

THERMO-TOLERANCE MECHANISM 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.

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. Terminal heat stress severely affects Wheat yield (Pandey *et al.*, 2013). For 85% and 82% of the world's population, wheat provides basic calories and protein, respectively (Sharma *et al.*, 2019 & 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.*). 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. Different mechanisms have been developed by plants to survive at higher temperatures (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, respectively, being the two states with the largest increases in growing season temperature since 1980, respectively (Jennifer & Ramanathan *et al.*, 2014).

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. Promising methods for examining the genetic basis of thermo tolerance involve the use of molecular markers (Maestri *et al.*, 2002). The marker-assisted selection (MAS) technique can be applied to traits that contribute to heat tolerance, such as Chl (Li *et al.*), in order to select these traits more efficiently. 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). Wheat genomic regions that are associated with variability in physiological traits require much more information. 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).

When temperatures reach a certain level for a limited amount of time, they can be reduced to yield. 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. The ability to tolerate high temp. is one of the ways a plant maintains self-integrity to avoid high temperature and create a good metabolic pathway as a result (Anand *et al.*, 2020).

3. Morphological mechanisms

3.1 Grain filling duration (GFD)

Maintaining high grain yield is one of the most important factors for improving wheat under heat stress (Aziz *et al.*, 2018). According to Dwivedi *et al.* (2017), the wheat reproductive phase is highly sensitive to heat stress, and in regions with the largest wheat production, the grain filling period experiences the highest temperatures that have an impact on the process of grain filling (Pradhan and Prasad *et al.*, 2015; Singh *et al.*, 2011). 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)

CTD describes the difference in canopy temp. from ambient temp. (Deva *et al.*, 2020). When wheat is exposed to heat stress, CTD is critical in maintaining the physiological basis for grain yield. 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. Drought and heat stress are strongly associated with lower canopy temperature (CT), and CT appears to have some common genetics basis under both conditions (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).

4.3. Chlorophyll Content

In wheat, chlorophyll content is related to heat tolerance and stay-green traits (Cao *et al.*, 2015; Feng *et al.*, 2014). During heat stress, wheat biomass and yield are both affected by chl (Tattaris *et al.*, 2016). A high chl concentration in wheat can be a criterion for selecting heat-resistant wheat (Munjaj & Dhanda 2016; Ramya *et al.*, 2014). A high chl concentration under thermal stress has a low photo inhibition (Choudhary *et al.*, 2020; Talebiet *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).

5. Biochemical mechanism

5.1. Starch synthesis

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

Studies have shown that under heat stress, damage to membranes increases and antioxidant levels decrease in wheat during seedling, anthesis (Narayanan *et al.*, 2015) & grain filling. (Suzuki *et al.*, 2014). 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 (Chakraborty & Pradhan *et al.*, 2011). The highest antioxidant activity was shown at 35-40°C in tolerant wheat varieties, and at 30°C in susceptible varieties (Chakraborty & 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).

6. Molecular mechanism:

6.1. Protein synthesis

During heat stress, plants develop some defense mechanisms, such as expressing specific genes that are only expressed under stress conditions (Feder *et al.*, 2006). Stress-Induced Proteins (SIPs) are heat-shock proteins. When wheat leaves are exposed to heat stress, they synthesize heat-shock proteins. A membrane association must be considered when explaining the role of HSPs in adapting to heat stress since two thirds of chloroplast HSPs are transferred to thylakoids under heat stress (Bernfur *et al.*, 2017). In wheat, heat stress leads to unfolding of proteins in the ER and cytosol via ROS regulation mechanisms (Kataoka *et al.*, 2017; Sun and Guo, 2016).

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). The role of genes in wheat heat tolerance has been determined

by genomic screening and genome expression studies (Yeh *et al.*, 2012). A transcriptome is produced by mRNA of heat tolerance genes; a proteome is produced by translating the mRNAs into functional proteins. A small non-protein coding RNA plays a role in post-transcriptional gene expression in plants. Wheat heat tolerance mechanisms can be better understood by studying microRNAs and micromics (Chinnusamy *et al.*, 2007). A metabolomics 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, 2009).

Conclusion:

Wheat is suffering from heat stress more frequently due to high temperatures across the globe. Ultimately, grain yield is reduced because of heat stress' substantial effects on grain filling duration and rate. A grain yield's impact on heat stress depends on its timing, duration and intensity. 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. This review paper quickly explains the morpho-physiological, biochemical, and molecular bases of heat tolerance as well as numerous elements of heat stress. 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

- 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 Naesan, 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

Ciucu M and E Petcu. (2009). SSR markers associated with membrane stability in wheat (*Triticum aestivum* L.). *Romanian 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

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. Vol. 2006.

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.

Halford NG. 2009. New insights on the effects of heat stress on crops. *Journal of Botany*. 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.

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/pnas.1317275111>

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, 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 Marmioli. 2002. Molecular genetics of heat tolerance and heat shock proteins in cereals. *Plant Molecular Biology* 48:667-681.

Mamrutha HM, Singh R, Sharma D, Venkatesh K, Pandey GC, Kumar R, Tiwari R and Sharma I. 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.

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 (*T.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.

Poudel PB and Poudel MR. 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

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

Queitsch C, SW Hong, E Vierling and S Lindquist. 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. The Role of Transcription Factors in Wheat Under Different Abiotic Stresses. In: K. Vahdati, C. Leslie (eds), *Abiotic Stress*. 201; 367-385.
- 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., Bowne, J., 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.
- Tattaris M, MP Reynolds and SC Chapman. 2016. A direct comparison of remote sensing approaches for high-throughput phenotyping in plant breeding. *Frontiers in Plant Science* 7, 1131.
- 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.
- 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, 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, 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.