyen (1996); Basha *et al.* (1999); Sumesh *et al.* (2008), Sharma-Natu *et al.*(2010), Chauhan *et al.* (2012); Zhang *et al.* (2013); Xue *et al.* (2014)
Over-expression of DHN-5	Brini *et al.* (2010)
Over expression of glutaredoxin (GRX)	Lillig *et al*. (2008); Cheng *et al.* (2009); Wu *et al.* (2012)

Table 4. Potential traits/characters for screening wheat for heat tolerance.

Traits/characters	References
Photosynthesis rate	Reynolds *et al*.(1994), Dwivedi *et al*. (2017b)
Spike photosynthesis	Cossani and Reynolds (2012),
Leaf chlorophyll content	Reynolds *et al*.(1994)
Canopy temperature depression	Shanahan *et al.* (1990); Reynolds *et al.* (1994, 1998); Amani *et al*.(1996); Blum *et al.* (2001), Dwivedi *et al.* (2017b)
Membrane stability	Talukder *et al.* (2014), Dwivedi *et al.* (2017b)
Flagleafstomatal conductance	Reynolds *et al.* (1994)
Grain weight	Tyagi *et al.* (2003); Singha *et al.* (2006); Dias and Lidon (2009), Bennani *et al.* (2016),Rezaei *et al*. (2018)
Early heading	Tewolde *et al*.(2006), Hussain *et al*. (2016)
High temperature index/ Heat Susceptibility Index	Rane and Nagarajan (2004), Dwivedi *et al.* (2017b)
Stay-green	Xu *et al.* (2000); Reynolds *et al.* (2001) Lopes and Reynolds (2012), Nawaz *et al.* (2013),Abdelrahman *et al.* (2017)
Stem carbohydrate re-mobilization	Cossani and Reynolds (2012), Dwivedi*et al*. (2017b)
Pollen viability	Dwivedi*et al*. (2017b)
Number of fertile spikes	Khan and Kabir (2014), Bennani *et al*. (2016)
Anti-oxidants activity	Sairam *et al*. (2000), Gupta *et al.* (2013)
Grain filling durations	Song *et al.* (2015), Dwivedi *et al.* (2017b)

vegetation index, stay-green trait (Harris *et al*., 2007), and stomatal conductance (Reynolds *et al.,* 1994) have been reported as the marker traits to differentiate heat susceptible and tolerant wheat genotypes. Canopy temperature depression (CTD) is considered to be the most efficient to assess heat tolerance since one single reading integrates scores of leaves (Reynolds *et al*., 1994), CTD is highly heritable and easy to measure using a hand-held infrared thermometer on sunny days (Reynolds *et al*., 1994).Even though an association between the stay green trait and yield and yield traits has been reported in various crops, published studies on a possible association between the stay green trait and CTD in different crops are scarce. Under hot and irrigated conditions, using infrared thermometers has been successfully used to screen wheat genotypes for their performance by measuring the difference between canopy and air temperature (CTD) (Reynolds *et al*., 1994). Gibson and Paulsen (1999) reported yield loss up to 3 to 5 % for 1 ^{0}C rise in temperature which also influences physiology, growth and yield traits. High temperature at anthesis decreases the grain number per spike (Prasad *et al.,* 2008) and grain size (Viswanathan and Chopra, 2001), both of which have significant effects on grain yield. The grain yield was affected by decreasing size of individual grains due to high temperature at the grain filling stage. Ferris *et al.* (1998) reported that in wheat, both number of grains and grain weight seem to be sensitive to heat stress, as, at maturity there is a decline in the number of grains per head with rising temperature. Mahrookashani *et al.* (2017) reported that single grain weight was reduced under drought stress by 13%–27% and by 43%–83% under combined stress (heat and drought stress). Further responses at cultivar level were similar for heat stress but different for combined stress (heat and drought stress) and drought alone. The magnitude of reduction in grain number was more under combined stress (heat and drought stress) than under drought or high temperature stress alone. Reproductive processes are clearly affected by high temperatures in most plants, which eventually affect fertilization and post-fertilization processes leading to reduced crop yield. Recommended wheat cultivars for sowing under delayed sowings of the Indo-Gangetic Plains of India are PBW 373, UP 2425, and RAJ 3765for the NWPZ and NW 1014, HD2643, HUW 510, HUW 234, HW 2045, DBW 14, NW 2036 and HP 1744 for the NEPZ.

MECHANISM OF HEAT TOLERANCE

The mechanism for heat tolerance can be understood by investigating the physiological responses of tolerant and susceptible genotypes at various stages of plant development, especially during grain filling stage of wheat. Plants adopt various mechanisms to survive under high temperature condition *viz.,* phenological and morphological adaptations and avoidance or acclimation responses such as changing the leaf angle, cooling through transpirational system, and alterations in membrane lipid compositions. As per earlier studies, smaller yield losses in different plants correlated with early maturity under high temperature which indicates earliness as one of the escape mechanisms (Adams 2001). Plants experience many types of environmental stresses at different growth stages and their mechanisms of response may vary at the tissue level (Queitsch *et al*., 2000). The initial stress signals in terms of ionic effects or membrane composition triggers downstream signaling processes and transcriptional control, which lead to the activation of stress-responsive mechanisms and creation of homeostasis through protection and repair of damaged proteins and membranes (Bohnert *et al.,* 2006). Several key tolerance mechanisms, including osmolyte accumulation and compartmentalization, ROS scavengers, late embryogenesis, abundant proteins and factors involved in signaling process, and gene level regulation are major drivers to counteract the heat stress effect (Wang 2004). The tolerance process begins with the sensing of heat stress, their signaling, and production of many metabolites that enable the plant to counteract the ill effect of high temperature stress. The ROS scavengers like CAT, SOD, POX, APX, and ascorbic acid are also important players in the tolerance mechanism of heat stress (Maestri *et al*., 2002). Furthermore, at the molecular level, the induction and expression of heat shock proteins (HSPs) is highly correlated with the thermos-tolerance mechanism of the plant. HSPs act as a molecular chaperone and provide protection to the cellular machinery. Many studies pointed out the role of HSPs in various stress responsive mechanisms (Wang 2004).

CONCLUSION AND FUTURE OUTLOOK

It is obvious that heat stress negatively influenced the wheat plant's physiology and yield. Furthermore, despite the vital need to identify heat tolerance genotypes and improve the heat tolerance level in wheat, a very limited number of heat-tolerant wheat varieties have been developed. Moreover, due to the complex nature of heat stress, the physiological and molecular mechanism happening inside plant system under heat stress is still not very clear. Therefore, it is very important that physiological and molecular variations for the trait be identified and characterized efficiently in order to introduce them in a breeding program. Furthermore, knowledge on the molecular physiology of the plant heat response can play an important role in speeding up the breeding programs for heat tolerance in wheat. QTLs identified in various mapping studies can, once validated, be exploited in breeding program to develop heat tolerant wheat genotypes. However, a major finding is that the plant heat stress response is highly complex, with challenges that may be tissue-, developmental stage specific. Thus, heat tolerance should not be regarded as a solitary trait and, as such, it is important to develop a comprehensive approach instead of a single, general strategy for generating heat tolerant wheat genotypes.

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