

Effects of high temperature stress and traits associated with tolerance in wheat

Abstract

Wheat (*Triticum aestivum* L.) is the most important crop in the world in terms of area harvested and the second most important food crop in the developing world after rice. To meet the increased demand of the exploding world population by 2050, wheat production needs to increase by 60%. However, wheat yields are currently limited by several environmental stresses, and high temperature stress is a major one among them. This review focuses on the impact of high temperature stress on wheat plants and traits associated with tolerance which would help formulate management strategies for wheat yield improvement under high temperature stress and breeding for high temperature tolerant varieties.

Keywords: *Triticum aestivum*, wheat plants, photosynthesis, wheat yield, tolerant varieties, biomass production high temperature stress

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Abbreviations: PS II, photosystem II; CTD, canopy temperature depression; SS, starch synthase; SSS, soluble starch synthase; HSP, heat shock proteins; ROS, reactive oxygen species; SG, sterol glycoside; OH, hydroxyl ion; HIS, heat susceptibility index; TDF, time of day of flowering; TTC, triphenyl tetrazolium chloride

Introduction

Wheat (*Triticum aestivum* L.) is the most important crop in the world in terms of area harvested.¹ It provides about 20 % of the total dietary calories and proteins worldwide.¹ It is a widely adapted crop grown in a vast range of environments ranging from temperate, irrigated areas to tropical, high-rainfall areas and from warm, humid conditions to cold, dry conditions.² Wheat is one of the earliest domesticated food crops in the world³ and is believed to have originated in south-western Asia or more specifically, in the fertile crescent about 8000 to 10000 years ago.⁴ In recent years, wheat production levels were unable to meet the demand, leading to price instability and hunger riots. To satisfy the increased demand of 9 billion people by 2050, wheat production needs to increase by 60%. This will require at least 1.6% annual wheat yield increases, which in turn will necessitate tolerance to abiotic and biotic stresses and improved input use efficiency. High temperature stress is a major environmental factor that limits yield in wheat. Every 1°C increase above a mean temperature of 23°C decreases wheat yield by ~10%.⁵ More than 40% of total wheat area in the world is affected by high temperature stress.⁶ High temperature affects wheat yield either through chronic stress by prolonged, moderately high temperatures up to 32°C or through heat-shock, which is sudden, but comparatively brief exposure to 33°C and above.⁷⁻⁹ The impact of high temperature stress on crop depends up on intensity, rate of increase, duration of stress and stage of crop development.^{10,11} High temperature stress induces several alterations in physiological, biochemical and molecular components of wheat crop production. The objective of this review is to discuss the impact of high temperature stress on wheat plants and traits associated with tolerance which would help formulate management strategies for wheat yield improvement under high temperature stress and breeding for high temperature tolerant varieties.

Effect of high temperature stress on physiological traits

Photosynthesis

Photosynthesis is one of the most sensitive processes to high temperature in wheat.¹² Photosynthetic rates exhibit a sharp decline when wheat plant is exposed to high temperature stress during vegetative or reproductive phase.^{12,13} Optimum temperature for photosynthesis has a broad range (20 to 30°C) in wheat, however, the rate photosynthesis declines rapidly at temperatures >30°C.¹⁴ Net photosynthetic rate throughout the crop cycle is a major parameter controlling biomass production and grain yield of wheat under high temperature stress.^{15,16} reported that high temperature (32/27°C day/night) at seedling stage or from anthesis to maturity decreased average leaf photosynthetic rate of wheat by 32 and 11%, respectively.^{17,18} reported reduction in photosynthetic rates due to high night temperatures (>14°C) in wheat. Photosynthesis happening at awns is more temperature tolerant compared to that in leaves.¹⁹ Mobilization of stem reserves from pre-anthesis photosynthesis to developing grains is increasingly important for grain filling when current photosynthesis is inhibited by high temperature stress.⁹ Considerable genetic variability has been reported in wheat for net photosynthetic rate under high temperature conditions.²⁰ Disruptions in the structure and function of chloroplasts, reduction in chlorophyll content and inactivation of chloroplast enzymes under high temperature are major reasons for decreased photosynthesis in wheat under high temperature stress.^{20,21} Reduction in net photosynthetic rate under high temperature stress during grain filling period is closely associated with chlorophyll loss⁹ and variation in the ratio between chlorophyll *a* and chlorophyll *b* due to premature leaf senescence.^{22,23} High temperature initially accelerates thylakoid membrane breakdown, which leads to electrolyte leakage and disruption of all photochemical reactions, especially, photosystem II (PS II) and cytochrome *f/b6*-mediated reactions, which ultimately lead to drastic reduction in rate of photosynthesis.^{22,23} Photosystem II has a major role in the responses of photosynthetic reactions to high temperature. Photosystem II is more sensitive to high temperature than PS I.²⁴ In wheat, high temperature causes significant damage to

different sites of PS II.²⁵ Since wheat is a cool season crop, its PS II is more sensitive to high temperature stress compared to warm season crops such as rice and pearl millet (*Pennisetum glaucum*).²² High temperature stress also causes cessation of photophosphorylation due to damage of thylakoid membrane.²⁶

Stomatal conductance

Increased stomatal conductance ($\text{mmolm}^{-2}\text{s}^{-1}$, measure of rate of CO_2 entering or water vapor exiting through the stomata) leads to transpirational cooling and canopy temperature depression (CTD). Higher stomatal conductance and associated leaf cooling provides an avoidance type of heat resistance to high temperature.^{27,28} showed a positive correlation between stomatal conductance and yield in wheat grown under hot environments. identified stomatal conductance as a useful selection criterion in wheat for high yields. Positive correlation is reported between CTD and stomatal conductance and between CTD and yield in wheat grown under hot environments.²⁸⁻³⁰ reported that stomatal conductance remained unaffected across night temperatures of 14, 17 and 20°C and slightly increased by 10% at night temperature of 23°C.

Respiration

Impact of high temperature stress on respiration is relatively less understood.²² With increases in temperature, respiration cost increases and reaches the point that rate of photosynthesis cannot compensate for respiratory losses, and that leads to carbon starvation.³¹ Responses of respiration to high temperature vary with the age of organs in crop plants.²⁷ Generally, respiration exponentially increases with increasing temperatures from 0 to 35 or 40°C, reaches the maximum around 40 to 50°C and then decreases with further increases in temperature above 50°C.^{32,33} reported high temperature (35/25°C day/night) significantly increased the flag leaf respiration rates, compared to control (23/18°C day/night) in heat susceptible varieties.

Effect of high temperature stress on biochemical traits

Enzyme activities

Response of photosynthesis to high temperature stress is closely related to temperature dependence of the major photosynthetic enzyme, Rubisco.²⁷ Under high temperature conditions, rate of inactivation of Rubisco exceeds activase's ability to promote Rubisco activation,³⁴ which leads to reduced activation and activity of Rubisco. In addition, under high temperature stress, solubility of CO_2 is decreased at a greater extent than O_2 , which favors the oxygenation activity of Rubisco, which leads to increased photorespiration and reduced photosynthesis.³⁵ Endogenous levels of Rubisco activase plays an important role in determining wheat productivity under high temperature stress conditions.³⁶ High temperature (40°C) decreases the abundance of large and small subunits of Rubisco and Rubisco activase.^{37,38} observed genetic variability in wheat for synthesis of the small subunit of Rubisco at 34°C. Starch synthase (SS) is one of the key enzymes responsible for endosperm starch biosynthesis and grain filling. High temperatures above 25°C decrease the activity of SS in wheat.³⁹⁻⁴¹ In addition, high temperature also regulates SS gene expression at the transcriptional level and reduces the relative levels of transcripts for that enzyme more than for other starch biosynthetic enzymes in wheat.³⁹ Considering the enzymes involved in endosperm starch synthesis pathway, soluble starch synthase (SSS) is highly thermosensitive, especially at temperatures above 34°C.⁴⁰ Soluble starch synthase has a T_{opt} of 20–25°C and temperatures above

25°C adversely affect the activity of this enzyme, which results in reduced grain growth and starch accumulation.⁴² This effect is found to be apparently reversible in wheat after a short period of exposure to elevated temperature.⁴¹ However, prolonged exposure to elevated temperature causes knockdown or complete loss of activity of SSS, which is much slower to reverse in wheat endosperm.⁴¹ Even short periods of high temperature stress (30–40°C) causes a decline in the rate of starch deposition due to reduction in the activity of SSS.⁴¹ reported that several other enzymes in starch biosynthesis pathway, including alkaline pyrophosphatase, phosphoglucomutase, UDP-glucose pyrophosphorylase, hexokinase, phosphoglucoisomerase, sucrose synthase, ADP- glucose pyrophosphorylase and bound starch synthase remained unaffected under elevated temperatures (25–45°C).

Membrane stability

Membrane thermostability is highly correlated with yield in wheat under hot environments.^{43,44} Studies have documented high genetic variability and heritability of this trait in wheat.⁴⁵ reported that membrane thermostability of heat-acclimated flag leaves under field conditions as well as seedlings grown in controlled conditions was associated with heat tolerance in 16 spring wheat cultivars at several hot environments. Level of unsaturation of membrane-phospholipids is linked to the extent of heat induced damage to membranes.⁴⁶ Thylakoids harbor chlorophyll, and damage of thylakoid membrane under high temperature stress leads to chlorophyll loss in wheat.^{47,48} reported increased membrane stability in heat tolerant wheat genotypes and association of that character to activity of antioxidant enzymes. Even though cell membrane thermostability has been identified as a potentially powerful selection criterion for high temperature tolerance in wheat, some studies have reported that this trait alone cannot serve for that purpose.⁴⁹

Heat shock proteins

Plants produce specific proteins termed as heat shock proteins (HSP) in response to high temperature stress. Heat shock proteins are usually undetectable at non-stressed conditions.⁵⁰ They can be categorized in to high molecular weight (ranges from 68 to 110kD) and low molecular weight groups (ranges from 15 to 27kD). High molecular weight HSPs are present in all organisms studied to date. Low molecular weight HSPs are the most abundant class of HSPs in higher plants, and the 15 to 18kD HSPs are unique to plants.^{50,51} Most, but not all, heat shock proteins are molecular chaperones. Molecular chaperones are proteins produced in plants in response to high temperature stress.^{52,53} They bind with partially unfolded or denatured proteins to stabilize them, and protect them from thermal aggregation and facilitate their re-folding during recovery when stress is relieved.⁵⁴⁻⁵⁶ Some HSPs are also involved in eliminating potentially harmful proteins arising from misfolding, denaturation or aggregation and play an important role in maintaining cellular homeostasis.⁵⁷ Heat shock proteins consists of classical and non-classical proteins. Most of the classical HSPs exhibit chaperon activity, binding with denatured proteins to prevent their thermo-aggregation. Non-classical HSPs include plastid protein synthesis elongation factor EF-Tu and peptidyl-prolyl cis/trans isomerases.⁴⁷ showed a positive correlation between synthesis of specific low molecular weight HSPs and heat tolerance in wheat. Wheat exhibits genetic variability for the synthesis of HSPs in response to high temperature stress.³⁸⁻⁵⁷ reported that acquired heat tolerance in wheat is associated with the level of expression of HSP genes during the initial 2 h of high temperature stress. It is reported that HSPs are synthesized even before leaf

temperatures reach lethal levels for growth and development.^{58,59} reported that EF-Tu is upregulated in wheat under high temperature stress and genotypes with increased accumulation of this protein are tolerant to high temperature stress. EF-Tu improves heat tolerance through its chaperone activity.⁶⁰ reported that transgenic wheat carrying an EF-Tu gene from maize (*Zea mays* L.) exhibited decreased thermal aggregation of leaf proteins and thylakoid membrane damage and increased rate of photosynthesis under high temperature stress. Transgenic wheat plants with EF-Tu gene produced superior grain yield based on number of grains per plant, total grain weight per plant and individual grain weight, compared to their non-transgenic counterparts under high temperature stress (Fu and Ristic, 2010). Modification of the expression of plastidial EF-Tu and/or selection of genotypes with increased activity might help improve heat tolerance of wheat.⁶⁰

Reactive oxygen species

High temperature stress often induces accumulation of reactive oxygen species (ROS) including hydrogen peroxide (H_2O_2), superoxide radical (O_2^-), hydroxyl ion (OH^\cdot) and singlet oxygen (O^1) in plant tissues, which leads to oxidative stress.^{61,62} Chloroplast, mitochondria and peroxisomes are major cellular organelles that generate ROS under stress.⁶³⁻⁶⁵ High temperature stress induced membrane and protein damage results in increased ROS content.^{66,67} Over-excitation of chlorophyll molecules under high temperature also results in accumulation of ROS.⁶⁸⁻⁷⁰ In general, high temperature induced imbalance between photosynthesis and respiration leads to oxidative damage in plants.⁷¹ Accumulation of ROS causes disruption of DNA strands and activation of cell wall hydrolyzing enzymes such as nucleases, proteases and lipases resulting in loss of cell structure.^{72,73} It also causes denaturation of proteins and lipid peroxidation in membranes, which lead to membrane damage and membrane leakiness, and ultimately results in decreased photosynthetic rate and enhanced cell death.^{74,75}

Antioxidants

The antioxidant defense system in plants has both enzymatic and non-enzymatic components. Major antioxidant enzymes in plants include superoxide dismutase, catalase, peroxidase, ascorbate-glutathione pathway enzymes such as ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase and glutathione reductase, Halliwell-Asada pathway enzymes and dehydroascorbate reductase. Non-enzymatic antioxidants include glutathione, ascorbic acid, β -carotene and tocopherols. Under non-stressed conditions, antioxidants scavenge ROS and protect cells from oxidative damage. Under stressed conditions, the general antioxidant status diminishes or antioxidants reduce their activity and the amount of ROS increases in the cell.⁷⁶⁻⁷⁸ Superoxide dismutase, catalase and peroxidase system converts ROS to O_2 and water. As a result of ascorbate-glutathione pathway, H_2O_2 will be reduced to water. Superoxide dismutase is the only enzyme that can scavenge O_2^- , whereas catalase and peroxidase scavenge H_2O_2 . Increased antioxidant enzyme (superoxide dismutase, catalase, glutathione reductase and peroxidase) activities are reported in heat tolerant genotypes in wheat.^{79,80} Non-enzymatic antioxidants, such as ascorbic acid is also important for protection of wheat plants from heat-induced oxidative damage.^{81,82} found that application of abscisic acid and salicylic acid increased the activity of antioxidant enzymes and decreased the amount of ROS in high temperature stressed wheat plants, and this decreased oxidative damage resulted in increased chlorophyll and

carotenoid contents, relative water content, membrane stability index, leaf area and total biomass compared to control plants.

Effect of high temperature stress on lipid metabolism

Identified lipid metabolic changes⁸³⁻⁸⁵ during high temperature stress in wheat and coordinated metabolism of lipid groups during high temperature stress responses⁸³⁻⁸⁵ they found that wheat leaf and pollen lipid compositions are significantly altered by high temperatures, in which some lipids are highly responsive to high temperatures, and that two wheat genotypes, chosen for their differing physiological responses to high temperature, differ in leaf lipid profiles under high temperatures. The wheat plants decreased the unsaturation levels of plastidic and extraplastidic glycerolipids of leaf and/or pollen in order to adapt to high temperature stress, and underwent lipid remodeling, likely to prevent the phase transition of membranes from a bilayer to non-bilayer phase. The lipid remodeling included decreases in the amount of more unsaturated lipids and increases in the amounts of less unsaturated lipids, phospholipids containing odd-chain fatty acids, sterol lipids [sterol glycoside (SG) and 16:0 acyl containing SG], 18:3-acyl-containing TAGs, and ox-lipids. Increases in activities of desaturating, oxidizing, glycosylating, and acylating enzymes led to simultaneous changes in levels of multiple lipid species during stress, leading to existence of co-occurring lipid groups.⁸⁴ Their results suggested that (1) SGs and ox-lipids might be associated with plant heat tolerance and susceptibility, respectively, (2) TAGs play a role in high temperature stress adaptation by sequestering fatty acids from the membrane lipids, and (3) changes in the amounts of phospholipids with odd-chain fatty acyl components under high temperature stress might be a diagnostic of the extent of heat damage, and (4) lipids can undergo coordinated metabolism during high temperature stress, leading to existence of co-occurring lipid groups.

High temperature sensitive stages in wheat

Vegetative stages

High temperature, usually, decreases the duration of all growth stages in wheat.⁸⁶ reported that high temperature from emergence to anthesis significantly decreased duration of all the development stages, GS1 (emergence to double-ridge), GS2 (double ridge to anthesis) and GS3 (anthesis to grain maturation) in wheat; and duration of GS2 was most sensitive to high temperature. The developmental stage at which wheat plant is exposed to high temperature stress will determine the degree of damage.⁸⁷ The double-ridge stage is highly sensitive to high temperature stress.⁸⁷ High temperature at double-ridge stage damages the development of spikelet primordia on the apex.⁸⁸ reported that plant height and tiller number remained unaffected, whereas, biomass showed a curvilinear decrease under high night temperatures ($>23^\circ C$) in wheat.

Reproductive stages

High temperature stress during reproductive development is a major constraint to wheat production in most parts of the world. Wheat plant suffers from greater damage when high temperature stress occurs during the reproductive phase than vegetative phase due to the direct effect of high temperature on grain number and grain weight.⁸⁹ Generally, plant reproductive tissues have less temperature tolerance compared to vegetative tissues. Reproductive development is accelerated when wheat is grown in hot environments.^{90,91}

Pollen and ovule formation

The most heat sensitive stage of reproductive development in wheat is the period from the onset of meiosis in pollen or embryo sac mother cells to the early development of micro or megaspores.⁹²⁻⁹⁴ Pollen formation is one of the most heat sensitive processes in cereals including wheat.⁹²⁻⁹⁴ High temperature induced pollen sterility is mainly due to the irregularities during microsporogenesis.⁹⁵ Inability of pollen to synthesize HSP is thought to be the reason for its increased sensitivity to high temperature.⁹²⁻⁹⁵ reported 35% reduction in pollen viability in wheat plants exposed to high temperature of 30°C for 3 d compared to normal temperature (20°C). Female fertility is also affected by high temperature in wheat.⁹²⁻⁹⁴ High temperature stress that coincides with meiosis in megaspore mother cells leads to abnormal ovary development with small sized or no embryo sac and reduced nucellus.⁹³ High temperature stress causes many ultra-structural changes to pollen grains which lead to pollen sterility in wheat.⁹³ reported that high temperature (30°C for 3d) during meiosis caused premature degeneration of tapetal cells which resulted in pollen sterility in wheat. These sterile pollen grains contained apparently normal exine, very little or no intine or cytoplasm and no starch.

Anthesis

High temperature stress causes severe damage to plants when it occurs during or soon after anthesis. Wheat plants are highly susceptible to high temperature stress during the period between flower initiation and anthesis, and the effect is marked by the reduction in kernel number. T_{min} , T_{opt} and T_{max} for successful anthesis are reported as 9, 18–24 and 31°C respectively in wheat.⁹⁷

Seed set

Generally, high temperature stress just before or during anthesis is associated with reduced seed set percentage in wheat, mainly due to (a) production of nonviable pollen or ovule, (b) hindered pollen tube growth and (c) inability of fertilized embryo-sac for the transition to a seed.⁹²⁻⁹⁴ Seed set in wheat is most sensitive to high temperature stress when the stress coincides with the time period between the onset of meiosis in pollen mother cell to the formation of microspores and their early development.⁹²⁻⁹⁴ High temperature stress at this highly sensitive stage hinders pollen performance, which leads to drastic reduction in seed set. High temperature stress during meiosis in megaspore mother cell results in abnormal ovary development and reduced pollen tube growth in wheat, which leads to reduced seed set. Embryo abortion has been reported in wheat due to high temperature stress.⁹⁸ reported that high temperature induced increase in ethylene production presumably causes embryo abortion and decreased kernel weight in wheat.

Yield components and yield

Grain number

Grain number is a major component of yield in wheat.⁹⁹ High temperature accelerates the development of the spike and reduces the number of spikelets and grains per spike.²¹ Genetic variation is reported in wheat for grain number under high temperature stress.^{44,45} Temperatures above 31°C just before anthesis cause reduction in grain number due to pollen sterility.¹⁰⁰ reported 4% reduction in number of wheat grains per unit area for each degree increase (from 15–22°C) in mean temperature during the one month period before anthesis. reported that 10°C increase in maximum temperature at mid anthesis caused 40% reduction in grain number per spike.¹⁰¹⁻¹⁰³ examined 21

spring wheat cultivars and found that heat tolerance was associated with increases in grain number per spike documented a linear decrease in grain number per spike with increases in night temperatures from 14 to 23°C.

Individual grain weight

Reported that high temperature (32/27°C) from anthesis to maturity caused 20% reduction in average grain weight of wheat.¹⁰⁴ observed that high temperature (40/21°C) during grain filling decreased individual grain weight of wheat by 14%, compared to the control (21/16°C).⁵ imposed high temperature stress starting from 15 d after anthesis (grain number was set by this time) until maturity, and quantified yield reduction due to decreased individual grain weight as 18%. Elevated temperatures reduce the time period between anthesis and physiological maturity, which results in a reduction in individual grain weight.¹⁰⁵ Decreased size of endosperm cells in grains and reduced starch deposition due to reduced activity of SSS are major reasons for decreased individual grain weight under high temperature stress.¹⁰⁶ reported that a sudden increase in temperature (from 20 to 40°C) caused a greater reduction in individual grain weight than a gradual increase in temperature (6°C h⁻¹, from 20 to 40°C) in a heat sensitive wheat variety, but this trend was absent in the heat tolerant wheat variety. Considerable genetic variability has been identified in wheat for individual grain weight under high temperature stress.

Grain filling duration

High temperature-induced decrease in grain filling duration results in a reduction of individual grain weight.⁸⁴⁻¹⁰⁴ Grain filling duration decreases by 2-8 d for every 1°C increase above 15–20°C in wheat (reviewed by Streck, 2005). Prasad et al. (2008b) reported that grain filling duration in wheat was decreased by 3 and 7 d at night temperatures of 20 and 23°C, respectively, compared to a night temperature of 14°C.

Grain filling rate

Under optimum temperature conditions, decreased grain filling duration is compensated by increased grain filling rate, but this compensation does not happen under high temperature stress, which results in a significant reduction in individual grain weight.¹⁰⁷ Reduction in leaf and spike photosynthesis and decreased remobilization of stem reserves are major reasons for decreased grain filling rate at high temperatures. Increased grain filling rate is a useful trait that can be used for the improvement of heat tolerance in wheat.²⁶

Total grain yield

Found that high temperature stress of 35/20°C from 10 d after anthesis until maturity decreased grain yield by 78%,⁵ grain number by 63% and individual grain weight by 29%. Reduction in number of spikes per unit area, number of fertile spikes per plant, number of grains per spike and grain weight lead to reduction in grain yield of wheat under high temperature stress.¹⁰⁸ reported that grain yield in wheat is more sensitive to increases in daily T_{min} than T_{max} . The same authors observed 10% decrease in wheat yield for every 1°C increase in night temperature above optimum in Mexico.

Grain quality

High temperature stress during the post-heading period adversely affects grain quality in wheat.¹⁰³ High temperature stress influences grain protein content and composition.¹⁰² It reduces starch deposition

in grains¹⁰⁹ and leads to more nitrogen per unit of starch.⁴¹ High temperatures (>35 °C) during grain filling negatively affect dough properties in wheat since it increases the ratio between gliadin and glutenin in grains, which produces a weak dough (Blumenthal et al., 1993). High temperature stress also reduces noodle swelling power of wheat flour (Stone and Nicolas, 1994).

Breeding for high temperature tolerance

Genetic resources available for the improvement of bread wheat consist of primary, secondary and tertiary gene pools.¹¹⁰ Genetic variability for heat tolerance has been identified in cultivated wheat^{111–114} and its wild relatives.^{115,116} Genetic variability for heat tolerance has been reported in wild *Triticum* and *Aegilops* species as well. These authors tested accessions from nine different countries of the world and found that all of the heat tolerant accessions were from eastern Israel, western Jordan and southwestern Syria. The authors also suggested that these three regions can be exploited for heat tolerant genotypes of bread and durum wheat that could be incorporated into wheat breeding programs. Landraces also exhibit significant genetic variability for heat tolerance. Heat tolerant accessions belonging to *Aegilops geniculata*, *A. speltoides*, *A. searsii* and *A. longissima* have been identified.¹¹⁷ screened 52 accessions of *Aegilops sp.* for tolerance to an extended period (16d) of high temperature stress at anthesis and identified tolerant genotypes of *A. speltoides* and *A. geniculata* based on grain number and grain size. They also reported that tremendous genetic variability exists in *Aegilops sp.* for heat tolerance that can be exploited in breeding for heat tolerance at reproductive stage. High temperature tolerance have also been reported in different genotypes of synthetic wheat.^{118,119} Synthetic wheats are valuable genetic stocks and can act as bridges for introgression of alien genes into cultivated wheat varieties.^{120,121}

Traits associated with heat tolerance

Canopy temperature depression

Canopy temperature depression is the difference between air temperature and canopy temperature. Canopy temperature depression shows high genetic correlation with yield in wheat in both warm and temperate environments. Canopy temperature depression is significantly correlated with biomass, grains m⁻², spikes m⁻² and grains spike⁻¹ under high temperature conditions in wheat. It is a heritable trait and can serve as a useful criterion for evaluating heat tolerance in both early and advanced generations. Canopy temperature depression is a function of many important physiological mechanisms such as metabolism, partitioning and vascular transport, and is therefore, a powerful trait for selection. However, this trait is highly sensitive to environmental factors such as radiation, evapotranspiration and wind. It shows highest potential as a selection criterion in low relative humidity environments.

Early heading

Early heading is an important and effective trait of wheat genotypes that contribute to heat tolerance.¹²² concluded that early-heading cultivars out-yielded later-heading cultivars in environments with risks of post-heading high temperature stress. Compared to later heading cultivars, early heading cultivars showed many important tolerant traits including (a) longer post-heading period and grain-filling duration, (b) completion of significant fraction of grain-filling duration earlier in the season before the onset of high temperature

stress, (c) retention of more number of green leaves at anthesis and (d) less number of leaves lost due to senescence at anthesis. However, early heading may not be a useful trait to select cultivars suitable for locations where cool temperature or frost limits the early heading trait.

Time of day of flowering

Another dehiscence, pollen shed, pollen tube growth, pollination and fertilization are highly sensitive to high temperature stress, while the embryo formed after fertilization is comparatively more tolerant. The time of day of flowering (TDF) is the time of the day at which anthesis commences in a crop.¹²³ Air temperature increases rapidly after sunrise and exceeds the critical temperature of 35°C at around 10:00 AM in high temperature damage-prone areas.¹²⁴ Therefore, shifting of TDF to early hours of the morning is one way to escape high temperature-induced spikelet sterility in plants.¹²⁴ Genetic variability has been reported for TDF in cereals such as rice, where TDF varied from 7:00 AM to 12:30 PM.

Increased partitioning

Grain filling under high temperature stress is largely associated with partitioning of stem reserves in wheat. Increased ability to utilize mobilized stem reserves contributes to increased grain number and grain weight under high temperature stress. Increased partitioning of reserves from leaves, stem or other plant parts is a potential strategy to improve grain filling and yield in wheat under high temperature stress. Considerable genetic variability is reported for assimilate partitioning under high temperature stress in wheat. Increased partitioning under high temperature stress is a 'true tolerance mechanism' exhibited by tolerant genotypes.

Heat susceptibility index

Heat susceptibility index (HSI) for grain yield is calculated using the formula, $HSI = (1 - Y/Y_p)/D$; where, Y is the average grain yield per plant of a genotype at high temperature, Y_p is the average grain yield per plant of the same genotype at optimum temperature, D is the stress intensity, which is calculated as $1 - X/X_p$, in which X is the mean Y of all genotypes, and X_p is the mean Y_p of all genotypes.¹²⁵ Low HSI is a useful criterion to select heat tolerant genotypes in cultivated and wild wheat. Generally, genotypes with HSI ≤ 0.5 are considered as highly heat tolerant, genotypes with HSI > 0.5 to ≤ 1.0 are considered as moderately tolerant and genotypes with HSI > 1.00 are considered as susceptible.

Chlorophyll content

Measurement of chlorophyll content in leaves is useful for high throughput screening for heat tolerance among wheat genotypes.⁴⁷ Chlorophyll loss is closely associated with heat-induced thylakoid membrane damage in wheat.⁴⁷ Genetic variability exists in wheat for the ability to retain chlorophyll content under high temperature stress.¹²⁵

Decreased membrane damage

Increased membrane stability, which is an indication of decreased membrane damage is a selection criterion used to select heat tolerant wheat genotypes under both controlled and field conditions. Genotypes vary in the extent of membrane damage under high temperature stress. Since cellular membrane stability is a highly heritable trait, it has a potential application in breeding wheat for heat tolerance. found that increased membrane stability was associated with

increased grain weight per spike in wheat. Measurement of electrical conductivity quantifies heat induced electrolyte leakage from tissues, thus, it evaluates the damage to plasma membrane measurement of chlorophyll *a* fluorescence indicates damage to thylakoid membranes specifically,¹²⁶ and triphenyl tetrazolium chloride (TTC) assay can quantify damage to mitochondrial membranes.^{127–130}

Decreased ROS production and increased amount of antioxidants

Protection against oxidative damage is an important component in the determination of heat tolerance in plants.^{131–134} Increased antioxidant activity is correlated with reduced oxidative damage and acquired thermotolerance in wheat. The beneficial effects of increased antioxidant enzyme activity and decreased oxidative damage is reflected in many physiological and biochemical parameters such as increased chlorophyll and carotenoid contents, relative water content and membrane stability and whole plant characteristics such as increased leaf area and total biomass. To exploit the association between antioxidant activity and heat tolerance, external growth regulators are applied in wheat to increase the activity of antioxidants and to reduce heat damage.^{135–137} For example,^{137–142} abscisic acid and salicylic acid when sprayed on leaves of wheat genotypes increase the activity of antioxidant enzymes such as superoxide dismutase, ascorbate peroxidase,^{142–145} glutathione reductase and catalase and decrease the contents of ROS such as hydrogen peroxide and thiobarbituric acid reactive substances.⁶⁴

Heat Shock Proteins

Since the synthesis of HSPs is related to acquisition of heat tolerance in wheat,^{54,55} it offers a useful trait for selecting for heat tolerance. Manipulation of expression patterns of HSPs has the potential to improve temperature tolerance of wheat. Transgenic wheat plants with increased heat tolerance have been developed using HSP (plastid protein synthesis elongation factor- EF-Tu genes from maize.^{145–148}

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Conflict of interest

The author declares there is no conflict of interest.

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