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Morpho-physiological and biochemical mechanism for terminal heat stress in bread wheat (*Triticum aestivum* L.)

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Abstract

Wheat is grown in tropical and subtropical regions of the world that experience different biotic stresses. India's wheat production is affected by heat stress on about 13.5 million ha Uttar Pradesh (UP) produce over 30% of India's wheat production and about 14% of its rice production. Several agronomic traits are affected by heat stress conditions. Physiological and biochemical traits are controlled by multiple genes that affect heat tolerance. The CTD is dependent on many factors, including air temperature, humidity, soil conditions, and incident radiation. Using RWC, plants can be evaluated for their water status relative to their fully turgid state. In these conditions, however, plants often adapt osmotically, which maintains turgor pressure and makes the definition of 'full turgidity' difficult to determine. In wheat, chlorophyll content is related to heat tolerance and stay-green traits. The chlorophyll estimation will determine the relative amount of chlorophyll in the plant and absorbance will be measured at 663nm and 645nm, as well as other traits. GFD in bread wheat refers to the period of time between an thesis and physiological maturity. HSPs are a family of proteins that play a crucial role in protecting plants from heat stress by preventing the aggregation and denaturation of other proteins in the plant cell.

Keywords - *Relative water content (RWC), Chlorophyll content, Canopy temperature (CTD), Grain filling duration (GFD), Heat shock protein (HSP).*

1. Introduction

Wheat (*Triticum aestivum* L.) is India's second-most significant food crop, after rice (Gupta *et al*., 2008). A winter crop is wheat, and India ranks second in production worldwide. Heat & cold stress have a negative impact on crop germination, growth, and development. Wheat production can be significantly reduced under certain conditions such as terminal heat stress during grain formation or when grown under late sowing conditions in certain regions like India and the Mediterranean. These challenges can affect the overall productivity and quality of the wheat crop (Tewolde *et al.,* 2006). Wheat is grown in almost every continent and is traded globally, making it an important commodity. The production of wheat is influenced by various factors, including weather patterns, soil fertility, disease and pest infestations. Efforts are being made to improve wheat production and ensure its sustainability (Chaves *et al.,* 2013). Generally, heat tolerance refers to a plant's capacity to survive and make a profit in an environment with a variety of biotic challenges. (Rahaie *et al*., 2013).

Wheat is grown in tropical and subtropical regions of the world that experience different biotic stresses. In this regard, even related species and even various tissues and organs within the same species may differ greatly from one another (Rodriguez *et al*., 2005 & Wang *et. al*., 2004). India's wheat production is affected by heat stress on about 13.5 million ha (Joshi *et al*., 2007) Uttar Pradesh (UP) produce over 30% of India's wheat production and about 14% of its rice production. UP and Rajasthan have both had relatively large climate impact on wheat since 1980, with 0.87°C and 0.52°C (Jennifer & Ramanathan *et al*., 2014).

The harmful impacts of high temperature during reproductive stages can be aggravated, leading to reduced grain yield. (Hatfield *et al*., 2011). Given these challenges, breeding heat-tolerant wheat genotypes is necessary for sustainable wheat production (Asseng *et al.*, 2011). These genotypes can withstand high temperatures during reproductive stages and maintain grain yield even in adverse climatic conditions. It appears that certain components can help crops withstand osmotic stress caused by high temperatures (HT). These components act as osmoprotectants, meaning they protect the plant by helping it maintain its water balance and prevent dehydration (Rivero *et al.*, 2014 and sattar *et al.*, 2020). Heat tolerance genes in wheat are one of the major focus areas for developing future heat tolerance strategies. The new crop varieties will have to be adapted to the future climate by improving heat tolerance and responding to prominent temperature (Halford *et al*., 2009). A wheat's terminal heat tolerance is useful in screening it. The purpose of these screening techniques is to simulate the effects of heat stress in the target environment.

Physiological changes induced by heat stress which cause leaf senescence in winter season (Dhyani *et al.,* 2013, Almeselmani *et al.,* 2011). Under heat stress, plants respond in a variety of morphological, physiological, biochemical, and molecular ways. Wheat is morphologically adapted to heat stress in a number of ways, including enhancing germination capacity, vegetative development, leaf rolling and folding, and delaying early leaf senescence. Under heat stress, early maturation may also be an avoidance mechanism (Adams *et al.,* 2001). The synthesis of stress-related proteins can also be triggered by molecular changes such as altered gene expression and transcript accumulation (Iba et al., 2002). Physiological and biochemical traits are controlled by multiple genes that affect heat tolerance (Maestri *et al*., 2002). Physiological selection traits such as canopy temperature (CT) are ideal in many ways since they can be measured quickly, easily, and inexpensively (Cossani & Reynolds *et al*., 2012). A quantitative trait locus (QTL) has been identified in a mapping population where yield and stay green traits are correlated (Kumar *et al*., 2010; Vijayalakshmi *et al*., 2010). It has been reported that membrane thermo tolerance in wheat can result from both additive and dominant gene action (Dhanda & Munjal *et al*., 2012) as well as QTL with SSR markers (Ciuca & Petcu *et al*., 2009). Heat-tolerant cultivars have not been significantly affected by MAS (Tuberosa & Salvi *et al*., 2006; Ortiz *et al*., 2008). An investigation was made into the genotypes of Indian wheat's chlorophyll content, heat tolerance, and correlation to molecular markers.

2. Mechanism of heat tolerance

The physiological reactions of thermal and susceptible genotypes during different plant development stages, especially grain filling, can provide insight into heat tolerance mechanisms. Early maturity under high temperature is linked to lower yield losses in different plants, which indicates early maturity is a mechanism of escape (Adams *et al*., 2001). In different growth stages, plants experience a variety of environmental stresses and their mechanism of responding may vary based on the type of stress (Queitsch *et al*., 2000).

Temperatures should be in the normal range of 18-22°C for higher yields. In order for plants to mature at an early stage, high temperature must change their anatomy (Porter *et al*., 2005). The high temp. causes cellular damage that may result in cell death. Injuries due to heat lead to protein denaturation. If the temperature is low, enzymes are inactive and protein synthesis is reduced (Howarth *et al*., 2005). There are a variety of ways in which plants can be affected by high temperatures, low temp. and high soil temp. Additionally, many crops are very sensitive to high temperatures (Anand *et al*., 2020).

3. Morphological mechanisms

3.1 Grain filling duration (GFD)

GFD in bread wheat refers to the period of time between anthesis (the time at which the flowers of wheat plants open and pollination occurs) and physiological maturity. During this period, the grain accumulates dry matter, primarily in the form of starch and protein, which are important components of the wheat grain. Generally, the grain filling period in wheat ranges from about 30 to 45 days, with some varieties taking longer or shorter periods. Research studies have shown that the rate and GFD in bread wheat can have a significant impact on yield and quality. For example, longer GFD can lead to higher grain yields and better grain quality, while shorter periods can result in lower yields and poorer quality grain.

Heat stress has been proven to have a significant negative impact on the quantity, weight and quality of wheat kernels (Mohammadi *et al*., 2012; Hutsch *et al*., 2019). Due to heat stress during anthesis and grain filling, grain yield drastically decreases (Semenov and Stratonovitch *et al.,* 2015). Wheat's maturity period and grain filling time are both reduced by heat stress by up to 15%. (Ahamed *et al*., 2010).

4. **Physiological Mechanism:**

4.1. Canopy temperature (CTD)

CT may well be an extraordinary trait for screening of tolerant genotypes (Mason *et al*., 2014). CT measurements will be taken after anthesis between 12:00 p.m. and 15:00 p.m., through infrared thermometer placed under a clear, bright sky with no wind. Two readings were taken at 7-day intervals per plot and averaged. (Rehman *et al*., 2021). It seems that the describing a method for measuring the difference between the ambient air temp. and the canopy temperature, which is commonly referred to as the canopy-air temperature difference (CTD). When wheat is exposed to heat stress, CTD is critical in maintaining the physiological basis for grain yield. (Deva *et al*., 2020). The cool canopy is a significant principle for wheat’s ability to tolerate heat during grain filling. The CTD is dependent on many factors, including air temperature, humidity, soil conditions, and incident radiation. (Pinto *et al.*, 2010). Wheat genotypes with a greater CTD have been found to have increased photosynthetic enzyme activity and greater leaf conductance (Sarkar *et al*., 2021).

4.2. Relative water content (RWC)

Using RWC, plants can be evaluated for their water status relative to their fully turgid state. In these conditions, however, plants often adapt osmotically, which maintains turgor pressure and makes the definition of 'full turgidity' difficult to determine (John *et al*., 2008). The RWC of a cell is a measure of its water state that has been linked to biotic and abiotic conditions such as heat stress. RWC and water potential are thought to be more desirable indicators of drought stress than other biochemical and physiological properties of the plants (Farooq *et al*., 2019 and Hussain *et al*., 2018). It can be utilized as an accurate predictor of drought resistance.

4.3. Chlorophyll content

In wheat, chl content is related to heat tolerance and stay-green traits (Cao *et al*., 2015; Feng *et al*., 2014). A high chl conc. in wheat can be a criterion for selecting heat-resistant wheat (Munjal & Dhanda 2016; Ramya *et al*., 2014). A high chl conc. under thermal stress has a low photo inhibition (Choudhary *et al*., 2020; Talebi *et al*., 2011). A chl content that is associated with transpiration efficiency can contribute to heat tolerance (Raynolds & Trethowan *et al*., 2007). The chlorophyll estimation will determine the relative amount of chlorophyll in the plant and absorbance will be measured at 663nm and 645nm (Kamble *et al*., 2015). Several studies have successfully used chlorophyll content assessment to screen for heat-tolerant wheat genotypes. Heat-tolerant genotypes have been found to maintain high chlorophyll content. It is important to note that while chlorophyll estimation can provide valuable information about plant health, it should not be the sole method used to assess heat tolerance or any other plant trait.

5. Biochemical mechanism

5.1. Starch synthesis

Starch synthesis is a complex process that plays a critical role in determining grain yield and quality in bread wheat. Terminal heat tolerance is an important trait in bread wheat, as high temperatures during grain filling can lead to reduced grain yield and quality. To improve terminal heat tolerance in bread wheat, researchers have focused on identifying genes that play a role in starch synthesis and that are also responsive to high temperatures. Overall, understanding the mechanisms of starch synthesis and how they are affected by high temperatures is critical for developing more resilient and productive bread wheat varieties that can withstand the challenges of a changing climate.

Wheat grain contains a significant amount of starch, which accounts for 55% to 75% of its dry weight (Gillies *et al*., 2012). The wheat grain produces two types of starch granules during the GFD (Zheng *et al*., 2014). As a result of amylopectin readily decreasing under high temperatures, starch is more heat sensitive than protein (Farooq *et al*., 2011), thereby reducing starch content. During heat stress, wheat grain starch content reduces at a critical level, resulting in a reduction in kernel weight and diameter (Poudel & Poudel *et al*. 2020). Soluble starch synthase (SSS) is the enzyme responsible for starch synthesis. It is extremely heat-sensitive. Wheat under heat stress loses SSS activity, which inhibits grain maturation and starch storage (Prakash *et al*., 2004).

5.2. Antioxidant response

Thermal stress causes plants to accumulate antioxidants from different pathways (Bokszczanin & Fragkostefanakis *et al*., 2013). Wheat's antioxidant defense systems are classified as enzymatic or non-enzymatic (Sattar *et al.,* 2020). In addition to converting superoxide into H2O2, SOD is one of the most important antioxidants. In contrast, GPX, APX and CAT regulate ROS detoxification (Buttar *et al.,* 2020). Superoxide dismutase, catalase, and ascorbate peroxidase activities are extenuated at 50°C, but they are initially enhanced at this temperature (Chakrabortty & Pradhan *et al*., 2011). In wheat, catalase and superoxide dismutase activities are capable of achieving thermo tolerance (Almeselmani *et al*., 2009) and demonstrate a strong relation with thermal stress during the reproductive stage (Zhao *et al*., 2007).

Lower oxidative damage was typically maintained by tolerable genotypes due to their better antioxidant capability. (Slesak *et al.,* 2007). Enzymatic activity increases and declines in oxidative damage have both been documented. Certain enzymes are activated to protect plants against oxidative damage.

6. Molecular mechanism:

6.1. Protein synthesis

HSPs are a family of proteins that play a crucial role in protecting plants from heat stress by preventing the aggregation and denaturation of other proteins in the plant cell. They are induced in response to a variety of stressors, including high temperature, and can be found in various cellular compartments, such as the cytoplasm, nucleus, and mitochondria (Feder *et al*., 2006). In wheat, exposure to heat stress can induce the synthesis of HSPs, which can help protect the plant from the negative effects of high temperatures. SIPs, which are a type of HSP, are also induced in response to heat stress and can help protect plants from oxidative stress and other forms of cellular damage caused by high temperatures. Overall, the induction of HSPs and SIPs is an important defense mechanism employed by plants to protect themselves from the negative effects of heat stress. In plant cells, chloroplasts are one of the major sites of heat stress response, and studies have shown that under heat stress conditions, many chloroplast HSPs are translocated from the stroma to the thylakoid membranes, where they are involved in protecting and stabilizing membrane-bound proteins such as the photosynthetic complexes (Bernfur *et al.,* 2017). This membrane association of HSPs is crucial for their protective function under heat stress. By associating with thylakoid membranes, HSPs can prevent protein denaturation, maintain membrane integrity, and help to restore normal photosynthetic function. Therefore, understanding the dynamics of HSPs in relation to membrane association is an important aspect of elucidating their role in heat stress adaptation.

Wheat plants exposed to high temperatures can experience protein unfolding and aggregation in both the endoplasmic reticulum (ER) and the cytosol. Kataoka *et al*. (2017), Sun and Guo *et al*., (2016) studied the effect of heat stress on wheat leaves and observed similar results. They found that the heat stress induced the production of ROS, which in turn led to protein unfolding and aggregation in both the ER and cytosol. Overall, these studies demonstrate the importance of ROS regulation mechanisms in protecting proteins from heat stress-induced damage in wheat plants.

6.2. Omics approaches

Among the major components of omics are genomics, transcriptomics, metabolomics & proteomics. In wheat plants, several genes containing genomic DNA are involved in heat stress tolerance (Deshmukh *et al*., 2014). According to the study by Yeh *et al*. (2012), genomic screening and genome expression studies have determined the role of genes in wheat heat tolerance. Through these methods, the researchers were able to identify a number of heat-responsive genes in wheat, including those involved in stress signaling, heat shock proteins, and genes involved in photosynthesis and carbohydrate metabolism. The researchers also identified several QTLs associated with heat tolerance, which could be useful in breeding programs aimed at improving wheat's ability to tolerate high temperatures. Overall, the study by Yeh *et al*., (2012) highlights the importance of genetic factors in wheat heat tolerance, and provides valuable insights into the molecular mechanisms underlying this trait.

A transcriptome is produced by mRNA of heat tolerance genes; a proteome is produced by translating the mRNAs into functional proteins. These small RNAs are processed from longer RNA molecules and can target messenger RNAs (mRNAs) for degradation or translational repression. Wheat heat tolerance mechanisms can be better understood by studying microRNAs and micromics (Chinnusamy *et al*., 2007). A metabolicomics approach can be used to phenotype genetically modified plants as well as to test for similarity, determine gene functions, and observe responses to biotic and abiotic stresses (Abdelrahman *et al*., 2020). Plant metabolites can be altered under heat stress based on metabolomics studies (Roessner and Bowne *et al.,* 2009).

Conclusion

Wheat is suffering from heat stress more frequently due to high temperatures across the globe. With global temperatures rising due to climate change, heat stress is becoming more frequent and severe, making it a significant concern for wheat farmers worldwide. Heat stress can impact wheat in several ways. Heat stress can also affect the quality of wheat grain, leading to changes in the composition of proteins and other nutrients. To address this issue, researchers and farmers are working to develop and implement heat-tolerant wheat varieties that can withstand high temperatures and maintain productivity under stressful conditions. One of the main issues with wheat production worldwide is heat stress. In order to create wheat varieties that are both thermo tolerant and high yielding, it is important to thoroughly comprehend the various metabolic and developmental processes that plants use to cope with heat stress. Morpho-physiological bases of heat tolerance, this refers to the physical and structural features of an organism that help it tolerate high temperatures. For example, plants may have smaller leaves or thicker cell walls to reduce water loss and prevent damage from heat. Biochemical bases of heat tolerance, this refers to the chemical processes that occur within an organism that help it cope with high temperatures. Molecular bases of heat tolerance, this refers to the genetic and molecular mechanisms that allow an organism to survive and thrive in high-temperature environments. For example, some organisms may have genes that enable them to repair DNA damage caused by heat. Heat stress, this refers to the negative effects that high temperatures can have on organisms, such as reduced growth or reproduction, or even death. Heat stress can result from a variety of factors, including exposure to high temperatures for prolonged periods of time, inadequate water or nutrients, or exposure to other environmental stressors.

It is commonly recognized that molecular analysis could support increasing economic crop output, but wheat under heat stress must have its full potential yield expression estimated at the field level. It is necessary to combine several agronomic alternatives with biochemical and molecular methods in order to examine the true impact of heat stress at the field level.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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References

Asseng, S, IAN Foster and NC Turner. 2011. The impact of temperature variability on wheat yields. *Global Change Biology 17*: 997–1012.

Abdelrahman M, DJ Burritt, A Gupta, H Tsujimoto and LSP Tran. 2020. Heat stress effects on sourcesink relationships and metabolome dynamics in wheat. *Journal of Experimental Botany* 71 (2):543–554.

Adams SR, KE Cockshull and CRJ Cave. 2001. Effect of temperature on the growth and development of tomato fruits. *Annals of Botany* 88 (5):869–877.

Almeselmani M, F Abdullah, F Hareri, M Naaesan, MA Ammar and OZ Kanbar. 2011. Effect of drought on different physiological characters and yield component in different Syrian durum wheat varieties. *Journal of Agricultural Science* **3**:127-33.

Almeselmani M, P Deshmukh and R Sairam. 2009. High temperature stress tolerance in wheat genotypes: role of antioxidant defence enzymes. *Acta Agronomica Hungarica* 57 (1):1–1

Bernfur K, G Rutsdottir and C Emanuelsson. 2017. The chloroplast-localized small heat shock protein Hsp21 associates with the thylakoid membranes in heat-stressed plants. *Protein Science* 26 (9):1773–1784.

Bokszczanin KL and S Fragkostefanakis. 2013. Perspectives on deciphering mechanisms underlying plant heat stress response and thermotolerance. *Frontiers in Plant Science* 4:315

Boyer JS, RA James, M Rana, TAG Condon and JB Passioura. 2008. Osmotic adjustment leads to anomalously low estimates of relative water content in wheat and barley. *Functional Plant Biology* 35:1172–1182

Buttar ZA, SN Wu, MB Arnao, C Wang, I Ullah and C Wang. 2020. Melatonin Suppressed the Heat Stress-Induced Damage in Wheat Seedlings by Modulating the Antioxidant Machinery. *Plants* 9(7): 809

Cao X, S Mondal, D Cheng, C Wang, A Liu, J Song, H Li, Z Zhao and J Liu. 2015. Evaluation of agronomic and physiological traits associated with high temperature stress tolerance in the winter wheat cultivars. *Acta Physiologiae Plantarum* 37(4):90

Chakraborty U and D Pradhan. 2011. High temperature-induced oxidative stress in Lens culinaris, role of antioxidants and amelioration of stress by chemical pre-treatments. *Journal of Plant Interactions* 6(1):43–52

Chaves MS, JA Martinelli, C Wesp-Guterres, FAS Graichen, SP Brammer and S Scagliusi. 2013. The importance for food security of maintaining rust resistance in wheat. *Food Security*. 5:157-176.

Chinnusamy V, J Zhu, T Zhou and JK Zhu. 2007. Small RNAs: big role in abiotic stress tolerance of plants. Advances in Molecular Breeding Toward Drought and Salt Tolerant Crops. *Springer, Dordrecht*, 223–260

Choudhary M, M Yadav and R Saran. 2020. Advanced screening and breeding approaches for heat tolerance in wheat. *Journal of Pharmacognosy and Phytochemistry* 9 (2):1047–10

Ciuca M and E Petcu. (2009). SSR markers associated with membrane stability in wheat (Triticum aestivum L.). *Romanion Agricultural Research* 26:21–24

Cossani CM and MP Reynolds. 2012. Physiological traits for improving heat tolerance in wheat. *Plant Physiology* 160:1710–1718

Deshmukh R, H Sonah, G Patil, W Chen, S Prince, R Mutava, T Vuong, B Valliyodan and HT Nguyen. 2014.

Integrating omic approaches for abiotic stress tolerance in soybean. *Frontiers in Plant science* 5, 244

Deva CR, MO Urban, AJ Challinor, P Falloon and L Svitakova. 2020. Enhanced leaf cooling is a pathway to heat tolerance in common bean. *Frontiers in Plant Science* 11, 19.

Dhanda SS and R Munjal. 2012. Heat tolerance in relation to acquired thermo tolerance for membrane lipids in bread wheat. *Field Crops Research* 135:30–37

Dhyani K, MW Ansari, YR Rao, RS Verma, A Shukla and N Tuteja. 2013. Comparative physiological response of wheat genotypes under terminal heat stress. *Plant Signaling and Behavior* 8(6):245-264

Farooq M, H Bramley, JA Palta and KHM Siddique. 2011. Heat stress in wheat during reproductive and grain filling phases. *Critical Reviews in Plant Sciences*. 30:1-17

Farooq M., Hussain M., Ul-Allah S., Siddique K. H. 2019. Physiological and agronomic approaches for improving water-use efficiency in crop plants. *Agricultural Water Management* 219:95–108.

Feder ME. 2006. Integrative biology of stress: molecular actors, the ecological theater, and the evolutionary play. In: Proceedings of the International Symposium on Environmental Factors, *Cellular Stress and Evolution*, Varanasi, India.

Feng B, P Liu, G Li, ST Dong, FH Wang, LA Kong and JW Zhang. 2014. Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. *Journal of Agronomy and Crop Science* 200 (2):143–155

Gillies SA, A Futardo and RJ Henry. 2012. Gene expression in the developing aleurone and starchy endosperm of wheat. *Plant Biotechnology Journal* 10 (6):668–679.

Gupta PK, RR Mir, A Mohan and J Kumar. 2008. Wheat Genomics: Present Status and Future Prospects Hindawi Publishing Corporation. *International Journal of Plant Genomics*, doi:10.1155/2008/896451.

Hatfield JL, KJ Boote, BA Kimball, LH Ziska, RC Izaurralde, D Ort, AM Thomson and DW Wolfe. 2011. Climate impacts on agriculture: Implications for crop production. *Agronomy Journal 103*: 351–370.

Halford NG. 2009. New insights on the effects of heat stress on crops. *Journal of Botanay.* 60:4215-4216.

Howarth CJ. 2005. Genetic improvements of tolerance to high temperature, in Abiotic Stresses: Plant Resistance Through Breeding and Molecular Approaches (eds M. Ashraf and P.J.C. Harris), *Howarth Press, Inc.*, New York 277–300.

Hussain M, S Farooq, W Hasan, S Ul-Allah, M Tanveer, M Farooq M. 2018. Drought stress in sunflower: Physiological effects and its management through breeding and agronomic alternatives. *Agricultural Water Management*, 2018; 201:152–166.

Iba K. 2002. Acclimative response to temperature stress in higher plants: approaches of gene engineering for temperature tolerance. *Annual Review of Plant Biology* 53(1):225–245.

Jennifer B and V Ramanathan. 2014. Recent climate and air pollution impacts on Indian agriculture. *Proceedings of the National Academy of Sciences*. https ://doi.org/10.1073/.13172 75111

Joshi AK, B Mishra, R Chatrath, FG Ortiz and RP Singh. 2007. Wheat improvement in India: present status, emerging challenges and future prospects. *Euphytica* 157:431–446

Kamble PN, SP Giri, RS Mane and A Tiwana. 2015. Estimation of chlorophyll content in young and adult leaves of some selected plants. *Universal Journal of Environmental Research and Technology* 5(6):307.

Kataoka R, M Takahashi and N Suzuki. 2017. Coordination between bZIP28 and HSFA2 in the regulation of heat response signals in Arabidopsis. *Plant Signaling and Behavior* 12 (11):1376159.

Kumar A, and VP Singh. 2020. Wheat Heat Tolerance: Mechanism, Impact and Quantitative Trait Loci Associated with Heat Tolerance. *International Journal of Current Microbiology and Applied Sciences ISSN: 2319-7706*

Kumar U, AK Joshi, M Kumari, R Paliwal, S Kumar and M Röder. 2010. Identification of QTLs for stay green trait in wheat (*Triticum aestivum* L.) in the ‘Chirya 3’ 3 ‘Sonalika’ population. *Euphytica*174: 437–445

Li R, P Guo, M Baum, S Grande and S Ceccarelli. 2006. Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. *Agricultural Science in China* 5:751–757

Maestri E, N Klueva, C Perrotta, M Gulli, HT Nguyen and N Marmiroli. 2002. Molecular genetics of heat tolerance and heat shock proteins in cereals. *Plant Molecular Biology* 48:667-681.

Mamrutha HM, R Singh, D Sharma, K Venkatesh, GC Pandey, R Kumar, R Tiwari and I Sharma. 2019. Physiological and molecular basis of abiotic stress tolerance in wheat. Genetic Enhancement of Crops for Tolerance to Abiotic Stress: Mechanisms and Approach 1:100-106.

Munjal R and SS Dhanda. 2016. Assessment of drought resistance in Indian wheat cultivars for morpho-physiological traits. *Ekin Journal of Crop Breeding and Genetics* 2 (1):74–81.

Narayanan S, PVV Prasad, AK Fritz, DL Boyle and BS Gill. 2015. Impact of high nighttime and high daytime temperature stress on winter wheat. *Journal of Agronomy and Crop Science* 201 (3): 206–218.

Ortiz R, KD Sayre, B Govaerts, R Gupta, GV Subbarao, T Ban, D Hodson, JM Dixon, JI Ortiz-Monasterio and M Reynolds. 2008. Climate change: can wheat beat the heat. *Agriculture Ecosystem and Environment* 126:46–58

Pandey GC, J Rane, S Sareen, P Siwach, NK Singh and R Tiwari. (2013). Molecular investigations on grain filling rate under terminal heat stress in bread wheat (*Triticum aestivum* L.). *African Journal of Biotechnology* 12(28):4440-4441

Pandey GC, G Mehta, P Sharma and V Sharma. 2019. Terminal heat tolerance in wheat: An overview. *Journal of Cereal Research* 11(1):1-16 doi. org/10.25174/2249-4065/2019/79252

Pinto RS, MP Reynolds, KL Mathews, CL McIntyre, JJ Olivares-Villegas and SC Chapman. 2010. Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. *Theoretical and Applied Genetics* 121:1001-1021.

Porter JR. 2005. Rising temperatures are likely to reduce crop yields. *Nature* 436(7048):174-174.

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Poudel PB and MR Poudel. 2020. Heat stress effects and tolerance in wheat: a review. *Journal of Biology and Today's World* 9 (3):1–6.

Prakash P, P Sharma-Natu and MC Ghildiyal. 2004. Effect of different temperature on starch synthase activity in excised grains of wheat cultivars. *Indian Journal of Experimental Biology* 42, 227-230

Queitsch C, SW Hong, E Vierling and S Lindquest. 2000. Heat shock protein 101 plays a crucial role in thermotolerance in Arabidopsis. *Plant Cell* 12: 479-492.

Ramya P, N Jain, GP Singh, PK Singh and KV Prabhu. 2015. Population structure, molecular and physiological characterization of elite wheat varieties used as parents in drought and heat stress breeding in India. *Indian Journal of Genetics and Plant Breeding* 75, 250–252.

Rahaie M, GP Xue and MP. 2013. The Role of Transcription Factors in Wheat Under Different Abiotic Stresses. In: K. Vahdati, C. Leslie (eds), *Abiotic Stress*. 201; 367-385.

Rivero RM, TC Mestre, RON Mittler, F Rubio, F Garcia-Sanchez and V Martinez. 2014. The combined effect of salinity and heat reveals a specific physiological, biochemical and molecular response in tomato plants. *Plant Cell Environ 37* :1059–1073.

Rehman HU, A Tariq A, I Ashraf, M Ahmed, A Muscolo, SMA Basra and M Reynolds. 2021. Evaluation of Physiological and Morphological Traits for Improving Spring Wheat Adaptation to Terminal Heat Stress. Plants, 10, 455. https://doi.org/10.3390/ *plants*10030455.

Reynolds MP and RM Trethowan. 2007. Physiological interventions in breeding for adaptation to abiotic stress. *Frontiers* 127–144.

Rodríguez M, E Canales and O Borrás-Hidalgo. 2005. Molecular aspects of abiotic stress in plants. *Biotecnología Aplicada 22*, 1–10.

Roessner U and I Bowne. 2009. What is metabolomics all about? *Biotechniques* 46 (5): 363–365

Sarkar S, AKM Aminul Islam, NCD Barma, JU Ahmed. 2021. Tolerance mechanisms for breeding wheat against heat stress: A review. *South African Journal of Botany* 138:1-16

Sattar A, A Sher, M Ijaz, S Ul-Allah, MS Rizwan, M Hussain, K Jabran and MA Cheema. 2020. Terminal drought and heat stress alter physiological and biochemical attributes in flag leaf of bread wheat. *Plos One* 15 (5), e0232974.

Sharma D, R Singh, R Tiwari, R Kumar and V Gupta. 2019. Wheat Responses and Tolerance to Terminal Heat Stress: A Review. In: M Hasanuzzaman, K Nahar, M A Hossain (eds), *Wheat Production in Changing Environments: Responses, Adaptation and Tolerance*. 149-173

Sun AZ and FQ Guo. 2016. Chloroplast retrograde regulation of heat stress responses in plants. *Frontiers in Plant Science* 7, 398.

Suzuki N, RM Rivero, V Shulaev, E Blumwald and R Mittler. 2014. Abiotic and biotic stress combinations. *New Phytologist* 203 (1):32–43.

Talebi R. 2011. Evaluation of chlorophyll content and canopy temperature as indicators for drought tolerance in durum wheat (*Triticum durum* Desf.). *Australian Journal of Basic Applied Science* 5, 1457–1462.

Tewolde H, CJ Fernandez and CA Erickson. 2006. Wheat cultivars adapted to post-heading high temperature stress. *Journal of Agronomy and crop Science* 192:111-120.

Tuberosa R and S Salvi. 2006. Genomics-based approaches to improve drought tolerance of crops. *Trends Plant Science* 11(8):405–412

Vijayalakshmi K, A Fritz, G Paulsen, G Bai, S Pandravada and B Gill. 2010. Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. *Molecular Breeding* 26:163–175

Wang W, B Vinocur, O Shoseyov and A Altman. 2004. Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. *Trends Plant Science. 9*, 244–252.

Yeh CH, NJ Kaplinsky, C Hu and YY Charng. 2012. Some like it hot, some like it warm: phenotyping to explore thermotolerance diversity. *Plant Science* 195, 10–23.

Zhao H, T Dai, Q Jing, D Jiang and W Cao. 2007. Leaf senescence and grain filling affected by post-anthesis high temperatures in two different wheat cultivars. *Plant Growth Regulation* 51 (2): 149–158.

Zhang Y, H Lou, D Guo, R Zhang, M Su, Z Hou, H Zhou, R Liang, C Xie, M You and B Li. 2018. Identifying changes in the wheat kernel proteome under heat stress using iTRAQ. *The Crop Journal* 6 (6):600–610.