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REVIEW ARTICLE

TOLERANCE MECHANISM AGAINST IMPACT OF HEAT STRESS ON WHEAT : A REVIEW

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ABSTRACT

Wheat (*Triticum aestivum)* of the family Poaceae is an important cereal crop and is regarded as a basic source of calories and protein demands of the increasing population. With regards to change in global temperature, the impact of rising temperature on crop production is gaining concern worldwide. Among the various abiotic stresses observed in wheat, heat and drought are the major abiotic stresses. An increase in temperature results in the reduction of grain number, photosynthetic activity, chlorophyll content, and starch synthesis in the endosperm interrupting the important morphological, physiological, and biochemical processes of the plant causing considerable variation like reduction in grain weight per ear, single kernel weight, kernel number, grain size. Spikelet formation, seed size, etc. along with decreased plant size under morphological changes. Similarly, under physiological changes, water potential, photosynthesis, respiration, etc. are adversely affected due to heat stress in wheat. Content of starch, protein, and different types of amino acid present in wheat grain is also affected due to heat stress which comes under biochemical changes. Heat shock proteins (HSPs) and stay green are the mechanisms for the heat tolerance in wheat. The present review was carried out to summarize the various effects of heat stress on wheat at morpho-anatomical, physiological, and biochemical behavior with a brief discussion on suitable breeding strategies to improve the production of wheat crops.

KEYWORDS

wheat, heat stress, yield

1. INTRODUCTION

Wheat (*Triticum aestivum)*, which belongs to the family Poaceae, is one of the most important cereal crops contributing to world grain production with 30% and world grain trade with 50% (Akter and Rafiqul Islam, 2017). As wheat is cultivated in a large area and has the potentiality to give high productivity along with its prominent position in the international food grain trade, it is considered as 'King of Cereals' (Iqbal et al., 2017). Cultivation of wheat can be done from high hill to the Terai region in the winter season of Nepal. According to FAO, 198 million tonnes of wheat should be produced to meet the future demand of the world. The average productivity of wheat is assessed to be 2.53 tons per hectare of Nepal (Bist et al., 2017). Wheat is mainly cultivated in the winter season under a rice-wheat cropping pattern in Nepal. More than 60 percent of wheat production is done in the Terai region of Nepal (Subedi et al., 2019). Nepal agriculture research council has suggested more than 40 improved varieties (26 for terai and 17 for hills) (Timsina et al., 2019). 703,993 hectares of land is utilized for the cultivation of wheat and 2,005,665 and average yield is found to be 3.3 metric tons per hectare in the context of Nepal (MOALD, 2020).

Lack of improved varieties, technical knowledge, farm machinery, quality seed are major constraints in the wheat production of Nepal. The production of wheat is insufficient to cover the demand of the world population which may lead to food insecurity (Narayanan, 2018). 20^0C is the optimum temperature for germination and 16^0C-22^0C is optimum for the vegetative growth of wheat in the context of Nepal. The average productivity of wheat is assessed to be 2.53 tons per hectare of Nepal (Bist et al., 2017). An increase in global temperature has become one of the major concerns in the field of agriculture. Wheat experiences various abiotic stresses like heat, drought, salinity, excess water, chemical and cold among which the major abiotic stresses are heat and drought stresses affecting the production of wheat globally (Lesk et al., 2016). With a $1^{\circ C}$ increment in temperature, global wheat production declined by 6% (Asseng et al., 2015).

It is predicted that heat stress has a generally negative impact on the growth and development of plants which may cause loss of productivity of crops (Bita and Gerats, 2013). Different physiological, biological, and biochemical processes are altered in wheat due to high temperatures (Asseng et al., 2015). Alteration of plant water relations, reduction of photosynthetic capacity, a decrease of metabolic activities, changes of hormones, reduction of pollen tube development ad increase of pollen mortality are caused due to heat stress in wheat (Hasanuzzaman et al., 2013; Almeselmani and Viswanathan, 2012; Ashraf and Harris, 2013; Krasensky and Jonak, 2012; Farooq et al., 2011; Oshino et al., 2011). The climatic factors such as changes in temperature, precipitation, CO2, weather variability, and deficit of soil moisture may produce positive or negative effects on crop production (Joshi and Kar, 2009).

The food security of the world is being deleteriously impacted on crop production due to climate change and it has also been predicted that the increasing temperature will have more impact on sustaining wheat production (Tripathi et al., 2016). So it is necessary to research to assess

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the major impacts of high temperature on wheat to develop improved varieties as well as to mitigate adverse impacts of heat stress. This review enfolds the heat stress effects on morphology, physiology, and biochemistry of wheat. In addition to this, different heat tolerance mechanisms such as HS-induced HSPs production and SG traits linked with heat tolerance have also been explained.

2. METHODOLOGY

For this review article, we used all secondary sources of information. We gathered all of the necessary information from many journals, articles, books, and significant reports, research papers published by other organizations such as the FAO, NARC, etc. The biggest sources of literature with the terms heat stress and wheat are Google Scholar and Research Gate. Then we have selected approximately 40 articles for the preparation of the final manuscript. Desk study helps in guiding the further processes of methodology. All the possible information was thoroughly searched and surfed. Major findings and data were gathered to assess the significant information and finally summarized in this review paper.

3. RESULTS AND DISCUSSION

After the thorough study of various articles on the effect of heat stress on wheat, it has been found that the plant responses to high temperature differ with the degree of temperature, plant type, environment, and the duration of growing. Almost all the aspects of the plant's physiological processes like germination, respiration, transpiration, growth and development, reproduction, yield, etc. are affected by the increasing temperature. The effect of heat stress on wheat wholly along with its effect on its morphology, biochemical processes, and physiological processes has been discussed below in separate headings:

3.1 Heat stress effect on wheat

The increase in temperature beyond a certain limit of a threshold for enough time that induces irreversible damage to the growth and development of the plant is known as heat stress, whereas the capability of the plants to grow and develop to produce economic yield under high temperature is referred as heat tolerance (Hall and A.E., 2018). Morph anatomical, physiological, and biochemical behavior of wheat are mainly affected due to heat stress which ultimately results in the declination of the duration of grain filling, starch synthesis in the endosperm, and pollen viability (Sharma et al., 2019).

Appropriate mechanisms like escape, stay green, avoidance has been developed by wheat to cope with HS (Wahid et al., 2007). Plants shorten their GFD by accelerating the GF rate with the help of stem reserves for escaping so that the yield can be maintained. Similarly, the maintenance of an optimum plant water status by the reduction of water loss and exploitation of water availability is the method of avoidance from the THS for the plants. Tolerance of low water potential, cooler canopies, active photosynthetic state to maintain the supply of current assimilate, better use efficiency of radiation, and long GFD to maintain GF in elevated temperatures comes under stay green behavior (Sharma et al., 2016).

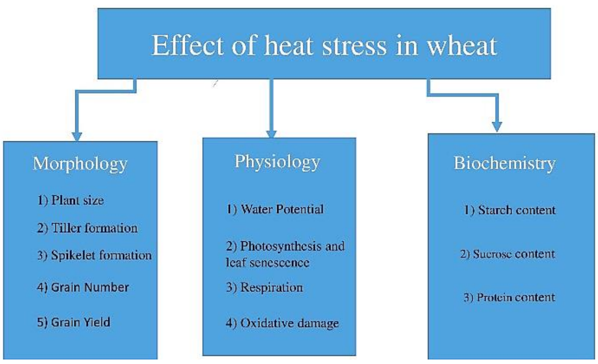

Figure 1: Effect of heat stress in wheat

3.1.1 Effect of heat stress on wheat morphology

The adverse effect of heat stress on wheat morphology are numerous including germination, emergence, root, stem, leaf development, seed growth, seed quality, etc. Due to high stress, seed germination and crop establishment are negatively influenced in wheat along with various other crops (Hossain et al., 2013). Crop production is ultimately affected as root growth is decreased due to heat stress (Huang et al., 2012).

3.1.1.1 Plant size

Genetic diversity in plant height is shown by different varieties of wheat. Plant height is significantly reduced by heat stress. Fast phasic change is the main cause of reduction in plant height which results in the short vegetative phase and the reproductive phase is attained very early (Weider and Georg, 2005). At heat stress conditions, 25.8% is the average reduction of plant height (Hamam and Khaled, 2009).

3.1.1.2 Tiller formation

Productive tiller's survivability is affected by the high temperature resulting in the decrement of the yield (Akter and Rafiqul Islam, 2017).

3.1.1.3 Spikelet formation

Spike enlargement and reduction in the number of spikelets are promoted during heading and anthesis(Semenov, 2009). Heat stress has negative impacts on pollen cell and microspore development which will induce male sterility (Anjum et al., 2008).

3.1.1.4 Grain number and size

Declines in photosynthesis during floret development have reduced grain number (Demotes-Mainard and Jeuffroy, 2004). The structure of endosperm cells and aleurone layer is changed due to heat stress which induces shrinkage of grain size (Dias et al., 2008). A decrease in grain number results in the reduction of harvest index under heat stress conditions (Lukac et al., 2012).

3.1.1.5 Grain yield

The phenomenon of grain development mainly depends upon the grain filling rate and duration that is very much sensitive to heat stress (Gourdji et al., 2013). A decrease in grain filling duration by the rise of 1◦C-2◦C temperature lowers the seed weight (NAHAR et al., 2010). High stress in wheat can result in the decrement of grain yield up to 53.37% and tiller number up to 15.38% (Riaz-Ud-Din et al., 2010). A higher loss in grain yield has been attained due to an increase in average temperature by 1◦(Asseng et al., 2015; Yu et al., 2014). Under heat stress, considerable variations like reduction in grain weight per ear, single kernel weight, kernel number, etc. were seen in different cultivars.

3.1.1.6 Seed quality

Degradation of mitochondria alters protein expression profiles, diminishes ATP aggregation and uptake of oxygen in soaking wheat embryos which will ultimately reduce the quality of seed (Hampton et al., 2013). Kernel weight, photosynthetic rate, viable leaf area, shoot, and grain mass and sugar content at maturity and reduced water use efficiency, etc. are decreased due to high temperature (Shah and Scheufele, n.d.).

3.1.2 Effect of heat stress on wheat Physiology

The most important physiological process; photosynthesis is highly affected by heat stress. The products of photosynthesis need to be translocated to different parts of the plant for the proper growth and development but due to an increase in temperature, the rate of assimilatory translocation from source to sink is reduced owing to a decrease in membrane stability (Farooq et al., 2011). Along with photosynthesis, water potential, respiration, transpiration, etc., are also affected due to heat stress.

3.1.2.1 Water potential

When a plant is exposed to high temperatures it will cause dehydration which may affect the growth and development of a plant. The water content of a cell is reduced owing to heat stress which affects the both size of the cell and its growth (Rodríguez et al., 2005). The water potential of wheat will decrease when the plant is exposed to a high temperature (35) after tillering. Dehydration due to heat stress occurred along with a reduction in osmotic potential (Ahmad et al., 2010). Individual heat stress results from a 25% decrease in relative water potential as compared to the control environment (Sattar et al., 2020).

3.1.2.2 Photosynthesis and leaf senescence

Photosynthesis is known to be the most heat-sensitive physiological process in plants. It was observed that stomata will close under high-stress conditions affecting grana and middle lamella of chloroplast which leads to a decrease in photosynthesis (Mathur et al., 2014). The amount of chlorophyll is reduced by 55.5% under heat stress (Sattar et al., 2020).

Under high temperatures, the activity of photosystem II (PSII) is highly reduced or even stops (Morales et al., 2003). The number of photosynthetic pigments is also reduced by the heat shock(Marchand et al., 2005). Reduction insoluble proteins, RUBP, large subunits, small subunits of Rubisco in darkness, an increase of those in light are considered to be some of the reasons to hinder the photosynthesis under heat stress (Sumesh et al., 2008). Leaf senescence in wheat may be hastened due to inhibition of chlorophyll biosynthesis under leaf stress (> 34°C) (Lopez-Ridaura et al., 2013). Leaf senescence is enhanced, the loss of chloroplast integrity is accentuated, and the turn-down of photosystem-II mediated electron transport is accelerated when the wheat plant is exposed to heat stress (Haque et al., 2014).

3.1.2.3 Respiration

Respiration is affected by the change in mitochondrial activities due to heat stress. Initially, the rate of respiration will increase with temperature increment up to a certain limit then decrease due to disruption in photorespiration (Mathur et al., 2014). Due to heat stress, the rate of respiratory carbon loss is increased in the rhizosphere which reduces the production of ATP and enhances the generation of ROS (Huang et al., 2012). The rate of respiration becomes maximum at 40-50 and decreases with an increase in temperature beyond 50 . Heat stress has a positive impact on photorespiration because of the alteration in solubility of oxygen and carbon dioxide (Cossani and Reynolds, 2012).

3.1.2.4 Oxidative damage

Destructive ROS (Reactive Oxygen Species) along with singlet oxygen, superoxide radical, hydrogen peroxide are generated in the plants when they are exposed to heat stress and oxidative stress is generated by hydroxyl radical (Marutani et al., 2012; Suzuki et al., 2012). Membrane peroxidation is increased and membrane thermo-stability is decreased in wheat due to oxidative stress (Savicka and Škute, 2010). Accumulation of ROS in the cell plasma membrane with depolarization of cell membrane, activation of ROS producing enzyme RBOHD can be caused by continual heat stress in plants and programmed cell death is also triggered (Mittler et al., 2011). O_2 production in root is increased by 68% and malondialdehyde (MDA) content I leaf by 27% at the early stage and the later stage of seedling development by 59% due to heat stress (Miller et al., 2009). Even so, for escaping the excess ROS, plants have antioxidants Superoxide dismutase (SOD), ascorbate peroxide (APX), and catalase (CAT), glutathione reductase (GR), and peroxidase (POX) having ameliorating effects of heat stress in wheat (Caverzan et al., 2016; Suzuki et al., 2011).

3.1.3 Effect of heat stress on wheat biochemistry

After checking the influence of heat stress on the quality of starch in bread, biscuit, and durum wheat, it was found that there is a reduction in the weight and diameter of the kernels which ultimately results in the reduction of starch level to a significant level (Labuschagne et al., 2009). Starch (amylose+ amylopectin), is one of the important constituents of wheat in which amylose content is a major factor to determine the quality of starch. Increase in amylose content and the ratio of amylose: amylopectin is dependent upon high temperature (Sharma et al., 2019). The starch content of the wheat grain is badly affected resulting in poor grain quality, grain size, and yield due to heat stress during grain development (Chinnusamy and Khanna-Chopra, 2003). From the proposal of Jenner, it has been found that the content of sucrose in the endosperm was either not affected or amplified by the increase in temperature.

Similarly, a differential effect on the content of glucose and fructose has been noticed due to an increase in temperature. Important enzymes involved in starch biosynthesis are ADP-Glucose Pyro phosphorylase (AGPase) and starch synthase (Soluble Starch Synthase and Granule bound Starch Synthase). Out of total endosperm, one-third of starch content in grain is decreased at high temperature because of the decreased efficiency of enzymes involving in starch biosynthesis (Liu et al., 2011). Due to the reduced activity of starch synthase at high temperatures, there was a decrease in starch deposition and grain size was also lowered (Chauhan et al., 2011). It has been observed that under high stress, there was a decrement of starch biosynthesis in wheat grain but there was an increment in total soluble sugar and protein (Asthir and Bhatia, 2014). Protein content and composition is the main factor to determine the quality of grain (Lizana and Calderini, 2013). Iqbal et. al reported the increment in grain protein content along with the increment in essential amino acids fractions, leaf nitrogen content, and sedimentation index.

3.2 Mechanism of heat tolerance in wheat

Among the different adaptation mechanisms for adapting under HS, avoidance, tolerance, and escape are considered to be the main mechanisms that help plants to survive and grow and develop in an environment having high temperatures. Generation of heat shock proteins (HSPs) i.e., antioxidant defense and stay green are major heat tolerance mechanisms in wheat. Protein folding and synthesis which are the function of protein is interrupted at HS condition which disturbs the major metabolism processes along with DNA replication, transcription, mRNA transport, and translation till the cell recuperate (Biamonti and Caceres, 2009; Sharma et al., 2019).

To win over this problem, the HS-induced proteins are produced by the plant to speed up the defense mechanism which is called Heat Shock Proteins (HSPs) (Gupta et al., 2010). To avoid the denaturation of protein and aggregation, HSPs function as molecular chaperones under HS (Hasanuzzaman et al., 2013). Stay Green (SG) is an associated genotype that helps to maintain photosynthesis and grain filling by the late expression of genes related to senescence (Vijayalakshmi et al., 2010). Stay Green is an important mechanism for HS tolerance in wheat as it helps in conserving photosynthetic area and increase nitrogen remobilization to the maturing grain (Poiroux-Gonord et al., 2013). Due to SG, photosynthetic activity is increased that maintains continuous sugar supply in growing anther and pollen, thus helping to retain pollen and ovules viability (Ruan, 2014). Hence, in wheat genotypes, the SG trait can be considered as a major HS tolerant mechanism (Huang et al., 2012).

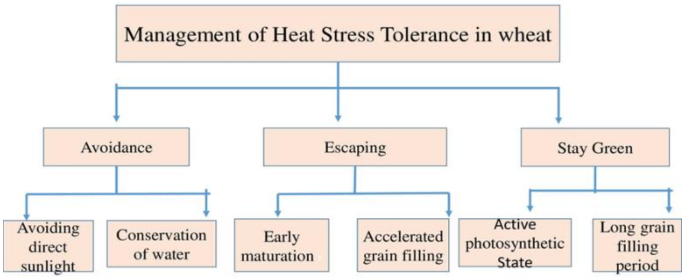

Figure 2: Tolerance mechanism of wheat against heat stress

Table 1: Functions of heat shock proteins (HSPs) for heat stress tolerance

Heat shock protein	Functions
HSP27	Stabilize microfilament, antiapoptotic
HSP40	After the formation of fully refolded protein, small HSPs involved in refolding are set free by HSP70, HSP100 (Hasanuzzaman et al., 2013)
HSP60	Helps to refold protein and prevent denaturation of protein accumulation (Sharma et al., 2019)
HSP70	Protein folding is properly facilitated and newly synthesized protein is stabilized by preventing aggregate formation (Park and Seo, 2015)
HSP90	HS associated signal transductions are mediated (Xu et al., 2012)
HSP100	Dissociation of ATP dependent and aggregate protein are also degraded (Sharma et al., 2019)
Small HSPs	Helps to refold the denatured protein by preventing thermal aggregation (Gupta et al., 2010)

4. Conclusion

The growth, development, and productivity of plants have been greatly affected by the high-temperature stress thus becoming a major concern for crop production worldwide. Heat stress caused due to high temperatures in wheat is expected to increase in frequency across the world. Heat stress's negative influence on wheat production could lead to food insecurity in the future, hence it's necessary to mitigate heat stress's impact on wheat yield. Grain setting, duration, rate, quality, tiller formation, spikelet formation, and ultimately grain yield, seed quality are adversely affected due to heat stress. However, the duration, timing, and intensity of heat stress can be utilized to determine its impact on the grain yield of wheat. Dehydration of cells, reduction of chlorophyll content, reduction of respiration rate are caused by the high temperature which harms the physiology of wheat. Synthesis of starch is reduced but the content of sucrose and protein is increased under heat stress. An increase in temperature interrupts the major morphological, physiological, and biochemical processes of wheat. Therefore, the effects of heat stress can be minimized by the development of heat-tolerant varieties by using the mechanism of heat shock proteins (HSPs) and stay green. Management and manipulation of cultural practices, such as timing and methods of sowing, weed management, irrigation management, and selection of cultivars and species can considerably help to minimize the adverse effects of heat stress.

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