

Review Article

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Terminal Heat Stress and its Effects in Wheat Crop: A Review

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ABSTRACT

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Wheat is a major cereal crop and considered as source of basic calories and protein for more than 80% of the world population. The impact of rising temperature, due to global climate change, on wheat production is of major concern worldwide. The wheat production is limited majorly by heat and drought stress. Heat stress effects and alters the important physiological and biochemical processes of the plant like grain number, photosynthetic activity, chlorophyll content, plant height, stay green etc. Plants detect changes in ambient temperature through membrane fluidity and protein conformation which further activates adaptive processes like expression of heat shock proteins. However, unfavourable high temperatures can be deleterious, causing injury which is generally called 'heat stress'. The present article reviews the recent findings on responses, adaptation and tolerance to Heat stress at various structural levels of plant.

Introduction

Wheat (*Triticum aestivum*) is a cool season crop, but its cultivation extends well beyond its typical adaptation zone. In India alone, about 13.5 million ha of wheat crop (about half of the total acreage) is estimated to be heat stressed (Joshi *et al* 2007). With the current trends of climate change, the heat stressed wheat production environments around the world are apprehended to increase about three fold by 2050 (Trethowan *et al* 2005). Wheat represents world's maximum cereal area with over 220 million ha cultivated worldwide which is often heat stressed. Heat stress (HS) can impair wheat

growth at any developmental stage and in the future scenarios predict even warmer temperatures (Easterling and Apps 2005).

Plants detect changes in ambient temperature through perturbations in metabolism, membrane fluidity, protein conformation and assembly of the cytoskeleton (Ruelland and Zachowski 2010). Heat shock proteins are expressed by such reactions until new cellular equilibriums are reached. However, temperatures above the optimum for growth can be deleterious, causing injury or irreversible damage, which is generally called 'heat stress' (Wahid *et al* 2007). Heat stress is a function of rate of temperature increase and

the magnitude and the duration of exposure to the raised temperature as well (Wahid *et al* 2007). Heat stress causes damage to various cellular components, so it is obvious that in order to survive a large number of different protective pathways are required. Induction of any one of these pathways makes the plant thermotolerant to some extent and the loss of any specific pathway merely limits that tolerance (Larkindale *et al* 2005).

Wheat is very sensitive to high temperature and increasing growing season temperatures trends have already been reported for the major wheat-producing areas (Alexander *et al* 2006, Hennessy *et al* 2008). Wheat experiences heat stress at different phenological stages, but during the reproductive phase heat stress is more harmful than during the vegetative phase due to the direct effect on grain number and dry weight (Wollenweber *et al.*, 2003). Hence the main focus is on responses to elevated temperatures during reproductive and grain-filling stages and processes that affect grain yield.

Heat-tolerant cultivars' development is concerned majorly in wheat breeding programs. An understanding of the genetics and physiology of heat tolerance in detail as well as the use of the proper germplasm and selection methods will lead the development of heat tolerant cultivars of wheat (Fokar *et al* 1998b). Heat tolerance is not controlled by a single gene in cereals. Different components of tolerance determined by different sets of genes are critical for heat tolerance at different stages of the life cycle and in various tissues (Maestri *et al* 2002). Yield potential of any variety is the combined effect of genotypes and environmental interaction. Nowadays, due to global warming, climatic conditions are changing and temperature begins to rise in late February and March coupled with hot dry winds during the post

anthesis stages, especially during grain development terminate grain growth prematurely and reduces yield considerably. Hence, there is need to breed new genotypes having genetic mechanism to tolerate high temperature by involving novel genes from diverse parents to sustain and maximize productivity of wheat under warmer areas of India.

Under high temperature (HT) stress, plant can survive with the ability to perceive the HT stimulus, generate and transmit the signal and initiate appropriate physiological and biochemical changes. Tolerance is improved substantially by HT-induced gene expression and metabolite synthesis. Hence, Current research areas are the physiological and biochemical responses to heat stress and the molecular approaches are adopted to develop HT tolerance in plants. The present article reviews the various findings on response and tolerance to HT at the cellular, organelle and whole plant levels.

Heat stress

Multidisciplinary research involving genetic resources enhancement and crop physiology at CIMMYT have led to a physiological trait based approach to breeding for abiotic stress which has merit over breeding for yield per se by increasing the probability of successful crosses resulting from additive gene action. Advances have already been made in the drought-breeding program (Reynolds and Borlaug 2006, Ortiz *et al* 2007) and this strategy will be used to breed wheat for the high temperature stressed Environments. A limiting factor in wheat production in many countries is the occurrence of temperature stress at grain filling stage especially in West Asia and North Africa. In another study by Singh *et al* (2001), it was found that for every 1°C increase in mean temperature above normal, grain yield was reduced by 12-23%.

Pollen sterility, tissue dehydration, lower CO₂ assimilation and increased photorespiration can be caused by heat stress during the reproductive phase. Though growth is accelerated by high temperatures, the phenology is also reduced, which is not compensated for by the increased growth rate (Zahedi and Jenner 2003). During reproductive and grain-filling phases, water is required for stem and peduncle elongation to raise the ear up through the unfolding leaf to the top of the canopy and growth of all parts of the ear, pollen ripening, rapid extension of stamen filaments and fertilization, grain growth and filling. Water flow for these processes involves crossing membranes, possibly facilitated by aquaporins. High temperature tends to increase hydraulic conductivity of membranes and plant tissues due to increase in aquaporin activity, membrane fluidity and permeability (Martinez- Ballesta 2009) and reduced water viscosity to a greater degree (Cochard *et al* 2007).

Nawaz *et al* (2013) found that heat stress negatively influences the chlorophyll and grain filling processes in plants. Heat stress drastically reduces the performance of all wheat cultivars at all stages; severity being at booting and heading stages than anthesis and grain filling stages. Heat stress is more harmful when it occurs at reproductive and grain filling stages (Hays *et al* 2007, Farooq *et al* 2011).

Heat stress affects photosynthetic capacity of plants, promotes the production of oxidative reactive species (Wang *et al* 2011), reduces pollen tube development and causes pollen mortality (Saini *et al* 2010), improves ethylene production thus increasing grain abortion (Hays *et al* 2007) and also causes oxidative damage to the chloroplast which results in minimum grain yield (Farooq *et al* 2011).

Heat stress also interrupts the grain filling in plants through reduction in grain weight and grain number (Wollenweber *et al* 2003, Schapendonk *et al* 2007), resulting in less grain yield (Mullarkey and Jones 2000, Tewolde *et al* 2006). For example, increase of just 1°C temperature above 15–20°C at grain filling stage can reduce grain weight by 1.5 mg per day (Streck 2005).

Effects of Heat Stress

Physiological parameters

Early maturing genotypes have the ability to possess greater grain weight and longer grain formation period thereby having the ability to tolerate heat stress as compared to long duration genotypes (Singh *et al* 2005). Some of the studies in late conditions revealed that days to heading, days to maturity, plant height, number of tillers per plant, spikelets per spike, 1000 grain weight, grain yield per plant, biomass per plant and harvest index were under the control of additive genetic effects and direct selection methodologies can be adopted in the selection of these traits (Chandrashekhar and Kerketta 2004). Comparison of mean of two sowing extremes revealed that plant height, days to heading, days to maturity, spikelets per spike, grains per spike and grain yield are greatly reduced as a result of different sowing times (Mahboob *et al* 2005). Similarly the yield is greatly reduced due to late sowing as reported by Arain *et al* (2002). M Qasim *et al* (2008) reported that the plant height decreased progressively with each delayed sowing. The earlier sown crop had longer vegetative growth period than late sown crop which resulted in more plant height.

Canopy temperature

Amani *et al* (1996) also used canopy temperature depression (CTD) to select for

yield under a hot, dry, irrigated wheat environment in Mexico. It had been pronounced that CTD is usually expressed as canopy temperature (T_c) minus air temperature (T_a) and it is positive when the canopy is cooler than the air. It has been used as a selection criterion in wheat breeding in terms of heat and drought stress tolerance (Reynolds *et al* 2001, Balota *et al* 2007). According to Munjal and Rana (2003) at grain filling period, cooler canopy and high stomatal conductance are assumed as the basic morpho-physiological criteria for higher grain yield under heat stressed conditions. Under more optimum (irrigated) conditions overall CTD showed relative high correlation with yield (Ginkel *et al* 2004). It is also recommended that CTD could be used to identify plants with cooler canopies with the aim of yield increasing under non-stressed conditions. The correlation study (Kumari *et al* 2012) showed that leaf area under greenness (LAUG) and canopy temperature depression (CTD) were strongly correlated. LAUG and CTD were also significantly associated with grain yield and biomass.

Photosynthetic Rate and Chlorophyll Content

Studies at CIMMYT demonstrated that under heat-stressed field conditions, photosynthetic rate has genetic variability (Delgado *et al* 1994). Physiological evidence indicates that loss of chlorophyll during grain filling is associated with reduced grain yield (Reynolds *et al* 1994). Wardlaw *et al* (1980) and Blum (1986) also revealed that in controlled environments, photosynthetic rate is genetically variable among wheat cultivars when exposed to high temperatures. Under heat stress, such differences in photosynthesis associated with a loss of chlorophyll and change in a:b chlorophyll ratio due to premature leaf senescence (Al-Khatib and Paulsen 1984, Harding *et al* 1990). Dhyani *et*

al (2013) observed that heat stress affects chlorophyll content and leaf area index (LAI) dramatically in sensitive genotypes under late sown conditions. At high temperature stress under late planting condition those genotypes are considered as heat tolerant that retain normal flag leaf chlorophyll for a longer period (Gupta *et al* 2006) and useful component for evaluating the tolerance of a crop to high temperature is proline which accumulates in plants under supra optimal temperature (Chaitanya *et al* 2001). When plants were stressed during vegetative and reproductive phases whole plant photosynthetic rates decline rapidly (Gupta *et al* 2006). Hasan *et al* (2007) reported that chlorophyll contents decreased with late sowing in all wheat genotypes.

Stem reserves

Important source of carbon for grain filling is stem reserves from pre-anthesis plant assimilation when current photosynthesis is inhibited by drought, heat or disease stress during this stage. The percentage of stem reserves in total grain mass or stem reserve mobilization is affected by sink size, cultivar and the environment. The relative study (in heat stress condition compared to normal condition) by Roy *et al* (2013) indicated that the heat tolerant genotypes had greater ability to utilize stem reserve compared to heat sensitive genotypes. Few studies suggested that the high capacity to utilize stem reserves for grain filling might be linked with accelerated leaf senescence (Yang *et al* 2000). Tahir and Nakata (2005) studied the dynamics of stored total nonstructural carbohydrates and nitrogen in leaves and stems under heat stress conditions.

These results suggest that rate of chlorophyll loss from flag leaf is positively correlated with nitrogen and total nonstructural carbohydrates remobilization efficiencies

under heat stress, suggesting a strong link between leaf senescence and remobilization efficiency.

Stay green

Stay Green genotypes retain chlorophyll in their leaves and the photosynthesis is carried for longer than the senescent types and are often shown to have a yield benefit (Borell *et al* 2001, Jordan *et al* 2003). Harris *et al* (2007) suggested three important components of tolerance were the SPAD reading at anthesis, the duration of senescence and rate of senescence. They suggest that important component of stay-green is rate of senescence rather than onset of senescence. Kumar *et al* (2010) have reported that stay green or delayed senescence is considered to play a crucial role in grain development in wheat when assimilates are limited, and stay green cultivars are well adapted to drought and heat stressed conditions. Nawaz *et al* (2013) reported that in heat sensitive cultivars, the imposition of heat increased the grain filling rate with a substantial decrease in grain filling duration. Thus, selection criteria for developing new wheat cultivars for heat resistance during reproductive stages would be stay green character and grain filling rate and duration under heat stress.

Yield related parameters

Number of Tillers

Tillering can be described as the degree of branching that determines the number of spikes per unit area, an important yield component, influencing light interception by the canopy and likely associated water use (Duggan *et al* 2005). To extent that high tiller number contributes to early season ground cover, this trait assists in competing against weeds and minimizing water loss due to soil evaporation in Mediterranean climates

(Borras-Gelonch *et al* 2010). Tahir *et al* (2009) reported that less number of tillers in late sowing was the result of less germination count per unit area which occurs due to low temperature. In case of delayed sowing the temperature was not according to the tillering requirement which results in less number of tillers per meter square. Differences in number of tillers per meter square among varieties might be attributed to their genetic diversity.

Number of Spikelets

Reduction in spike number per meter square is mainly due to higher tiller production in early sowing date with cooler temperatures during vegetative phase and decreasing in duration of vegetative phase in late sowing dates due to higher temperatures. This effect of sowing date on spike number per m² has also been reported by Ayeneh *et al* (2002). Rahman *et al* (2009) reported that green leaf area and productive tillers per plant were drastically reduced under high temperature (30/25°C, day/night).

Due to late sowing-induced heat stress, the spike length, number of spikelets per spike, number of tiller per meter row length were reduced significantly which further resulted in reduced grain yield (Ahamed *et al* 2010). Modaressi *et al* (2010) reported that high temperature could decrease grain yield upto 46.63%, 1000-grain weight, grain filling period upto 20% and spikelets per spike was reduced to 11%.

Grain Shrinkage

Elevated temperatures can also cause grain shrinkage through ultrastructural changes in the aleurone layer and endosperm cells as observed by Dias *et al* (2008) when day/night temperatures increased from 25/14°C to 31/20°C. As temperatures rise above 18-

22°C, the duration of starch biosynthesis and deposition to grain is reduced (Spiertz *et al* 2006). Heat stress accelerates the rate of grain filling whereas grain filling duration is shortened (Dias and Lidon 2009). For instance, 5°C increase in temperature above 20°C increased the rate of grain filling and reduced the grain filling duration by 12 days in wheat (Yin *et al* 2009). Under these conditions, the supply of photoassimilates may be limited (Calderini *et al* 2006).

Sarkar C K Guha *et al* (2001) noticed that the susceptible genotypes possessed relatively high grains number per spike as compared to tolerant types, while the 1000-grain weight was relatively high in the tolerant ones. High 1000-grain weight obtained in most of the tolerant types was likely because they could maintain high Grain Growth Rates (GGRs) under high temperature stress condition. Mian *et al* (2007) also observed that delayed sowing shortens the duration of each development phase which ultimately reduces grain filling period and lowers the grain weight. Decreasing in thousand grain weight with delay in sowing date is also due to high temperatures in March, April and May when temperatures raised and terminal heat stress coincided with grain filling period.

Grain development is impacted by heat stress because assimilate translocation and grain-filling duration and rate are influenced directly by changes in ambient temperature. The extent of heat-driven damage is dependent on the level of heat stress. Reduced number of ears per m², number of grains per ear and reduced grain size were the major responsible factors for reducing the grain yield under heat stress condition. Results from other studies showed that late planting heat stress caused lower grain yield in wheat compared to optimum sowing (Kosina *et al* 2007, Rehman *et al* 2009).

Reproductive Phase

Rane *et al* (2007) reported that decrease in duration of crop life cycle with delay in sowing date and coincidence of terminal heat stress in grain filling period caused lower biological yield. Minimum grain yield in wheat genotypes due to heat stress at reproductive stages may be due to least duration for resource utilization during grain filling (Dias and Lidon 2009, Yin *et al* 2009). Heat stress modifies the early dough and maturity stage, shorten the kernel desiccation period and cause grain yield loss in wheat (Zhang *et al* 2013). Post-anthesis heat stress in wheat induces several physiological effects which eventually result in smaller grain size due to reduced grain filling period and reduced grain filling rate or the combined effect of both (Hasan and Ahmed 2005). Choosing a suitable planting date and genotype with the appropriate phenology that matches crop growth to the climate conditions will lead to optimum grain yields (Chen *et al* 2003).

In conclusion with the current trends of climate change, the heat stressed wheat production environments around the world are apprehended to increase about three fold by 2050. Heat stress is a function of the magnitude and rate of temperature increase, as well as the duration of exposure to the raised temperature. Wheat experiences heat stress to varying degrees at different phenological stages, but heat stress during the reproductive phase is more harmful than during the vegetative phase due to the direct effect on grain number and dry weight.

It may be concluded that grain yield is an important selection criterion for breeding programmes. Grain yield is related with various traits such as morphological, physiological and yield components. These yield related traits like number of tillers per

plant, plant height, flag leaf area, and spike characteristics like spike length, spike density, spikelets per spike, 100-grain weight and grain yield per plant etc. under both conditions play important role to improve yield stability and potential. These plant traits may contribute towards high grain yield and can help the plant to perform well in normal and stress conditions. The information obtained from these traits may be used to evolve high yielding varieties which can produce economic yield and help the yield sustainability in those areas where terminal heat stress is a major threat.

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