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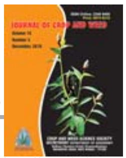

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# A review on conventional and molecular breeding approaches for exploring mechanisms underlying heat stress tolerance in wheat

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## ABSTRACT

*Wheat is one of the primary foods for more than 40 countries and for over 35% of the global population. The increased temperature during reproductive phase known as heat stress has emerged as a serious problem. Constant or transitory high temperatures may affect the plant growth and development which may lead to diverse morphological, physiological and biochemical changes in plants ultimately decrease in yield. Every 1°C rise in temperature above 28°C during grain filling, results in yield reduction by 3-4 %. To combat, the breeding for crops with enhanced heat tolerance is of pivotal importance to ensure global food security. The understanding of the mechanisms of the heat tolerance at the reproductive stage is the prerequisite for inducing toreance in wheat in particular. During recent past, a lot of information has been generated on classical as well as molecular breeding approaches. The present review aims to summarize those published data to give an insight into the underlying mechanism of heat stress tolerance in wheat.*

***Keywords***: Heat stress tolerance, morphological markers, molecular markers, QTLs and wheat

Wheat is a major cereal crop in the world occupying more than 220 million hectares of crop land for producing ~715 million tons of food grains with productivity of ~3.2 t ha-1 (FAO, 2015). A mathematical model, given by Paroda *et al*., 2013, indicated that the world will need around 1090 million tons wheat by 2050 through an annual production growth of 1.6% even under this changing climatic scenario. As evident from the global temperature rise (IPCC, 2014), ~ 40 % of the total wheat-growing area has been reported to be severely affected by heat stress (Reynolds *et al*., 2001). In India, the entire Indo-Gangetic plain has been reported to be under heat stress by 2050 (Ortiz *et al*., 2007). Naturally, breeding for crops with enhanced heat tolerance is of pivotal importance to ensure global food security (Rockström, 2003). Heat stress affects every physiological growth stage of wheat. The adverse impact of high temperature which is predominant during the grain filling stage, is regarded as terminal heat stress. It has been documented to result in yield loss even up to 40 % under severe condition (Hays *et al*., 2007). Every 1°C rise in temperature above 28°C during the grain filling stage has been shown to result in yield reduction by 3-4 % (Reynolds *et al*.,1994, 1998; Wardlaw et al., 1989). The major effects of heat stress in wheat include decreased grain weight, premature senescence, shriveled grains, reduced starch accumulation, altered starch-lipid composition in grains, lower seed germination, and loss of vigour (Balla *et al*., 2012). It can affect the integrity and functions of biological membranes by deforming the tertiary and quaternary structures of membrane proteins (Wahid *et al*., 2007; Hemantaranjan *et al*., 2014). As sole agronomic interventions to combat heat tolerance is not enough, breeding for heat-tolerant wheat has gained global importance. But due to the complex genetics of wheat (owing to its large and allohexaploid genome) and its heat tolerance mechanism, conventional breeding in this aspect has achieved insignificant success. Indirect phenotypic selection based on only associated traits like Grain Filling Duration (GFD), Thousand Kernel Weight (TKW), and Canopy Temperature Depression (CTD) has also remained as a major reason behind these limited achievements (Yang *et al*., 2002; Reynolds *et al*., 1994). However, the recent decoding of the wheat genome has broadened the scope of molecular breeding that can play a crucial role in achieving substantial success in developing wheat cultivars with enhanced heat tolerance. Both the molecular and classical approaches have been utilized by the researchers in order to understand the mechanisms as well as to induce heat tolerance in wheat. The present review is aimed to summerize the information generated through classical and molecular breeding approaches to deduce the heat stress tolerance mechanism in wheat.

## Heat stress and its manifestation in wheat

Almost all developmental stages including growth rate of wheat are affected by heat stress.Heat stress has

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been reported to alter different physiological processes of plants like assimilate partitioning, excess heat dissipation, electrolyte conductance, photosynthesis, plant water status, and senescence and all culminating in reduced yield (Wahid *et al*., 2007; Hasanuzzaman *et al*., 2013). Reduction in cell size caused due to loss of cell water has been documented to ultimately affect plant growth (Rodríguez *et al*., 2005). High evaporation demand lowers relative water content (RWC) of the plant (Hall, 2001) to cause senescence-related metabolic changes. Due to this, improper assimilate-partitioning takes place that has been found leading to a severe reduction in harvest index (Wahid *et al*., 2007) and thousand kernel weight (TKW; Ahmad *et al*., 2010). Relative water content is one of the measures of membrane stability and decreased membrane stability under heat stress has been documented to reduce the rate of assimilate transport from source to sink (Wahid *et al*., 2007; Farooq *et al*., 2011). An increase in electrical conductivity (EC) has been noticed due tomembrane malfunctioning and disruption (Hemantaranjan *et al*., 2014). Leaf RWC, stomatal conductance, and the rate of transpiration are influenced by canopy temperature CT (Farooq *et al*., 2009). It has been observed that CT lowers the plant water status (Pask *et al*., 2012) and stay green ability (Pinto *et al*., 2010; Lopes and Reynolds, 2012).

Photosynthesis is a sensitive process and affected most due to heat stress. Among different cell organelles, chloroplast stroma and thylakoid lamellae are the most affected parts (Ristic *et al*., 2008a; Mathur *et al*., 2014). Leaf exposed to ~40 °C has been found to cause irreversible changes in key enzymes likerubisco, rubiscoactivase, and to damage the important photosystem II (Mathur *et al*., 2014). Dissociation of rubiscoactivase under heat stress conditions has been found to significantly reduce photosynthetic activity in wheat (Raines *et al*., 2011). Additionally, the disordered fluidity of thylakoid membranes and dissociation of the light-harvesting complex II from the photosystem II have been reported as the major reason behind the heat sensitivity of photosystem II (Dias and Lidon, 2009; Iwaia *et al*., 2010). These consequences are attributed to the increased production of reactive oxygen species (ROS). Photorespiration in the flag leaf of wheat is significantly higher under heat stress because of change in solubility of O2 and CO2 and the affinity of rubisco for these gases (Almeselmani *et al*., 2006; Cossani and Reynolds, 2012). Moreover, premature leaf senescence has been observed as one of the most damaging outcomes of heat stress that results in chloroplast destruction, vacuolar collapse, and finally a break of plasma membrane integrity and cellular homeostasis (Akter and Islam, 2017).

The perception of heat stress by wheat is reflected by aberrant agronomical traits. Hence, agronomic traits like plant height, productive tillers, biomass, spike length, and thousand grain weight have been explored for indirect selection of heat-tolerant wheat lines. The inhibition of initiation and survival of productive tillers, a key determinant of wheat yield, have been reported (Hasanuzzaman *et al*., 2013). However, the pre-flowering and anthesis stages of wheat have been found most vulnerable (Cossani and Reynolds, 2012; Prasad *et al*., 2008), as even a short period of high-temperature exposure can significantly reduce the grain number per spike and size leading to yield reduction (Ferris *et al*., 1998). In wheat, 3-day heat shock during flowering has been found to result in structurally abnormal and/or non-functional florets (Hedhly *et al*., 2009). The lower ability of pollens to germinate coupled with restricted pollen tube growth has been observed under heat stress during anthesis. On the other hand, post-anthesis abortions of grains and decreased grain weight under heat stress conditions have been found to reduce wheat yield. Moreover, the early grain filling period is relatively more sensitive than later periods to high-temperature stress. Adverse impacts of heat stress on spikelet initiation, pollination, and fertilization (Porter and Gawith, 1999; Semenov, 2009; Anjum *et al*., 2008; Kaur and Behl., 2010) have been reported.

Apart from its impact on agronomical traits, heat stress has been found to adversely affect the wheat grain quality also (Spiertz *et al*., 2006; Borghi *et al*., 1995). Generally, starch synthesis has been documented to be reduced in developing wheat kernels owing to the high level of heat susceptibility of the enzyme starch synthase (Keeling *et al*., 1993; Jenner *et al*., 1994). Because of the reduced efficiency of starch biosynthetic enzymes, a reduction up to one-third of total endosperm starch has been documented under high temperatures (30-40°C) (Zhao *et al*., 2008; Liu *et al*., 2011). Furthermore, amylose content is a key determinant of starch properties in the endosperm, as variation in amylose content has been observed to alter starch gelatinization and pasting properties (Hurkman *et al*., 2003). The chain length distribution of amylopectin glucan chains may be modified under heat stress. Amylose content and the amylose: amylopectin ratio has been postulated to increase with the increasing temperature (Labuschagne *et al*., 2009; Sharma *et al*., 2015). Apart from starch, wheat grain quality vastly depends on the protein content and composition. In wheat, heat stress has been found to affect the grain protein concentration (Lizana and Calderini, 2013) and to diminish the flour quality by plunging gluten strength-related parameters, lactic acid retention capacity, and mixograph peak time (Li *et a*l., 2013). Furthermore, decreased sedimentation index due to a reduction in essential amino acid content has been observed under heat stress conditions (Dias *et al*., 2008).

### *Classical breeding aprroaches*

Plant breeding for wheat heat tolerance is now only in the early stage and much more attention needs to be given in the near future (Ortiz *et al*., 2007; Ashraf, 2010). Heat tolerance in wheat and other crops is a very complex trait due to the lack of any direct selection criteria. Due to the complex polygenic nature of the trait (Blum, 1988; Howarth, 2005; Bohnert *et al*., 2006), phenotypic selection using indirect selection parameters *viz*., grain filling duration (Yang *et al*., 2002), thousand grain weight (Sharma *et al*., 2008) and canopy temperature depression (Ayeneh *et al*., 2002; Reynolds *et al*.,1994, 2001) for selecting heat-tolerant wheat lines have been performed. Naturally, lack of precision and labour intensive nature of this selection criteria have remained as a bottleneck in this aspect. Despite that, several parameters have been suggested to identify heat-tolerant plants or lines in wheat. Among yield traits, plot yield (Fisher *et al*., 1998), Thousand grain weight (TGW) (Shpiler and Blum, 1991), grain filling duration (GFD) (Randal and Moss, 1990), number of effective tillers per plant (Richards, 1996) are important. Morphological traits like early ground cover (Richards, 1996), stay green (Zhao *et al*., 2007), leaf rolling (Araus, 1996) and biomass (Reynolds *et al*., 2001) have also been found useful. Among physiological traits, canopy temperature (Reynolds *et al*., 1994), photosynthetic rate (Rijven, 1986), chlorophyll content (Al-Khatib and Paulsen., 1984), stomatal conductance (Reynolds *et al*., 1994), membrane thermostability (Saadalla *et al*., 1990) have been considered. Susceptibility index (SI) has been used as an effective tool for heat tolerance and drought tolerance in both hexaploid wheat (Kirigwi, 2005) and durum wheat (Peleg *et al*., 2009). Consequently, attempts have been made to identify the concerned candidate quantitative trait loci (QTL) and/or gene(s). It has been suggested that mapping each yield component as a separate SI would allow the identification of QTL affecting individual traits that would collectively contribute to overall yield stability and heat tolerance (Mason *et al*., 2010). Therefore, it has been suggested that HSI may be used as an indicator of yield stability and as a proxy for indicating heat tolerance. However, the complexity of the wheat genome has made the work much more challenging. The wheat genome complexity lies not only upon its large size (5 times the size of the human genome!) but also to its very high proportion of relatively long, repetitive regions (Li *et al*., 2004). Another major challenge in this regard is assembling the wheat genome owing to its allohexaploid genome with three genomic components (A, B, and D), each comprising of seven chromosomes. The recent release of the draft genome sequence (Brenchley *et al*., 2012) has provided information regarding~96,000 genes and ~132,000 single nucleotide polymorphisms (SNPs) distributed over the A, B, and D genomic compartments. With the increasing knowledge of wheat genome sequence and currently available whole-genome next-generation sequencing (NGS) data, novel information is supposed to boost our understanding of complex traits in wheat, like heat tolerance. Sequence-based molecular markers have been and are being highly explored in this regard.

### *Molecular breeding aprroaches*

As mentioned earlier, heat tolerance is quantitative. That means it is controlled by several genes/QTLs. These QTLs may be involved in interactions with each other (QTL × QTL interaction) and/or with the environments (E) (QTL × E and QTL × QTL × E interactions). The QTLs for heat tolerance in wheat were reported using different parameter like GFD (Yang *et al*., 2002; Mason *et al*., 2010), senescence-related traits (Vijayalakshmi *et al*., 2010), and experiments were done to identify QTLs using other important parameters such as thousand grain weight (TGW) and canopy temperature depression (CTD). The heat susceptibility index (HSI) parameter for thousand grain weight (HSITGW), canopy temperature (HSICT) and grain filling duration (HSIGFD) have been utilized to identify the QTLs for heat tolerance in wheat (Paliwal *et al*., 2012). Senescence-related traits have been examined to detectnine QTLs for heat tolerance on chromosome 2A, 6A, 6B, 3A, 3B, and 7A in wheat, where both the parents have been found to contribute favourable alleles for most of the senescence-related traits (Vijayalakshmi *et al*., 2010). The simple sequence repeat (SSR) markers Xgwm356 and Xgwm5,linked to the senescence-related traits have been proposed to be useful in marker-assisted breeding. In tetraploid wheat genotypes, QTLs for chlorophyll content, flag leaf temperature depression (FLTD) and individual kernel weight (IKW) on chromosome 1B (QChlc.tamu-1B), 2B (QFlt.tamu-2B), and 5A (QIkw.tamu-5A), respectively, have been observed to be associated with heat stress tolerance (Ali *et al*., 2013). Most QTLs for drought tolerance and heat tolerance in wheat have been identified through yield and yield component measurements under water-limited conditions (Quarrie *et al*., 2006; Maccaferri *et al*., 2008; Mathews *et al*., 2008; Von Korff *et al*., 2008; McIntyre et al., 2009, Barakat *et al*., 2013, Zhang *et al*., 2013).The molecular markers Xcfd 22-7B and Xcfa2114-6A (for harvest index and TGW), Xgwm181-3B, Xwmc405-7B, and Xgwm148-3B (for spike harvest index), and

Xwmc166-7B (for grain weight per spike)have been reported to explain up to 20% of the phenotypic variation in durum wheat and the concerned mapped QTLs have been found to explain up to 49.5% of the phenotypic variation under drought stress environment (Golabadi et al., 2011). The QTLs for heat tolerance under hot and dry conditions have been reported on chromosomes 2B and 5B in a spring wheat population (Byrne et al., 2002). Three QTLs(on chromosomes 1B, 5B, and 7B) for heat tolerance in wheat have been detected using the Fischer susceptibility index (Mohammadi et al., 2008). Genes responsible for reproductive stage heat tolerance have been identified in a bi-parental population derived from a spring ? winter wheat cross (Esten and Hays, 2005). Previously, the QTLs linked to GFD have been mapped on short arms of chromosomes 1B and 5A, using single marker QTL analysis in an F2 population (Yang et al., 2002). Through this study, two markers, Xgwm11 and Xgwm293 have been proposed to be useful in molecular breeding for heat tolerance in wheat. The Xgwm11-linked QTL (with additive gene action) has been documented to contribute 11% to the total phenotypic variation in GFD in the F2 population. Similarly, the other marker Xgwm293-linked QTL have been found to have both additive and dominance gene action to explain 12% to the total variation in GFD. The results have helped to understand that heat tolerance of common wheat is controlled by multiple genes and marker-assisted selection with SSR markers might be useful for developing improved cultivars. As grain weight under heat stress during grain filling is an important measure of heat tolerance (Singha *et al*., 2006), the usefulness of grain-filling rate (GFR) and high potential grain weight has been proposed as a selection criterion for heat tolerance in wheat (Dias and Lidon, 2009). Three SSR markers (Xgwm132, Xgwm577, and Xgwm617) have been documented to be linked to grain filling rate through QTL analysis in an F2 population (Barakat *et al*., 2011). Similarly, thousand grain weight (TGW) is considered to be a very important yield contributing trait and has a role in thermo-tolerance in cereals. The QTL of TGW, which has been dissected into a single Mendelian gene on the short arm of chromosome 7D, has been mapped (Röder *et al*., 2008). As the number of effective tiller number per plant has been reported as an important parameter for heat stress tolerance (Richards, 1996), nine QTLs for effective tiller per plant have been mapped in the wheat genome (Li *et al*., 2010) using 168 doubled haploid (DH) lines, derived from a cross between two winter wheat cultivars (Li *et al*., 2010). Previously, one QTL for yield (on chromosome 7D) and three QTL for TKW (on chromosomes 2B, 5B, and 7A) have also been identified (Groos *et al*., 2003). In the recent past, the pleiotropic effect of QTL for grain yield in bread wheat is located on chromosome 3B, which could increase grain yield by 12.5 %, particularly in environments where both heat and drought stress occurred (Bonneau *et al*., 2013). Mason *et al*., 2013 have also reported 25 stable QTLs for the 15 traits measured with phenotypic variation ranging from 3.5 to 27.1% derived from a cross between the stress-tolerant cultivar 'Halbert' and heat stress-sensitive cultivar 'Karl92'. Subsequently, other QTLs for heat and drought tolerance in wheat have been identified (Acuña *et al*., 2014). Previously, the marker gwm11 on chromosome 1B is associated with yield under heat stress (Kuchel *et al*., 2007). The stable QTLs for HSI of single grain weight (on chromosome 1A and 2A), grain weight (on chromosome 3B), and grain number (on chromosome 2B and 3B), which explains up to 22% of phenotypic variation under short-term heat stress in wheat have also been identified previously (Mason *et al*., 2010).

'Stay green' has been considered as an important morpho-physiological trait for heat tolerance in wheat. It helps the plants to retain their leaves in the active photosynthetic state when any abiotic stress occurs (Rosenow, 1983). Stay green trait keeps leaves green and postpones the senescence and helps the plants to keep on photosynthesis for some extra time. The stay-green trait has been reported to influence the grain yield of different crops, especially under heat conditions. In wheat, stay green has been associated with increased leaf area, grain filling rate, and duration, and photosynthetic competence (Spano *et al*., 2003). Joshi et al., 2007have reported the additive nature for the stay-green trait in wheat. Previously, one gene with two alleles for a stay-green trait in wheat has been reported (Silva *et al*., 2000). The authors have also reported high heritability and partial dominance with an additive effect for the gene. Subsequently, other QTLs for stay-green trait has been documented (Kumar *et al*., 2010; Vijayalakshmi *et al*., 2010). Though different published works, the wheat genomic compartment B could be identified as a major source of QTLs for heat tolerance, one QTL on the short arm of chromosome 7D (near centromere) has been reported for heat tolerance (Paliwal *et al*., 2012), in a region that harboured the previously identified QTL for the stay-green trait (Kumar *et al*., 2010).

Cooler canopy temperature (CT), which appears to have some common genetic basis under both heat and drought stress (Pinto *et al*., 2010) is strongly associated with yield in both environments (Pinto *et al*., 2010). Recent data have shown CT to be associated with deeper roots under drought (Lopes and Reynolds, 2010) and heat stress (M.P. Reynolds, unpublished data). The QTL for canopy temperature has been reported previously on wheat chromosome 4A (Pinto *et al*., 2010). Subsequently, seven loci those co-localized for both HSI of main spike yield components and temperature depression of the main spike, explaining 32.1 % of phenotypic variations have been reported (Mason *et al*., 2011), indicating a strong genetic link between the cooler canopy and heat stress tolerance. Afterward, a significant association of chromosomal regions on 2B, 7B, and 7D with HSI of grain weight and GFD and with the expression of canopy temperature depression under the late sown condition in field experiment has been documented (Paliwal *et al*., 2012), which has explained more than 15% phenotypic variation for these traits. Seven stable QTLs related to HSI of GFD, TGW, GY, and CT on chromosomes 1D, 6B, 2D, and 7A, respectively have been reported (Tiwari *et al*., 2013). Under the greenhouse condition, five QTLs have been identified attached with plasma and thylakoid membrane damage and chlorophyll content on chromosomes 1B, 1D, 2B, 6A, and 7A (Talukder *et al*., 2014). These QTLs have been found to explain up to 33.5% of the phenotypic variation. Subsequently, stable QTLs, explaining up to 22% phenotypic variation associated with GFD, GN, and PT have been identified on chromosomes 1B, 2B, 3B, 5A, and 6B in a field experiment (Sharma *et al*., 2016).

Eight major QTL clusters related to drought and heat tolerance on chromosomes 1B, 2B, 2D, 4A, 4B, 4D, 5A, and 7A were found by QTL meta-analysis (Acuña-Galindo *et al*., 2015).The result demonstrated that fine-mapping techniques can be used to identify genes. With an experiment with 255 doubled haploid (DH) lines, Bennett *et al*.,2012 have identified two key QTL on chromosome 3B for canopy temperature and grain yield. Important QTLs related to canopy temperature were mapped on chromosome 3B by the group (Mondal *et al*., 2015). A drought and heat tolerance related QTL, qDHY.3BL, in an ~1 Mbp interval on chromosome 3B which contains 22 genes were mapped (Thomelin *et al*., 2016). Recently published sequencing information will be of great benefit for map-based cloning of major QTL controlling heat tolerance (Clavijo *et al*., 2017).

Traits like early ground cover, leaf glaucousness (Richards, 1996), leaf rolling (Araus, 1996), biomass, canopy temperature (Reynolds *et al*., 2001), etc. have been mapped independently in various genetic backgrounds.

To identify quantitative trait locus (QTL) and the potential candidate genes linked to Fv/Fm (maximum quantum efficiency of photosystem II) for improved photosynthesis under heat stress in wheat three bi-parental F2 mapping populations were generated by (Sharma *et al*., 2017). By doing inclusive composite interval mapping they identified one significant and heat-stress driven QTL in each population on day 3 of the heat treatment. Two of which were located on chromosome 3B and one on chromosome 1D.

Talukdar *et al*., 2014 found five QTL regions significantly associated with response to heat stress by Composite interval mapping. Tahmasebi *et al*., 2017 reported some important QTLs for days to heading (DHE), thousand grain weight (TGW), and grain yield (YLD) were detected on chromosomes 1B, 1D-a, and 7D-b, where QTLs related to canopy temperature, were on 3B. They also found three QTLs for chlorophyll content in the SPAD unit (on 1A/6B), leaf rolling (ROL) (on 3B/4A), and GM2 (on 1B/7D-b) showed significant epistasis × environment interaction.

A total of 854 individual QTL were reported, with 502 associated with drought stress, 234 with heat stress, and 118 with physiological traits in nonstressed environments by Acuna *et al.*, 2015. It is evident from the study that individual QTL clustered into 66 MQTL regions distributed throughout the genome. There were 43 MQTL that are co-localized for both drought and heat stress, 20 specifics for drought stress, 2 specific for heat stress, and 1 MQTL specific for physiological traits in nonstressed environments.

By the experiment of Shirdelmoghanloo *et al*., 2016, it was evident that molecular markers for the 3B or 6B loci, or the facile measurement of chlorophyll loss over the heat treatment, could be used to assist identification of heat-tolerant genotypes for breeding.

Three major and consistent QTLs for chlorophyll fluorescence, chlorophyll content, and leaf temperature associated with drought tolerance on chromosome 2B, 3B, and 4D were identified by Kumar *et al*., 2012. These QTLs explained up to 35% of the mean phenotypic variation with a LOD value of 6.3. Nezhad *et al*., 2012 detected six QTLs for thousand grain weight on chromosomes 7A and 7D under drought conditions, which explained phenotypic variation ranged from 8.9 to 21.0%.

Azam *et al*., 2015 mapped QTL for chlorophyll fluorescence kinetics parameters at the seedling stage as indicators of heat tolerance in wheat. In their study, a total of 37 QTLs were identified for the target traits, among which 13 were detected under the normal temperature of 250C and the remaining 24 under the stressful temperature of 380C. Stable or consistently expressed QTLs for initial, maximum, and variable fluorescence were detected on chromosomes 1A, 1B, 2B, 4A, and 7D. Besides, 24 QTLs were clustered in 9 clusters on chromosomes 1A, 1B, 2B, 3B, 3D, 4A, 5A, and 7D. These QTL hot spot regions along with stable QTLs should be targeted for better understanding the genetic basis of chlorophyll fluorescence kinetics parameters in future mapping studies. In 2018, Kumari and Maria identified QTLs and potential candidate genes for heat stress tolerance from the mapping populations specifically segregating for Fv/Fm in wheat. Beecher *et al*., 2012 identified QTLs associated with maintenance of wheat (Triticum aestivum Desf.) quality characteristics under heat stress conditions.

### *Whole genome association studies (WGAS)*

In contrast, a whole-genome association study (WGAS) or the genome-wide association study (GWAS) allows us to discover the tremendous allelic diversity existing in natural germplasm. GWAS helps in the understanding of the genetic basis and analysis of complex genes controlling important traits such as drought and heat tolerance. The objective is to discern genomic regions that could either be markers, genes, or QTL associated with key agro-morphological traits for marker-assisted breeding, gene discovery, or gene introgression (Tester and Langridg, 2010). GWAS mapping for abiotic stress tolerance in wheat is very limited compared to other crops. Studies have shown how GWAS has also been used to dissect the genetic basis of heat tolerance in wheat (Tian *et al*., 2011; Huang *et al*., 2012). Genotypic variation in ethylene production in spikes (SET) and the relationship of ethylene levels with spike dry weight (SDW) was examined by Valluru et al., 2017 in 130 diverse elite wheat lines and landraces under heat-stressed field conditions. It was clear by the study that SET was negatively correlated with SDW. GWAS uncovered 5 and 32 significant SNPs for SET and 22 and 142 significant SNPs for SDW in glasshouse and field conditions, respectively. Sukumaran *et al*., 2018 investigated QTL hotspots for yield and component traits in durum wheat under drought and heat stress through GWAS. A genome-wide association mapping study (GWAS) was conducted using 200 diverse representative lines of the hard red winter wheat association mapping panel to map quantitative trait loci (QTLs) along to recognize single-nucleotide polymorphism (SNP) markers related with seedling heat tolerance by Maulana *et al*., 2018. They genotyped those lines with the wheat Select 90K SNP array. With the use of mixed linear model (MLM), they detected multiple significant QTLs for seedling heat tolerance on different chromosomes. High sequence similarities of some significant loci with candidate genes involved in plant stress responses including heat was revealed by candidate gene analysis. This was the first GWAS to map QTLs associated with seedling heat tolerance targeting early planting of dual-purpose winter wheat. Tyagi *et al*., 2020 made an effort to mine SSR markers from 96 members of heat-responsive miRNA-genes of wheat followed by their validation using 37 contrasting (heat tolerance or susceptible) wheat genotypes. They first reported that the genic or miRNA markers could be successfully used to study wheat diversity, population structure and characterization of trait-specific germplasm. Identification of genotyping-by-sequencing tags associated with bread-making quality traits in spring wheat under heat stress was done by Barakat et al., 2020. They found one locus (JD_c4438_839) on the chromosome 5D was identified in two (Yecora Rojo × Ksu106 and Klasic × Ksu105) populations and was considered stable QTL. This locus was associated with QLFV.hs and QSLFV.hs in the population (Klassic × KSU105) and QLFW.n in the population (Yecora Rojo × KSU106). This marker can play a significant role in marker assisted selection of bread-making quality traits under heat stress. QTL mapping has limitations owing to the restricted allelic diversity and genomic resolution in the bi-parental populations. The allelic diversity can be increased to some extent by using multi-parental crosses.

### *Conclusion*

Heat stress will become one of the major challenges to the wheat breeders under the changing climatic scenario. Mathematically it has been shown a global need of around 1090 million tons of wheat by 2050. On the contrary, the global temperature rise in the coming decades has also been reported. The production of wheat will be severely affected globally and the entire Indo-Gangetic plain will also remain under threat. Naturally, breeding for developing wheat variety with enhanced heat tolerance is the need of the hour. The major effects of heat stress in wheat include decreased grain weight, premature senescence, shriveled grains, and reduced starch accumulation, altered starch-lipid composition in grains, lower seed germination, and loss of vigour. Almost all developmental stages including the growth rate of wheat are affected by heat stress. Heat tolerance in wheat and other crops is a very complex trait due to the lack of any direct selection criteria. Through classical breeding approaches, heat sensitive morphological descriptors like thousand grain weight, grain filling duration (GFD), number of effective tillers per plant, early ground cover, stay green, leaf rolling, and biomass have been identified. Among physiological traits, canopy temperature, photosynthetic rate, chlorophyll content, stomatal conductance, and membrane thermostability have been considered. Heat susceptibility index (HSI) is suggested to use as an indicator of yield stability and as a proxy for indicating heat tolerance in both hexaploid and durum wheat. Consequently, attempts have been made to identify the concerned linked markers and candidate quantitative trait loci (QTL) and or gene(s) by the molecular breeders. The wheat genome complexity due to its allohexaploid genome with three genomic components (A, B, and D), each comprising of seven chromosomes is another major challenge to the molecular breeders. Considerable number of heat sensitive traits linked SSR markers, *viz*., Xgwm356, Xgwm5, Xcfd22-7B, Xcfa2114-6A, Xgwm181-3B, Xwmc405-7B, Xgwm148-3B, Xwmc166-7B, Xgwm11 and Xgwm293 have been reported which could successfully utilized in marker assisted selection. The results have helped to understand that heat tolerance of common wheat is controlled by multiple genes and marker-assisted selection with SSR markers might be useful for developing improved cultivars. Lastly, good number of major QTLs as narrated in the report earlier may be incorporated into desired background following marker-assisted backcrossing method for elevating heat tolerance in wheat.

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