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Heat Stress Effects and Tolerance in Wheat: A Review

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ABSTRACT

Wheat is a major cereal crop and considered as source of basic calories and protein for more than 80% of the world population. Regarding the global climate change at the past few decades, the impact of rising temperature on wheat production is gaining concern worldwide. Heat and drought are the major abiotic stress limiting the wheat production. Heat stress interrupts the important physiological and biochemical process of the plant. High temperature stress reduces grain number, photosynthetic activity and chlorophyll content and starch synthesis in the endosperm. Reactive oxygen species accumulated under heat stress cause severe oxidative damage to the crop. Plant rapidly produces heat shock proteins to minimize the effect of heat stress. Several traits such as stay green, chlorophyll fluorescence and canopy temperature play significant role in heat tolerance. In order to develop new crop varieties that can cope with future climate, knowledge of heat stress effect and tolerance at physiological, biochemical and morphological level is highly important.

Keywords: Heat stress, Heat shock proteins, Oxidative stress, Wheat.

INTRODUCTION

Wheat (*Triticum* spp.) is one of the major cereal crops belonging to Poaceae family which contributes about 30% of world grain production and 50% of the world grain trade [1]. Wheat is considered as staple food in more than 40 countries of the world which provides basic calories and protein for 85% and 82% of the world population respectively [2,3]. FAO estimated that, the annual cereal production have to grow by almost one billion to feed the projected population of 9.1 billion by 2050. In order to meet the increase food requirement, increase in crop production and productivity is the demand of 21st century [4]. Wheat is grown in tropical and sub-tropical region of the world which experiences various abiotic stresses. Adverse environmental stress significantly reduces crop production [5]. The major abiotic stresses include heat, drought, salinity cold, chemical and water excess. However, heat and drought are the main abiotic stresses affecting the wheat production worldwide [6,7]. Considering global climate model, the mean ambient temperature is likely to rise by 6°C by the end of 21st century [8].

Wheat is much sensitive to heat stress. It is estimated that per 1°C increase in temperature cause decrease in global wheat production by 6% [9]. Even 1°C temperature increase over mean temperature during reproductive stage may leads to higher loss in grain yield [10,11]. High temperature alters different physiological, biological and biochemical process in wheat [12]. Heat stress (HS) in wheat cause poor seed germination, decrease in grain filling duration, reduction in grain number, deactivation of Rubisco enzyme, decrease in photosynthetic capacity, reduction in rate of assimilate translocation, premature leaf senescence, decrease chlorophyll content and ultimately decrease in yield [13-21]. HS also affect the starch and protein content in grain. HS induce production of reactive oxygen species (ROS) which cause change in membrane stability along with lipid peroxidation, protein oxidation and damage to nucleic acids [22,23]. However, in order to avoid injury and damage associated with HS, wheat has evolved different tolerance mechanisms to maintain its survival and growth. HS induced heat shock proteins (HSPs) maintain correct protein folding, refolding, synthesis and it also degrade the protein aggregate [2,24,25]. The accumulated ROS is detoxified by the antioxidative defense system through various enzymatic and non-enzymatic antioxidants [26]. Stay green (SG), chlorophyll fluorescence and canopy temperature are traits that are associated with heat tolerance in wheat [20].

This review covers the effect of HS on wheat morphology, physiology and biochemistry. Furthermore, we explained the different HS tolerance mechanisms such as antioxidative defense system and HS induced HSPs production along with SG traits associated with heat tolerance.

EFFECT OF HEAT STRESS ON WHEAT

HS affects the different growth and development stages of wheat which leads to high yield loss. However, effect of HS in plant depends upon the length of heat exposure and growth stage during the high temperature [27,28]. Poor germination, reduced leaf area, early leaf senescence and damaged photosynthetic machinery associated with heat stress cause decrease in photosynthesis in wheat [12,29,30]. Heat stress brings certain alteration on wheat morphology, physiology and biochemistry.

Effect on wheat morphology

In various crops, including wheat, HS negatively influence the seed germination and plant establishment [13]. High temperature

(45°C) has negative impact on embryonic cells, followed by improper germination and emergence which leads to poor crop stand [31]. High temperature affects the survivability of the productive tiller, which result in decrease in yield. HS in wheat result in decrease grain yield (53.57%) and tiller number (15.38%) [21]. HS causes decrease in root growth which ultimately affects the crop production [32]. The effect of HS is highly significant during reproductive phase [33]. Increase in average temperature by 1°C during reproductive stage may lead to higher loss in grain yield [10,11]. The optimum temperature for flowering and grain filling ranges from 12°C to 22°C [2]. Early stage of gametogenesis is harmed when HS occur during meiosis [34]. Microspore and pollen cell development is affected negatively due to HS at the time of floral initiation [35]. The grain development phenomenon depends upon the grain filling rate and duration which is highly sensitive to HS [36,37]. The life cycle of wheat shortens in HS than in normal temperature situation [38]. 1°C-2°C rise in temperature lowers seed weight due to decrease in grain filling duration [39]. Short term heat stress during grain filling may result in grain yield loss up to 23% [40]. HS negatively influence number of grain and grain quality. In HS condition, grain number is decreased causing reduction in harvest index [15]. Heat stress associated decrease in assimilate production and remobilization result in reduced grain quality [41]. Wheat productivity is reduced remarkably due to harmful effect of high temperature in growth process [42]. When wheat is subjected to ambient temperature (>35°C) for a short period of time can result in significant loss in grain yield [43].

Effect on wheat physiology

Photosynthesis is most important physiological process in plant which is highly influenced by high temperature. Stroma and thylakoid lamellae are most sensitive to heat stress in wheat [30]. High temperature (~ 40°C) results in permanent alternation of RuBisCO, Rubisco Activase and Photosystem II [44]. Upon exposure of wheat in HS condition, the RuBisCO enzyme was found to be deactivated in less than 7 days [16]. Rubisco activase breakdown under heat stress cause decrease in photosynthetic capacity [17]. HS cause change in the fluidity of thylakoid membrane and separation of light harvesting complex II from the photosystem II [45]. The photosynthetic product is necessary to be translocated to different plant parts for its growth and development. The rate of assimilate translocation from source to sink is reduced under high temperature stress caused by decrease in membrane stability [18]. Mobilization of water soluble carbohydrate to reproductive sink support grain growth and development [46]. Source and/or sink limitation reduce seed set and seed filling [47]. In case of source limitation caused by HS, plant to find another way to translocate the photosynthetic product into the grain [1]. There is increase in carbohydrate remobilization from stem to developing grain during pre-anthesis HS, which help to recover the effect on grain starch content in post-anthesis HS [48]. The availability of high O_2 concentration promotes photorespiration. The change in solubility of O_2 and CO_2 gases was observed under HS condition causing increase photorespiration in flag leaf in wheat [49].

Plant senescence is the process of aging in plant. A vacuolar collapse, loss in membrane integrity, disturbance of cellular homeostasis are distinctive feature of leaf senescence [50]. Moderate but extended duration of HS result in gradual senescence while intensive HS for short period of time leads to protein denaturation and aggregation, causing death of the plant [24]. HS during maturity promotes the leaf senescence in plant [19]. Also, high temperature (>34°C) accelerates the leaf senescence due to reduction in biosynthesis of chlorophyll [20]. High temperature affects the water relation and content in the plant. Cell dehydration is observed under HS due to reduction in osmotic potential [51]. Canopy temperature affects the leaf relative water content, stomatal conductance and rate of transpiration [2]. Whereas chlorophyll fluorescence is highly associated with yield which aid in the measurement of photosynthetic efficiency. Thus, chlorophyll fluorescence and canopy temperature traits can be used for selection of heat tolerant genotypes [20]. During drought condition and high temperature, canopy temperature is linked with deeper roots [52]. A research was conducted by Dhyani et al. on heat tolerant and heat sensitive wheat genotypes grown under normal and late sown condition and revealed that chlorophyll content and leaf area index was significantly decreased in heat sensitive genotypes but proline content was increased in heat tolerant genotypes grown under late sown situation [53]. Under HS, plant highly produce reactive element known as Reactive Oxygen Species (ROS). The ROS interrupt the cell function by their negative action on lipid, protein and DNA. Oxidative damage associated with heat stress cause decrease in membrane thermostability by 54% [54]. ROS accumulated under HS promotes protein denaturation and formation of unsaturated fatty acid, which finally increases cell membrane permeability [55].

Effect on wheat biochemistry

Starch is the major constituents of wheat and is made up of amylose and amylopectin. Amylose content is key parameter to mark starch quality. Starch characteristics are affected by variation in amylose content. High temperature is associated with increase in amylose content and amylose: amylopectin ratio [56]. ADP-Glucose Pyrophosphorylase (AGPase) and starch synthase is significant enzyme involved in starch biosynthesis. Soluble Starch Synthase and Granule bound starch synthase are the two forms of starch synthase [2]. At high temperature, there is decrease in starch content in grain up to one-third of total endosperm starch, which is caused due to decrease efficiency of enzymes involving in starch biosynthesis [57]. Lower grain size and decrease in starch deposition is caused by reduce activity of soluble starch synthase at high temperature around 40°C [58]. However, Sharma et al. reported that, starch deposition is not affected by the reduction of Soluble Starch Synthase activity up to 30°C, but it affects the starch composition. He also mentioned that HS in wheat, not remarkably affect the granule bound starch synthase activity [59]. Asthir and Bhatia observed remarkable decrease of starch biosynthesis in wheat grain under HS but there was increase in total soluble sugar and protein [60]. Wheat grain quality is highly dependent upon protein content and composition. Lizana and Calderini observed no significant effect on protein concentration under HS [41]. In contrast, Iqbal et al. reported that, in HS condition, there is increase in grain protein content with increase in essential amino acids fractions, leaf nitrogen content and sedimentation index [4].

HEAT TOLERANCE MECHANISM IN WHEAT

Plants have different adaptation mechanism to adapt under HS. Avoidance, Escape and Tolerance are main three mechanisms that allow plant to survive and grow in high temperature environment. Heat tolerance is defined as the capability of plant to survive, grow and produce economic yield under HS. Antioxidant defense, generation of Heat Shock Proteins (HSPs) and stay green are major heat tolerance mechanism in wheat.

Heat shock proteins

Protein function is highly dependent upon its synthesis and folding. Protein misfolding significantly affects the working mechanism of the cell. At HS condition, protein folding and synthesis is interrupted [2]. Stressing agents are produced in cell under HS. These agents instantly disturbs the major metabolism processes as well as DNA replication, transcription, mRNA transport and translation till the cell recuperate [61]. To overcome this plant speed up production of HS induced proteins as a defense mechanism which is known as Heat Shock Proteins (HSPs) [62]. HSPs can be classified into different families on the basis of their molecular mass, amino acid sequence homologies and functions [63]. The families include HSP100 family, HSP90 family, HSP70 family, HSP60 family and small HSPs family. These HSPs are associated with different function under HS condition (**Table 1**). Heat Stress transcription factors (Hsfs) are present in the cytoplasm in an inactive condition which acts as regulatory protein in the transcription of the genes which encodes for HSPs. Under HS, these Hsfs acts as transcriptional activators [64].

Various mechanisms are involved in the expression of genes that encodes for HSPs, particularly temperature sensing mechanism followed by mechanism of signal transfer to Hsfs and finally binding of Hsfs to heat shock element (HSE) in DNA for the initiation of gene expression [65]. Under HS, HSPs function as molecular chaperons to prevent protein denaturation, and aggregation [24,66].

Reactive oxygen species and antioxidative defense mechanism

HS affects the plant by producing unfavourable reactive oxygen species (ROS) which include singlet oxygen ($^1O_2$), superoxide ($O_2^{\bullet -}$) and hydroxyl radical (•OH) [67,68]. In normal cell, there exists equilibrium between production and scavenging of ROS which is known as redox homeostasis [69]. When there is more production of ROS then the scavenging capacity of cell, the cell comes under stress which is known as oxidative stress [70]. Also oxidative stress either can be occurred due to decrease in free radicals scavenging capacity of cell [71]. HS induced increased ROS production cause change in membrane potential (depolarization), lipid peroxidation, protein oxidation, damage in nuclei acids, obstruct enzyme function and activates the programmed cell death [22,23,72]. HS associated increase in ROS signals to switch on the antioxidative defense mechanism by activating the free radical scavenging related enzymes [73]. Detoxification of ROS by antioxidative defense system is necessary to save plant from oxidative damage [71]. In plant the antioxidative defense system is highly effective and is obtained through involvement of different enzymatic and non-enzymatic antioxidants [74]. The enzymatic antioxidant includes superoxide dismutase (SOD), ascorbate peroxidase, catalase (CAT), glutathione peroxidase (GPX), glutathione reductase (GR) and peroxidase (POX) while non-enzymatic antioxidants includes ascorbic acid, glutathione, tocopherols, carotenoids and phenolic compounds [69,75]. These antioxidants have different role in scavenging ROS (**Table 2**). The production of type of antioxidant enzymes depends upon the type of stress associated with plant. Under HS, there is increase in activity of SOD, CAT, POX [63,76]. Balla et al. Reported that, the activity of S-transferase (GST), APX and CAT is increased in the cultivar which showed tolerance to HS [77].

There is unavoidable leakage of electrons from electron transport chain occurring in mitochondria, chloroplast and plasma membrane. The ROS is produced from the acceptance of leaked electron by O_2 or as by product of several metabolic process limited to different cellular regions [78,79]. When oxygen molecule accepts the leaked electron, superoxide or singlet oxygen is produced. Superoxide radical is converted to hydrogen peroxide by two ways either by spontaneous dismutation or by catalytic action of SOD or otherwise metal ions (Fe^{3+} and Cu^{2+}) present in cell is reduced by superoxide radicals. The hydrogen peroxide is converted into •OH by Haber-Wiss reaction. There are two steps governing this reaction. In first step, the metal ion is reduced by superoxide radical and in second step, the reduced metal ion react with hydrogen peroxide to form •OH. The later step is known as Fenton reaction. •OH are very reactive than other ROS [26]. There is no any enzymatic mechanism that can eliminate •OH, thus higher production of •OH can result in cell death [80]. However, the •OH can be decreased by scavenging of hydrogen peroxide by

Table 1: Role of different heat shock proteins under heat stress.

Heat Shock Proteins	Functions	Reference
HSP100	Degradation of protein aggregate. It is ATP dependent process.	[2]
HSP90	Mediate HS associated signal transduction.	[90]
HSP70	Facilitate proper protein folding and stabilizes newly synthesized protein by preventing aggregate formation.	[88]
HSP60	Helps in Protein refolding and prevent denatured protein accumulation.	[2]
HSP40	Small HSPs involved in refolding are set free by HSP40, HSP70, HSP100 after the formation of fully refolded protein.	[24]
Small HSPs	Helps in refolding of denatured proteins, thus prevent thermal aggregation.	[62]

Table 2: Different role of antioxidants in scavenging ROS.

Antioxidants	Functions	Reference
Enzymatic antioxidants		
SOD	Catalyzes the dismutation of O2•– to H_2O_2 and O_2	[2]
CAT	Convert H_2O_2 into water and oxygen without using any reducing power.	[87,89]
GPX	Catalyzes the removal of H_2O_2	[74]
APX	Scavenging H_2O_2 by oxidizing ascorbate.	[80]
Non-enzymatic antioxidants		
Ascorbic Acid	Donate electron in various enzymatic and non-enzymatic reaction.	[26]
Glutathione	Scavengers of singlet oxygen, hydrogen peroxide and hydroxyl radical	[74]
Tocopherol	Scavengers of H_2O_2; up regulation of APX and GR	[86]
Carotenoids	Inhibit singlet oxygen formation	[80]

class of peroxidase like guaiacol peroxidase or by APX and CAT [81]. Although ROS production is associated with oxidative stress but it can function as signaling molecule under different abiotic stress and trigger tolerance against such stress. Therefore, ROS should not be eliminated completely and should be maintained in a level to avoid oxidative injury.

Stay green

Stay green (SG) associated genotype maintains photosynthesis and grain filling in HS condition through late expression of senescence related genes [82]. SG is an important mechanism for HS tolerance in wheat as it conserve photosynthetic area and increase nitrogen remobilization to the maturing grains [81]. During growing phases of ovaries, starch content in the ovary is depleted rapidly but under HS the accumulation of sugar decreases due to reduced photosynthetic activity which helps to seed abortion [82]. Increased photosynthetic activity due to SG, helps to maintain continuous sugar supply in growing anther and pollen , thus helps to retain pollen and ovules viability [83].A research was conducted by to relate SG traits with canopy temperature depression (CTD) [84]. They observed higher value of CTD (air temperature-canopy temperature) in SG genotypes under HS condition and concluded that SG is highly associated with CTD. Therefore, SG trait can be used as selection criteria under heat stress in wheat genotypes [32].

CONCLUSION

Regarding the global warming, the frequency of heat stress in wheat is projected to increase worldwide. HS significantly affect grain setting, duration, rate, quality and finally grain yield. The effect of HS is genotype specific and also depends upon the intensity, timing, and duration of HS. Therefore, the development of tolerant varieties helps to minimize the effect of HS. Plant produces different metabolites such as antioxidants and HSPs under HS condition. Molecular studies of such metabolites play crucial role to know the mechanism underlying stress tolerance [86-90].

REFERENCES

1. Akter N, Islam M. Heat stress effects and management in wheat: A review. Agron Sustain Dev. 2017; 37:37.
2. Sharma D, Singh R, Tiwari R, Kumar R, Gupta V. 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. 2019; 149-173
3. Chaves MS, Martinelli JA, Wesp-Guterres C, Graichen FAS, Brammer SP, Scagliusi S, et al. The importance for food security of maintaining rust resistance in wheat. Food Secur. 2013; 5:157-176.
4. Iqbal M, Raja NI, Yasmeen F, Hussain M, Ejaz M, Shah MA. Impacts of heat stress on wheat: A critical review. Adv Crop Sci Tech.2017; 5(1):1-9.
5. Rahaie M, Xue GP, MP. The Role of Transcription Factors in Wheat Under Different Abiotic Stresses. In: K. Vahdati, C. Leslie (eds), Abiotic Stress. 201; 367-385.
6. Lesk C, Rowhani P, Ramankutty N. Influence of extreme weather disasters on global crop production. Nature. 2016; 529:84-87.
7. Liu B, Asseng S, Müller C, Ewert F, Elliott J, et al. Similar estimates of temperature impacts on global wheat yield by three independent methods. Nat Clim Change. 2016; 6(12):1130-1136.
8. De Costa WAJM. Reviewa review of the possible impacts of climate change on forests in the humid tropics. J Natl Sci Found. 2011; 39(4):281-302.
9. Asseng, Senthold, Foster I, Turner NC. The impact of temperature variability on wheat yields. Global Change Biol. 2011; 17:997-1012.
10. Bennett D, Izanloo A, Reynolds M, Kuchel H, Langridge P, Schnurbusch T. Genetic dissection of grain yield and physical grain quality in bread wheat (Triticum aestivum L.) under water-limited environments. Theor Appl Genet. 2012; 125:255-271.
11. Yu Q, Li L, Luo Q, Eamus D, Xu S, Chen C, et al. Year patterns of climate impact on wheat yields. Int J Climatol. 2014; 34:518-528.
12. Asseng S, Ewert F, Martre P, Rötter RP, Lobell DB, Cammarano D et al. Rising temperatures reduce global wheat production. Nat Clim Change. 2015; 5:143-147.
13. Hossain A, Sarker MAZ, Saifuzzaman M, da Silva JAT, Lozovskaya MV, Akhter MM. Evaluation of growth, yield, relative performance and heat susceptibility of eight wheat (Triticum aestivum L.) genotypes grown under heat stress. Int J Plant Prod. 2013; 7(3):615-636.
14. Bala S, Asthir B, Bains N. Effect of terminal heat stress on yield and yield attributes of wheat. Indian J Applied Res. 2014; 4(6):1-2.
15. Lukac M, Gooding MJ, Griffiths S, Jones HE. Asynchronous flowering and within-plant flowering diversity in wheat and the implications for crop resilience to heat. Ann Bot. 2012; 109:843–850.
16. Kumar RR, Goswami S, Singh K, Dubey K, Singh S, Sharma R et al. Identification of putative RuBisCo activase (TaRca1)–The catalytic chaperone regulating carbon assimilatory pathway in wheat (triticum aestivum) under the heat stress. Front Plant Sci. 2016; 7:986.
17. Raines CA. Increasing photosynthetic carbon assimilation in C3 plants to improve crop yield: Current and future strategies. Plant Physiol. 2011; 155:3642.
18. Farooq M, Bramley H, Palta JA, Siddique KHM. Heat stress in wheat during reproductive and grain-filling phases. Crit Rev Plant Sc. 2011; 30(6):491-507.
19. Haque MS, Kjaer KH, Rosenqvist E, Sharma DK, Ottosen CO. Heat stress and recovery of photosystem II efficiency in wheat (Triticum aestivum L.) cultivars acclimated to different growth temperatures. Environ Exp Bot. 2014; 99:1-8.
20. Pandey GC, Mehta G, Sharma P, Sharma V. Terminal heat tolerance in wheat: An overview. J Cereal Res. 2019; 11(1):1-16.
21. Din R, Subhani GM, Ahmad N, Hussain M, Rehman AU. Effect of temperature on development and grain formation in spring wheat. Pak J Bot. 2010; 42(2):899-906.
22. Mishra S, Jha AB, Dubey RS. Arsenite treatment induces oxidative stress, upregulates antioxidant system, and causes phytochelatin synthesis in rice seedlings. Protoplasma. 2011; 248:565-577.
23. Mittler R, Vanderauwera S, Suzuki N, Miller G, Tognetti VB, Vandepoele K et al. ROS signaling: The new wave? Trends Plant Sci. 2011; 16(6):300-309.
24. Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci. 2013; 14:9643-9684.
25. Tripp J, Mishra SK, Scharf K. Functional dissection of the cytosolic chaperone network in tomato mesophyll protoplasts. Plant Cell Environ. 2009; 32:123-133.
26. Sharma, Pallavi, Jha, AB, Dubey RS, Pessarakli M. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot. 2012.
27. Balla K, Karsai I, Bencze S, Veisz O. Germination ability and seedling

vigour in the progeny of heat-stressed wheat plants. Acta Agron Hung. 2012; 60(4):299-308.

28. Ruelland E, Zachowski A. How plants sense temperature. Environ Exp Bot. 2010; 6:225-232.

29. Ashraf M, Harris PJC. Photosynthesis under stressful environments: An overview. Photosynthetica. 2013; 51(2):163-190.

30. Mathur, Sonal, Agrawal D, Jajoo A. Photosynthesis: Response to high temperature stress. J Photoch Photobio B. 2014; 137:116–126.

31. Essemine J, Ammar S, Bouzid S. Impact of heat stress on germination and growth in higher plants: physiological, biochemical and molecular repercussions and mechanisms of defence. J Biol Sci. 2010; 6:565-572.

32. Huang B, Rachmilevitch S, Xu J. Root carbon and protein metabolism associated with heat tolerance. J Exp Bot. 2012; 63(9):3455-3465.

33. Nawaz A, Farooq M, Cheema SA, Wahid A. Differential response of wheat cultivars to terminal heat stress. Int J Agric Biol. 2013; 15:1354-1358.

34. Ji X, Shiran B, Wan J, Lewis DC, Jenkins CLD, Condon AG et al. Importance of pre-anthesis anther sink strength for maintenance of grain number during reproductive stage water stress in wheat. Plant Cell Environ. 2010; 33:926-942.

35. Kaur V, Behl R. Grain yield in wheat as affected by short periods of high temperature, drought and their interaction during pre- and post-anthesis stages. Cereal Res Commun. 2010; 38(4):514-520.

36. Gourdji SM, Mathews KL, Reynolds M, Crossa J, Lobell DB. An assessment of wheat yield sensitivity and breeding gains in hot environments. P Roy Soc B-Biol Sci. 2013; 280(1752).

37. Lobell DB, Gourdji SM. The influence of climate change on global crop productivity. Plant Physiol. 2012; 160:1686-1697.

38. Alam M, Bodruzzaman M, Hossain M, Sadekuzzaman M. Growth performance of spring wheat under heat stress conditions. Int J Agric Res. 2014; 4(6):91-103.

39. Nahar K, Ahamed KU, Fujita M. Phenological variation and its relation with yield in several wheat (Triticum aestivum L.) cultivars under normal and late sowing mediated heat stress condition. Not Sci Biol. 2010; 2(3):51-56.

40. Mason RE, Mondal S, Beecher FW, Pacheco A, Jampala B, Ibrahim AMH et al. QTL associated with heat susceptibility index in wheat (Triticum aestivum L.) under short-term reproductive stage heat stress. Euphytica. 2010; 174(3):423-436.

41. Lizana XC, Calderini DF. Yield and grain quality of wheat in response to increased temperatures at key periods for grain number and grain weight determination: Considerations for the climatic change scenarios of Chile. J Agric Sci. 2013; 151:209-221.

42. Janjua P, Samad G, Khan N. Impact of Climate Change on Wheat Production: A Case Study of Pakistan. Pak Dev Rev. 2010; 49(4):799-822.

43. Sharma P, Sareen S, Saini M, Shefali. Assessing genetic variation for heat stress tolerance in Indian bread wheat genotypes using morpho-physiological traits and molecular markers. Plant Genet Resour. 2017; 15(6):539-547.

44. Mathur S, Jajoo A, Mehta P, Bharti S. Analysis of elevated temperature-induced inhibition of photosystem II using chlorophyll a fluorescence induction kinetics in wheat leaves (Triticum aestivum). Plant Biol. 2011; 13(1):1-6.

45. Iwai M, Yokono M, Inada N, Minagawa J. Live-cell imaging of photosystem II antenna dissociation during state transitions. Proc Natl Acad Sci USA. 2010; 107(5): 2337-2342.

46. Talukder ASMHM, McDonald GK, Gill GS. Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat. Field Crops Res. 2014; 160:54-63.

47. Lipiec J, Doussan C, Nosalewicz A, Kondracka K. Effect of drought and heat stresses on plant growth and yield: A review. Int Agrophys. 2013; 27:463-477.

48. Wang X, Cai J, Liu F, Jin M, Yu H, Jiang D et al. Pre-anthesis high temperature acclimation alleviates the negative effects of post-anthesis heat stress on stem stored carbohydrates remobilization and grain starch accumulation in wheat. J Cereal Sci. 2012; 55:331-336.

49. Almeselmani M, Viswanathan C, Deshmukh P. Effects of prolonged high temperature stress on respiration, photosynthesis and gene expression in wheat (Triticum aestivum L) varieties differing in their thermotolerance. Plant Stress. 2012; 6(1):25-32.

50. Khanna-Chopra R. Leaf senescence and abiotic stresses share reactive oxygen species-mediated chloroplast degradation. Protoplasma. 2012; 249:469-481.

51. Ahmad P, Jaleel CA, Salem MA, Nabi G, Sharma S. Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. Crit Rev Biotechnol. 2010; 30(3):161-175.

52. Lopes MS, Reynolds MP. Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. Funct Plant Biol. 2010; 37:147-156.

53. Dhyani K, Ansari MW, Rao YR, Verma RS, Shukla A, Tuteja, N. Comparative physiological response of wheat genotypes under terminal heat stress. Plant Signal Behav. 2013; 8(6): 1-6.

54. Savicka M, Škute N. Effects of high temperature on malondialdehyde content, superoxide production and growth changes in wheat seedlings (Triticum aestivum L.). Ekologija. 2010; 56:26-33.

55. Cossani CM, Reynolds MP. Physiological traits for improving heat tolerance in wheat. Plant Physiol. 2012; 160(4):1710-1718.

56. Sharma, Davinder, Mamrutha HM, Gupta VK, Tiwari R, Singh R. Association of SSCP variants of HSP genes with physiological and yield traits under Heat stress in wheat. Res Crop. 2015; 16(1):139-146.

57. Liu P, Guo W, Jiang Z, Pu H, Feng C, Zhu X et al. Effects of high temperature after anthesis on starch granules in grains of wheat (Triticum aestivum L.). J Agric Sci. 2011; 149(2):159-169.

58. Chauhan H, Khurana N, Tyagi AK, Khurana JP, Khurana P. Identification and characterization of high temperature stress responsive genes in bread wheat (Triticum aestivum L.) and their regulation at various stages of development. Plant Mol Biol. 2011; 75:35-51.

59. Sharma D, Tiwari R, Gupta VK, Rane J, Singh R. Genotype and ambient temperature during growth can determine the quality of starch from wheat. J Cereal Sci. 2018; 79:240-246.

60. Asthir B, Bhatia S. In vivo studies on artificial induction of thermotolerance to detached panicles of wheat (Triticum aestivum L) cultivars under heat stress. J Food Sci Technol. 2014; 51:118-123.

61. Biamonti G, Caceres JF. Cellular stress and RNA splicing. Trends Biochem Sci. 2009; 34(3):146-153.

62. Gupta SC, Sharma A, Mishra M, Mishra RK, Chowdhuri DK. Heat shock proteins in toxicology : How close and how far ? Life Sci. 2010; 86:377-384.

63. Gupta NK, Agarwal S, Agarwal VP, Nathawat NS, Gupta S, Singh G. Effect of short-term heat stress on growth, physiology and antioxidative defence system in wheat seedlings. Acta Physiol Plant. 2013; 35:1837-1842.

64. Hu W, Hu G, Han B. Plant Science Genome-wide survey and expression profiling of heat shock proteins and heat shock factors

revealed overlapped and stress specific response under abiotic stresses in rice. Plant Sci. 2009; 176:583-590.

65. Al-Whaibi MH. Plant heat-shock proteins: A mini review. J King Saud Univ Sci. 2011; 23:139-150.

66. Hemantaranjan A, Bhanu N, Singh M, Yadav D, Patel P, Singh R et al. Heat stress responses and thermotolerance. Adv Plants Agric Res. 2014; 1(3):1-10.

67. Marutani Y, Yamauchi Y, Kimura Y, Mizutani M, Sugimoto Y. Damage to photosystem II due to heat stress without light-driven electron flow: Involvement of enhanced introduction of reducing power into thylakoid membranes. Planta. 2012; 236:753-761.

68. Suzuki N, Koussevitzky S, Mittler R, Miller G. ROS and redox signalling in the response of plants to abiotic stress. Plant Cell Environ. 2012; 35:259-270.

69. Caverzan A, Casassola A, Brammer SP. Antioxidant responses of wheat plants under stress. Genet Mol Biol. 2016; 39(1):1-6.

70. Mullineaux PM, Baker NR. Oxidative Stress : Antagonistic Signaling for Acclimation or Cell Death ? Plant Physiol. 2010; 154:521-525.

71. Xin M, Peng H, Ni Z, Yao Y, Hu Z, Sun Q. Wheat responses and tolerance to high temperature. In wheat production in changing environments. 2019; 139-147.

72. Srivastava S, Dubey RS. Manganese-excess induces oxidative stress, lowers the pool of antioxidants and elevates activities of key antioxidative enzymes in rice seedlings. Plant Growth Regul. 2011; 64:1-16.

73. Kumar R, Goswami S, Sharma S, Singh K, Gadpayle K, Kumar N et al. Protection against heat stress in wheat involves change in cell membrane stability, antioxidant enzymes, osmolyte, H2O2 and transcript of heat shock protein. Int J Plant Physiol Biochem. 2012; 4(4):83-91.

74. Puthur JT. Antioxidants and cellular antioxidation mechanism in plants. South Indian j Biol Sci. 2016; 2(1):14-17.

75. Suzuki N, Miller G, Morales J, Shulaev V, Torres MA, Mittler R. Respiratory burst oxidases: The engines of ROS signaling. Curr Opin Plant Biol. 2011; 14:691-699.

76. Ibrahim MM, Alsahli AA, Al-Ghamdi AA. Cumulative abiotic stresses and their effect on the antioxidant defense system in two species of wheat, Triticum durum desf and Triticum aestivum L. Arch Biol Sci. 2013; 65(4):1423-1433.

77. Balla K, Bencze S, Janda T, Veisz O. Analysis of heat stress tolerance in winter wheat. Acta Agron Hung. 2009; 57(4):437-444.

78. Blokhina O, Fagerstedt KV. Reactive oxygen species and nitric oxide in plant mitochondria: Origin and redundant regulatory systems. Physiol Plant. 2010; 138:447-462.

79. Heyno E, Mary V, Schopfer P, Krieger-Liszkay A. Oxygen activation at the plasma membrane: Relation between superoxide and hydroxyl radical production by isolated membranes. Planta. 2011; 234:35-45.

80. Tiwari S, Tiwari S, Singh M, Singh A, Prasad SM. Generation Mechanisms of Reactive Oxygen Species in the Plant Cell: An Overview. In V Singh, S Singh, D Tripathi, S Prasad, D Chauhan (Eds.), Reactive Oxygen Species in Plants: Boon Or Bane-Revisiting the Role of ROS. 2018; 1-22.

81. Poiroux Gonord F, Santini J, Fanciullino A, Lopez Lauri F, Giannettini J, Sallanon H et al. Metabolism in orange fruits is driven by photooxidative stress in leaves. Physiol Plant. 2013; 149:175187.

82. Vijayalakshmi K, Fritz AK, Paulsen GM, Bai G, Pandravada S, Gill BS. Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. Mol Breeding. 2010; 26:163-175.

83. Ruan YL. Sucrose Metabolism: Gateway to Diverse Carbon Use and Sugar Signaling. Annu Rev Plant Biol. 2014; 65:33-67.

84. Dolferus R, Ji X, Richards RA. Abiotic stress and control of grain number in cereals. Plant Sci. 2011; 181:331-341.

85. Kumari M, Pudake RN, Singh VP, Joshi AK. Association of staygreen trait with canopy temperature depression and yield traits under terminal heat stress in wheat (Triticum aestivum L.). Euphytica. 2013; 190:87-97.

86. Kumar S, Singh R, Nayyar H. α-Tocopherol Application Modulates the Response of Wheat (Triticum aestivum L.) Seedlings to Elevated Temperatures by Mitigation of Stress Injury and Enhancement of Antioxidants. J Plant Growth Regul. 2013; 32:307-314.

87. Lata C, Jha S, Dixit V, Sreenivasulu N, Prasad M. Differential antioxidative responses to dehydration-induced oxidative stress in core set of foxtail millet cultivars [Setaria italica (L.)]. Protoplasma. 2011; 248:817-828.

88. Park CJ, Seo YS. Heat shock proteins: A review of the molecular chaperones for plant immunity. Plant Pathol J. 2015; 31(4):323-333.

89. Weydert CJ, Cullen JJ. Measurement of superoxide dismutase, catalase and glutathione peroxidase in cultured cells and tissue. Nat Protoc. 2010; 5(1):51-66.

90. Xu ZS, Li ZY, Chen Y, Chen M, Li LC, Ma YZ. Heat shock protein 90 in plants: Molecular mechanisms and roles in stress responses. Int J Mol Sci. 2012; 13:15706-15723.