

## Terminal heat tolerance in wheat: An overview

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### 1. Introduction

Heat stress is a serious threat to crop production globally. Mean temperature of 0.3°C will globally rise per decade (Jones *et al.*, 1998; Hossain *et al.*, 2013) above the present ambient, leading to approximately 0.3 and 1°C for years 2025 and 2100, respectively as stated by Inter-governmental Panel on Climatic Change (IPCC 2014) report. Increasing temperature may alter the crop season and crop gets mature earlier (Porter 2005; Gupta *et al.*, 2013). Tripathi *et al.* (2016) also reported that heat stress has deleterious effect on crop production and it is very challenging for the world food security and it is expected by increasing temperature that prolonged wheat production will be very much effected. The grain filling duration (GFD) in cereals is measured by temperature pattern at the crop growth period related to grain development (Sofield *et al.*, 1977; Slafer and Rawson 1994; Wheeler *et al.*, 1996a; Almeselmani *et al.*, 2009; Muhammad *et al.*, 2011).

The overall performance of genotype is also affected by genotype × environment interactions (Dia *et al.*, 2016). The

### Abstract

Since the beginning of the century, ambient temperatures have increased and are predicted to rise further under climate change. Heat stress is a rigorous threat, particularly during reproductive and grain-filling phases, that results into yield loss. Reductions in dry matter accumulation and grain yield, caused by reduced plant photosynthetic capacity through metabolic limitations and oxidative damage to chloroplasts due to heat stress. Wheat pre-breeding and breeding may be based on secondary traits like chlorophyll content, chlorophyll fluorescence and grain number under heat stress. On the other hand, grain yield under heat stress can be improved by selecting genotypes for the rate of grain filling and for grain size. Wheat varieties with improved grain yield can be developed by integrating physiology and biotechnological tools with conventional breeding techniques during reproductive and grain-filling phases. In this review, we have discussed the effect of heat stress on wheat reproductive and grain-filling stages and the strategies to improve terminal heat stress tolerance in wheat.

**Keywords:** Terminal heat tolerance, agronomic traits, physiological parameters, QTLs, Wheat

environments in that the plants live plays an important role in preparation of the key frame decisions that includes, sustainable farm management and cultivar selection for understanding of possible interactions among crop system with the soil (Dia *et al.*, 2016). The sufficient amount of nutrients and minerals are very much necessary in plants, exposed to temperature stress (Waraich *et al.*, 2012).

Heat stress causes physiological changes by reducing chlorophyll content that leads to leaf senescence in cool-season cereal species (Almeselmani *et al.*, 2011; Dhyani *et al.*, 2013). High temperature (> 31°C) post anthesis can decrease the rate of grain-filling in wheat (Al-Khatib and Paulsen 1990; Randall and Moss 1990; Stone *et al.*, 1995; Wardlaw and Moncur 1995) while the same imposed before anthesis can also decrease yield (Wardlaw *et al.*, 1989; Tashiro and Wardlaw 1990; Hunt *et al.*, 1991) by reducing the number of grains per spike (Wheeler *et al.*, 1996b). Heat stress in wheat has affect on the plant growth and development, physiological functions, reduced grain formation and yield (Mondal *et al.*, 2013; Iqbal *et al.*, 2017; Challinor *et al.*, 2014). Heat stress causes reduction

in photosynthetic capacity (Almeselmani *et al.*, 2012; Ashraf and Harris 2013), change of plant water relations (Hasanuzzaman *et al.*, 2012, 2013), hormonal changes (Krasensky and Jonak 2012), decreases of metabolic activities (Farooq *et al.*, 2011), production of oxidative reactive species (Wang *et al.*, 2011, 2012, 2014, 2016), increases of pollen mortality, reduction of pollen tube development and promotion of ethylene production in wheat (Oshino *et al.*, 2011). During the period from 1880 to 2012, the Earth's system warmed by 0.85°C (IPCC 2014). Genes associated with terminal heat tolerance traits are a major focus area for defining future strategy to characterize heat tolerance in wheat. We need to understand how heat tolerance can be improved and how crops respond to prominent temperatures for the new crop varieties to the future climate (Halford 2009). The important traits associated with terminal heat tolerance are helpful in screening of wheat. These techniques largely determine the efficiency of screening to simulate heat stress of the target environment. Through perturbations in metabolism, membrane fluidity, protein conformation and assembly of the cytoskeleton plants detect changes in ambient temperature (Ruelland and Zachowski 2010). Rehman *et al.* (2009) also screened genotypes for heat tolerance at terminal growth stage of wheat germplasm. Abrupt temperature rise at grain filling duration (GFD) negatively affect the plant growth, grain-quality and yield. During grain filling duration (GFD), sudden temperature rise is a major limitation to wheat production in many environments (Hays *et al.*, 2007). Under heat stress 36 million ha area is covered worldwide and out of this a major portion is located in south Asia (Reynolds *et al.*, 2001). In India, 13.5 ha<sup>-1</sup> (Joshi *et al.*, 2007a) area is covered under heat stress. Eastern Gangetic plains cover eastern UP, Bihar, Jharkhand and West Bengal while central and peninsular India covers MP, Maharashtra and Karnataka state of the India and Bangladesh are considered as extreme heat stress location of the south Asia. The north-western parts of the Indo-Gangetic plain are considered as moderate heat stress zone (Joshi *et al.*, 2007b; Singh *et al.*, 2007). Traits associated with morpho-physiological, yield and different growth stage of plants were affected by high temperature. Post anthesis temperature rise affected the grain filling rate (Stone and Nikolas 1994). Short duration (3-4 days) sudden temperature rise in form of heat wave (35-37°C) alter the morphology and size of grain (Wardlaw and Wrigley 1994). Yield is also reduced by up to 23% due to short duration (4 days) of heat exposure (>35°C) (Stone and Nikolas 1994) and 3-day heat treatment (~38°C from 8 am to 5 pm) reduced individual yield component up to 28.3% (Mason *et al.*, 2010). Terminal heat stress is major concern for India (Rane *et al.*, 2007; Joshi *et al.*, 2007b). Global warming in form of climate change

increased the risk for yield losses in wheat (Lillemo *et al.*, 2005). Improving heat tolerance in wheat is major goal for wheat breeder and morpho-physiological traits in plants are affected by heat stress (Nachit *et al.*, 1998). Temperate cereals are prone to rising temperature when compared to tropical cereals. Many traits contributing for heat tolerance are heritable, additive nature and show variation, these are indicative for scope of wheat improvement under terminal heat stress (Tuberosa and Salvi 2006). Physiological traits such as higher photosynthetic rates, stay-green, chlorophyll content, chlorophyll fluorescence etc. play significant role in heat tolerance. Crossing programmes are being carried out for such traits to assist in the breeding for abiotic stress tolerance in wheat.

Heat tolerance is a complex phenomenon and is controlled by multiple genes regulating different biochemical and physiological traits. To analyse the genetic basis of thermo-tolerance the promising approaches are molecular markers (Maestri *et al.*, 2002). Marker assisted selection (MAS) has been considered as helpful approach to develop crop stress tolerance because of the difficulty in phenotypic selection for tolerance and general complexity of abiotic stress tolerance. Identification of genetic markers that are associated with gene or quantitative trait loci (QTLs) or affecting whole plant stress tolerance or individual contributing components are required for MAS. The powerful tool for dissecting the genetic basis underlying complex traits into individual components is QTL analysis and the QTL analysis is based on high density molecular linkage maps. Limited information regarding the heat-responsive microsatellite markers in wheat is available on public domain. On the other hand, Akpinar *et al.*, (2017) reported 68, 592 SNPs from the *Aegilops tauschii* genotype MvGB589 mapped on to the chromosome 5D through genomic and transcriptomic approaches. High temperature also increases the rate of grain filling to compensate for genetic dissection of wheat kernel size and shape.

In this review, we explained common morphological, physiological, and molecular responses of wheat to high temperatures during the reproductive and grain-filling stages and investigate how these responses can be exploited to improve heat tolerance. Wheat (*Triticum aestivum* L.) sensitivity have already been reported for the major wheat-producing regions to high temperature and trends in rising temperatures during the growing season (Gaffen and Ross 1998; Alexander *et al.*, 2006).

## 2. Mechanism of heat tolerance in wheat

Crops have three different mechanisms to adapt for heat stress conditions, namely heat avoidance, heat tolerance and heat escape mechanisms. These mechanisms are

in turn governed by different associated traits, viz. leaf rolling, waxiness in heat avoidance, production of stress responsive genes in tolerance and adjusting the phenology of plants once it senses the heat stress to escape. By leaf rolling, reducing leaf size, leaf shedding, thickening leaves, transpirational cooling, reducing growth duration in morphology and ontogeny plants tend to reduce heat-induced damage (Wahid *et al.*, 2007).

### 3. Grain filling rate and duration

Grain-filling rate and duration are influenced directly by high temperature and it directly affects the process of grain development (Kumar *et al.*, 2012; Lobell and Gourdjji 2012; Gourdjji *et al.*, 2013). The degree of heat-driven damage is dependent on the intensity of heat stress. Grain filling duration is shortened because heat stress accelerates the rate of grain filling (Dias and Lidon 2009). For instance, 5°C increases in temperature above 20°C by 12 days in wheat increased the rate of grain filling and reduced the grain filling duration as the supply of photo assimilates may be limited under these conditions (Yin *et al.*, 2009; Calderini *et al.*, 2006). The RILs mapping populations derived from parental crosses of genotype RAJ 4014 and WH 730 showed clear-cut segregation pattern for differences in GFR between timely and late sown conditions. About 75% of the progenies showed no difference while 25% showed significant difference in GFR under high temperature stress created by late sown condition (Pandey *et al.*, 2013; Hossain ad Teixeira de Silva 2012; Hakim *et al.*, 2012). Other studies have also reported that the grain growth rate and duration were reduced by heat stress in genotypes differing in grain weight stability (Viswanathan and Khanna-Chopra 2001). Wu *et al.* (2018) conducted field trials during 2011–2013 in three locations on 10 wheat genotypes. Observations were recorded on grain weight, grain-filling duration, grain-filling rates and the lag phase from flowering to the initiation of grain filling. The grain-filling duration and rate were fitted by Richard's equation in thermal time (growing degree-days (GDD), base temperature 9°C. Grain filling takes place between 362 to 400 GDD and range of the lag phase from 67 to 86 GDD. There is found a positive correlation of lag phase with rates of grain filling and grain weight, while a significant negative correlation of days to anthesis with the lag phase and rates of grain filling. There's a negative correlation between temperature during grain filling and the lag phase. A positive correlation associated between variation in grain weight and the rate of grain filling, which, consecutively, was related to the grain number per unit area. Wang *et al.* (2018) in their study studied different varieties of wheat for the effects of heat stress on grain filling at different levels of thermotolerance. They demonstrated

a widely distributed mechanism for heat adaptation of metabolism, where the assimilation and energy needed for metabolism and protein synthesis are redirected to heat protection and accumulation of reserves, as a result storage protein accumulation is increased and a stable filling rate. Rampinoa *et al.* (2009) studied the durum wheat (*Triticum durum* Desf.) cultivars for the attainment of thermotolerance and HSPs gene expression

### 4. Agronomic traits

#### 4.1. Grain Number and weight:

Grain weight and number both are severely affected by increasing temperature (Ferris *et al.*, 1998). Each of these components of grain yield is affected by high temperature depends on the developmental phase at which the high temperature occurs (Balla *et al.*, 2012; Hampton *et al.*, 2013). Ovule abortion due to high temperature was also reported (Saini and Aspinall 1982; Thorne and Wood 1987; Tashiro and Wardlaw 1990; Mitchell *et al.*, 1993; Wheeler *et al.*, 1996b). Wheeler *et al.*, (1996a) showed that high temperatures at anthesis reduced grain numbers per spike in winter wheat 'Hereward'. Saini and Aspinall (1982) showed that low grain fertility was induced by exposure to high temperature for as little as 1°C during critical periods between booting and anthesis. When abiotic stress coincides with meiosis, the first phase of gametogenesis may be further impaired (Ji *et al.*, 2010). According to Ferris *et al.* (1998) maximum temperatures increase over four consecutive days near to anthesis affects grain number and that directly reduced grain yield at maturity. Around floral initiation heat stress has severe effects on grain number. For example, grain number per spike decreased by 4% for every 10°C (from 15–22°C) increase in the 30 days after anthesis (Fischer 1985).

The development of spikes is increases by heat stress, but reducing spikelet number and due to this number of grains per spike also reduces (Porter and Gawith 1999; Saini and Aspinall 1982). There is an inverse relationship between grain number per spike and duration of heat stress (Rawson and Bagga 1979). The reason for this sensitivity is that each spikelet meristem starts to produce florets and spikelets begin to form in the spike from the double ridge stage. However, the reduction in the spikelet number per spike and grain number per spikelet because of the reduction in the duration of appearance to double ridge and double ridge to anthesis (McMaster 1997). During floret development high temperature (>30°C) may cause complete sterility (Saini and Aspinall 1982), variation among wheat genotypes has also been observed (Anjum *et al.*, 2008; Zhao *et al.*, 2008; Gibson and Paulsen 1999). Heat stress severely effects the grain number around floral initiation. The one factor determining grain number for

floret development is availability of carbohydrates (Abbate *et al.*, 1995; Demotes-Mainard and Jeuffroy 2004) because insufficient availability of assimilates may cause floret most sensitive period to heat stress.

Maintaining optimum kernel weight under heat stress is used as a measure of heat tolerance (Tyagi *et al.*, 2003; Singha *et al.*, 2006). High temperature during grain-filling period decreases yield by decreasing kernel weight (Warrington *et al.*, 1977; Tashiro and Wardlaw 1990; Stone and Nicolas 1994). Kernel weight was decreased by 85% when the temperature rose from 20/16°C (day/night) to 36/31°C from 7 DAA until maturity (Tashiro and Wardlaw 1989). The distribution of differences in thousand grain weight (TGW) in RILs showed normal curve. About 15% progenies (18 RILs) had significant difference in TGW under late sown condition whereas 20 RILs had higher TGW under stress conditions (Pandey *et al.*, 2014). In the hard red winter wheat Karl 92, which is adapted to great plains conditions, kernel number was reduced by 63%, kernel weight by 29% and grain yield was reduced by 78%, when a temperature regime of 35/20°C was imposed from 10 DAA until maturity (Gibson and Paulsen 1999). The duration between anthesis and physiological maturity are reduced by the increasing temperature (Warrington *et al.*, 1977), which is related with reduction in grain weight (Warrington *et al.*, 1977; Shpiler and Blum 1986). For every 1°C above 15–20°C grain weight Reduces (1.5 mg per day) (Streck 2005). High temperature variability effects on wheat grain size and number appears to be related to genotypic differences in heat tolerance (Viswanathan and Khanna-Chopra 2001; Tahir and Nakata 2005). The main stem grain weight reduces by 20 to 44%, during reproductive phase by increasing temperature from 30 to 38°C (Tahir and Nakata 2005). If the standard temperature increases up to one degree throughout reproductive phase in wheat can cause greater loss of yield (Bennett *et al.*, 2012; Yu *et al.*, 2014). Shrinkage of grain through ultra structural changes in the aleuronic layer and endosperm cells can be caused by high temperature, as observed by Dias *et al.* (2008) when day/night temperatures increased from 25/14°C to 31/20°C. Viswanathan *et al.* (2008) studied that when the varieties of wheat is exposed to heat the stability of grain weight differed, by that rate and duration of grain growth is also affected.

#### 4.2. Yield

Integration of high temperatures (i.e. accumulated thermal time above 31°C over 8 d of the treatment during anthesis) has been reported to cause 50% reduction in grain yield (Ferris *et al.*, 1998). Even a brief period of exposure to high ambient temperature (>35°C) can drastically reduce the grain yield in wheat (Randall and Moss 1990; Hawker and Jenner 1993; Stone and Nicolas 1994; Sharma *et al.*, 2017).

Yields are reduced 3–4% per 1°C rise above the optimum temperature (15–20°C) during grain filling (Wardlaw *et al.*, 1989). In India most commercially sown wheat cultivars lost their yield about 50%, when exposed to 32–38°C temperature at the fundamental grain formation stage can be calculated by using this factor (3–4% loss per 1°C above 15–20°C). Among wheat germplasm a significant variation exists for heat tolerance (Reynolds *et al.*, 1994; Joshi *et al.*, 2007b,c), due to lack of understanding of dependable direct criteria, until now very slight progress has been made for selecting heat tolerant genotypes. Willey and Dent (1969) suggested that grain yield is neither limited by assimilate supply nor by the storage capacity of the ear alone, but by both. Grain yield in wheat could reduce if the temperature increased in variably during anthesis. According to Ferris *et al.* (1998) and Huang *et al.* (2012) further threat to crop production also occur if higher temperatures makes deleterious effects on root growth. The overall growth process of wheat is negatively affected by higher temperature thus resulting in rigorously hindered productivity (Janjua *et al.*, 2010). Temperature also effects spring wheat at period of grain formation under late sown conditions. They also observed the comparison of reduction in grain yield (53.75%) and reduction in tiller number (15.38%) (Din *et al.*, 2010). There are number of ways by which high temperature affects the crop, some of them are poor germination, less photosynthesis, leaf senescence and all finally leads to less yield (Asseng *et al.*, 2011).

### 5. Physiological traits

#### 5.1. Leaf senescence

Avacuolar collapse, disruption of cellular homeostasis and plasma membrane integrity lost, are some structural changes in chloroplast during leaf senescence (Lim *et al.*, 2007; Khanna-Chopra 2012). Delay in the expression of senescence-related genes permits stay green genotypes to maintain photosynthesis (Lim *et al.*, 2007). Leaf senescence is enhanced if plants are exposed to heat stress during maturity (Haque *et al.*, 2014). While stay green is recognized as an adaptive mechanism for stress conditions, chlorosis is an essential part of programmed senescence, where there are essential tradeoffs between preserved photosynthetic area and remobilization of nitrogen to the maturing grain (Vijayalakshmi *et al.*, 2010). QTLs for the association of yield and stay green have been shown in mapping populations (Kumar *et al.*, 2010; Vijayalakshmi *et al.*, 2010). Since chlorosis is expressed heterogeneously on all above ground organs and it is not simple to consider even within a single organ such as leaf. However, effortless and integrated approaches to assess stay green via spectral reflectance. Normalized Difference Vegetation Index (NDVI) explain substantial

relationship with yield in two large mapping populations under heat stress, making it a consistent tool for large-scale screening and gene discovery work (Lopes and Reynolds 2012). While NDVI is correlated with the heat tolerance, which is a consistent indicator of greenness combine all chlorophyll. Leaf senescence in wheat may speed up by inhibition of chlorophyll biosynthesis under high temperature ( $>34^{\circ}\text{C}$ ) (Asseng *et al.*, 2013). Photosynthesis mainly affected by heat stress, effects photosynthetic machinery, premature leaf senescence, decreased leaf area expansion and ultimately less yield (Mathur *et al.*, 2014; Feng *et al.*, 2014). Grain yield can be increased by foliar spray of potassium orthophosphate ( $\text{KH}_2\text{PO}_4$ ) after anthesis because of the delay in the heat stress-induced leaf senescence (Dias and Lidon 2010).

### 5.2. Spike Fertility

Grain set is actually sensitive and conservative towards carbohydrate supply even under relatively optimal conditions (Fischer 2011). The observation for reduction in grain number is more than expected, by reduction in biomass, leading to quite low harvest index during heat stress from hot wheat-growing environments (Reynolds *et al.*, 2007). Programmed cell death at high temperature induced by ethylene level that leads to grain abortion (Hays *et al.*, 2007). Structurally and functionally abnormal anthers are produced in 80% of the florets, if wheat plants are exposed to  $30^{\circ}\text{C}$  during a 3-d period around anthesis. Heat stress affects the morphology, pollen tube growth rate, metabolism, chemical composition and viability of pollens (Hedhly *et al.*, 2009). In other cereals like sorghum the carbohydrate metabolism has been linked to reduced pollen viability under heat stress (Jain *et al.*, 2007; Prasad and Djanaguiraman 2011). Abnormal ovary development resulted in reduced pollen tube growth and seed set when heat stress coincided with meiosis (Barnabás *et al.*, 2008).

### 5.3. Starch biosynthesis

Significant decrease in quantity of starch in wheat grains can be resulted by heat-shock treatment above  $30^{\circ}\text{C}$  (Liu *et al.*, 2011). Due to the small amount of soluble starch synthase at  $40^{\circ}\text{C}$ , about 97% of activity was lost and in result of this grain size and accumulation of starch is reduced in wheat (Chauhan *et al.*, 2011). Soluble sugar content and biomass is reduced by increased temperature stress ( $35/27^{\circ}\text{C}$ ) given at seedling stage (Wang *et al.*, 2014). Starch biosynthesis is significantly restricts by heat stress in wheat grains although caused a significant increase in total soluble sugar and protein (Asthir and Bhatia 2014).

### 5.4. Canopy temperature

Cooler canopy temperature (CT), is strongly associated with yield in drought and heat stress and also appear

to have some common genetic basis under both the conditions (Pinto *et al.*, 2010). Recent data show canopy temperature to be associated with deeper roots under drought and heat stress (Lopes and Reynolds 2010). While the genetic variation in stomatal conductance under heat is also linked with the cooler canopy, selection for canopy temperature can be helpful for the improvement of heat tolerance (Reynolds *et al.*, 1994, 2007).

### 5.5. Chlorophyll fluorescence and Chlorophyll content

Chlorophyll fluorescence (CFL) is one of the traits used extensively in field phenotype after CT and chlorophyll content (Chl). The roles of chlorophyll fluorescence (CFL) in relation to grain yield under water-stress conditions were suggested for selecting heat and drought tolerant genotypes of wheat. CFL is directly proportional to the yield i.e genotypes with higher yield have higher CFL, representing that in screening for tolerant genotypes CFL can be used. Photosynthetic efficiency can be calculated indirectly by CFL in wheat genotypes, mainly in terms of photosystem II (PSII) function. A study on RILs mapping populations derived from cross of heat sensitive genotype RAJ 4014 and heat tolerant genotype WH 730 showed that, out of 112 RILs, 17 RILs had their heat susceptibility index (HSI) less than 1 for all three traits viz., CFL, Chl and TGW. By virtue of low HSI (0.43) for thousand grain weight, group of genotypes showing tolerance to terminal heat stress were also found having values less than zero (-0.52) of Chl HSI indicating substantial increase in the Chl value under stress (Pandey *et al.*, 2015). However, contrasting HSI values of 2.07 and 2.19 were observed for TGW and Chl in another set of RILs depicting heat sensitivity (Pandey *et al.*, 2015). Sharma *et al.* (2012) screened 1274 contrasting wheat cultivars for heat tolerance of diverse origin, based on the maximum quantum efficiency of PSII ( $F_v/F_m$ ) and physiological trait. The role of CFL and Chl in relation to grain yield under water-stress conditions was suggested for the selection of heat and drought tolerant wheat plants (Blum 1988, 1989; Krause and Weis 1991). Wang *et al.* (2008) reported that the maintenance of the higher Chl in wheat plants is an effective strategy to increase its yield and biomass. Chl around flowering time were positively associated with yield in near-isogenic lines (NILs) of wheat (Quarrie *et al.*, 2005).

## 6. Molecular mechanism

Significant contribution of the molecular science for the understanding of the mechanism of stress response under heat stress conditions spread light on the information of protective mechanisms and molecular pathways to raise the plants that are tolerant to heat stress (Asthir, 2015a,b). At different growth stages the genotypic

differences in cell membrane thermo stability tolerance were also reported in wheat (Kumar *et al.*, 2013b; Asthir *et al.*, 2013). Identification of three known and one novel genome rearrangement of wheat is confirmed by Clavijo *et al.* (2016). Heat tolerance is quantitative and irregular in nature, so efficient selection of the traits is very much difficult for breeders. The normal distribution was typical of traits controlled by multiple genes (Prasad *et al.*, 1999) and supported the hypothesis of Blum (1988) that heat tolerance is quantitatively inherited. In several studies of wheat, QTL for yield and its components such as thousand grain weight (TGW) and grain numbers per ear (GNE), have been previously reported (Huang *et al.*, 2006; Kumar *et al.*, 2006). To record agronomically essential characters and yield enhancing traits in wheat, QTL analyses have been conducted (Campbell *et al.*, 2003; Kato *et al.*, 2000).

TGW is used to estimate yield of wheat genotypes because it is also one of the yield contributing traits and can be measured easily. Related to many studies of the yield components of wheat, recognition of QTL associated with TGW on different wheat chromosomes (Borner *et al.*, 2002; Huang *et al.*, 2006; Wang *et al.*, 2009). Significant association of differences in TGW between optimum and late sown of RILs with two markers, viz. Xpsp3094 and Xgwm282 with coefficients of determination ( $R^2$ ) values of 0.14 and 0.11, respectively analysed by regression analysis (Pandey *et al.*, 2014). In the earlier studies this had been reported that the markers, e.g. Xpsp3094, were found to be associated with dTGW in single marker analysis, (Quarrie *et al.*, 2005). On the other hand by using Xgwm282 marker, reported QTL for single kernel weight (Mason *et al.*, 2010). In wheat there is a major role of grain filling rate (GFR) in the final yield (BeiQuan and Kronstad 1994) and is positively associated with final grain weight. Three significant genomic regions on 2B, 7B and 7D were found to be associated with heat tolerance. Using single-marker analysis, Yang *et al.* (2002) found QTLs associated with markers Xgwm11 (1B) and Xgwm293 (5A) for heat tolerance in an  $F_2$  population (166 plants) that contributed 23 % of phenotypic variation. According to Campbell *et al.* (2003), a marker linked to a QTL for grain yield on wheat chromosome 3A was found to interact significantly with the temperature from emergence to anthesis. Mason *et al.* (2010) reported five stable QTL for HSI of single grain weight (1A and 2A), grain weight (3B), and grain number (2B and 3B) contributing 11.1–22.6 % of phenotypic variation. However, their phenotypic assessment was performed on 65 lines of  $F_5$  generation material in controlled conditions for a short period of heat stress (3 days). Another study was carried out by Mason *et al.* (2010) for detailed characterization of the effect of heat shock on plant yield and yield components during early grain-

filling and to identify molecular markers linked to QTL for heat susceptibility index (HSI) and other potentially beneficial phenotypic traits. HSI was calculated based on difference in yield and yield components between the heat stressed and control treated RIL replications and used as a phenotypic measure of heat tolerance for QTL mapping. Paliwal *et al.* (2012) reported 3 QTLs from using RILs populations derived from Indian parental lines under terminal heat stress. Groos *et al.* (2003) found that QTL affecting yield was located on chromosome 7D and QTL affecting kernel weight were located on chromosomes 2B, 5B and 7A. Borner *et al.* (2002) reported 210 QTL controlling 20 morphological and physiological traits. In an analysis of spring wheat populations for heat tolerance, loci on chromosomes 2B and 5B were most important (Byrne *et al.*, 2002). Bhusal *et al.* (2017) mapped maximum number of QTLs on chromosome 2A followed by 6D and 2B for grain yield components in wheat under heat stress.

In another study, HSP 18 got accumulated in developing grains of heat tolerant varieties more than susceptible types, where several wheat varieties were exposed to 3.2 to 3.6°C higher than normal (Sharma-Natu *et al.*, 2010). Dehydrins help to stabilize macromolecules against heat-induced damage and belong to Group 2 late embryogenesis abundant proteins (LEA) (Brini *et al.*, 2010). In wheat, the key enzymes to start metabolism is protect and stabilized by DHN-5 (Brini *et al.*, 2010).

The RuBisCo enzyme is deactivated by heat stress and the deactivity of RuBisCo has been observed within 7 days of imposed heat shock treatment (Kumar *et al.*, 2016). Staygreen has also been studied extensively in different crops. Major components for identifying terminal heat stress resistant genotypes of wheat are canopy temperature depression and stay green (Jangid and Srivastava 2018). Xu *et al.* (2000) found that regions that contained the QTL for stay-green coincided with the genes for key photosynthetic enzymes, heat shock proteins, and ascorbic acid response. For heat tolerance in wheat during the reproductive phase several QTLs have been identified. Three QTLs are identified for stay-green character (Kumar *et al.*, 2010). A QTL on chromosome 4A was also identified for canopy temperature under heat stress (Pinto *et al.*, 2010). On the other hand 15 and 12 QTLs were also identified associated with yield and yield associated traits (Mason *et al.*, 2010). The results suggest that the main spike should be used for the identification of QTLs genomic regions for heat tolerance (Mason *et al.*, 2011). The QTL influencing stay-green under high temperature stress in wheat have been mapped to date. Christopher *et al.* (2018) identified QTL for stay-green traits in well-watered and water-limited environments by using doubled haploid population. For stay-green traits

the associated genetic regions with QTL were identified in both the environments on chromosomes 4A, 4B, 4D (constitutive stay-green); 2A in wetter environments and 5B dryer environments. On the other hand 3B and 7B are the regions on which the QTL for stay-green were identified in a mixture of environment.

Heat tolerance contributed traits molecular markers can be used in marker assisted selection (MAS). Traits that could be selected more efficiently include photosystem (PS II, Fv/Fm) efficiency (Blum and Ebercon 1981), Chlorophyll content (CHL) (Li *et al.*, 2006) and canopy temperature are the ideal physiological selection trait in many ways since measurement is quick, simple and inexpensive (Cossani and Reynolds 2012). In crops like tomato and maize for the better understanding of the genetic basis of plant stress tolerance the very much contributed approach is Marker-assisted selection (MAS) (Liu *et al.*, 2006; Momcilovic and Ristic 2007) and, in some cases has led to the development of improved abiotic stress tolerance plants (Lopes and Reynolds 2010; Thomson *et al.*, 2010). Because of the difficulty in phenotypic selection and general complexity of abiotic stress tolerance MAS are considered as an effective approach. Therefore an urgent need exists to understand the genetic factors underlying heat tolerance and to recognize consistent markers to be deployed in molecular breeding leading to enhancement in grain yield of wheat.

## 7. Screening and breeding for heat tolerance

**Table 1** Selection criteria of wheat genetic resources for tolerance to heat stress

Sr. No.	Selection criteria for heat stress tolerance in wheat	References
<b>1.</b>	<b>Growth and phenology</b>	
a.	Rapid ground coverage	Cossani and Reynolds 2012, Khan and Kabir 2014 Nawaz <i>et al.</i> , 2013
b.	Leaf rolling, shedding and thickening	
c.	Biomass yield	Khan and Kabir 2014
d.	Early heading and phenology	Hussain <i>et al.</i> , 2016
<b>2.</b>	<b>Physiological traits</b>	
a.	Photosynthesis and stomatal conductance	Radhika and Thind 2014
b.	Stay green duration	Lopes and Reynolds 2012, Nawaz <i>et al.</i> , 2013
c.	Membrane stability	Sikder and Paul 2010, Dhanda and Munjal 2012, Talukder <i>et al.</i> , 2014
d.	Leaf chlorophyll content and chlorophyll fluorescence	Trethowan and Mujeeb-Kazi 2008; Bhusal <i>et al.</i> , 2018; Pandey <i>et al.</i> , 2015
e.	Stem reserves	Mohammadi <i>et al.</i> , 2009
<b>3.</b>	<b>Yield and yield attributes</b>	
a.	Grain weight	Sareen <i>et al.</i> , 2012), Bennani <i>et al.</i> , 2016 Pandey <i>et al.</i> , 2014
b.	Grain filling rate and duration	Nawaz <i>et al.</i> , 2013, Khan and Kabir 2014, Song <i>et al.</i> , 2015, Pandey <i>et al.</i> , 2013
c.	Number of fertile spikes	Khan and Kabir 2014, Bennani <i>et al.</i> , 2016

Various physiological approaches have been found to be effective in breeding programs. This includes screening genetic resources for identification of genetic bases for heat tolerance in crops. Thereby, a preferred new plant types can be established following physiological crossing of new trait combinations, to combat future climate that comprises high temperature events (Reynolds and Langridge 2016). It is very well understood that screening wheat genotypes under natural heat stress condition in several environments is problematic. Therefore, no dependable selection criterion has been established to evaluate diverse genetic materials for heat tolerance. In this concern, researchers recommended some indirect selection criteria for developing heat tolerance in wheat (Table 1).

## 8. Strategies to improve thermo-tolerance in wheat

High temperature severely affects the plant growth by affecting the quality of grain and wheat productivity. One of the key step to increase the yield in wheat is to develop the thermotolerance varieties therefore, at present a number of techniques are being used to increase the thermotolerance in wheat. In addition to this researchers also reported superior propagation of different plants on large scale using tissue culture technique (Ali *et al.*, 2013; Hussain *et al.*, 2016a; Hussain *et al.*, 2016b; Iqbal *et al.*, 2016a; Iqbal *et al.*, 2016b). For enhancement in germination potential of wheat there are number of growth enhancers that are exogenously applied (Iqbal *et al.*, 2016c). On the other hand transcriptomic and proteomic data play a key role for the identification of genes and proteins that affects quality and yield. So we need to know more about this process for the development of new wheat variety that can adapt to increasing temperature (Altenbach 2012). For the improvement of heat tolerance the inoculation of seed with rhizobacteria also significantly used (Anderson and Habiger 2012). On the other hand effects of heat stress can be managed chiefly by developing genotype collectively with modification of relevant agronomic properties (Asseng *et al.*, 2011; Chapman *et al.*, 2012). Similarly there are several growth-promoting protectants that are applied exogenously; few of them are osmoprotectants, phytohormones, signaling molecules and trace elements having potential to protect the plants by unfavorable effects of heat and up regulating the antioxidant capacity (Upreti and Sharma 2016; Hemantaranjan *et al.*, 2014). Some other adaptation procedures under heat stress are surface cooling by irrigation, antioxidants defense, osmoprotectants, choice of cultivars and change in date of sowing (Lobell *et al.*, 2008; Suzuki *et al.*, 2011; Caverzan *et al.*, 2016; Kaushal *et al.*, 2016; Deryng *et al.*, 2014).

## 9. Concluding remarks

Frequency of heat stress in wheat is increasing across the globe due to high temperature. The substantial effects of heat stress on grain setting duration and rate ultimately leads to reduction in grain yield. However the timing, duration and intensity of heat stress determine its impact on grain yield. By developing tolerant genotypes and agronomic strategies the effect of heat stress can be minimized. Although in wheat, physiological basis of heat tolerance are quite well-understood, research into phenotypic flexibility and assimilate partitioning are required. Molecular basis of response and tolerance mechanisms to harvest higher grain yields on a sustainable basis must be explored by the use of functional genomics approaches. The important area for future research are conventional breeding blended with modern biotechnological tools for identification and introgression of heat tolerance gene into elite lines. For the understanding of genotypes and the environment interactions the most recent genomics resource combined with ecophysiological research may be useful. To study the complex quantitative traits like yield stability under heat stress an integrated system approach should be designed.

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