REVIEW ARTICLE

Effect of heat stress on wheat production in semi-arid region of Rajasthan

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Producing sufficient food to meet the demands of India's growing population, projected to reach 10 billion by 2050, presents significant challenges due to declining arable land, water scarcity and unpredictable weather patterns magnified by climate change. Wheat (*Triticum aestivum* L.), a staple crop providing 20% of global caloric and protein intake, faces severe threats from heat stress, which has already reduced global productivity by approximately 5% since the 1980s. This review examines the impact of heat stress on wheat production, focusing on physiological, biochemical and yield-related aspects, with a particular emphasis on the semi-arid region of Rajasthan, India. High temperatures during significant growth stages disrupt photosynthesis, reduce enzymatic activities and alter starch accumulation in grains, ultimately decreasing yield and grain quality. Additionally, heat stress induces oxidative damage through the accumulation of Reactive Oxygen Species (ROS), impacting membrane stability and protein expression. The synthesis of Heat Shock Proteins (HSPs) plays a vital role in mitigating heat-induced damage, although their efficacy is often overwhelmed under extreme stress. This review underscores the necessity of developing heat-tolerant wheat cultivars to sustain productivity in the face of rising temperatures and highlights the complex exchange between temperature stress and wheat physiology.

Key Words: *Heat stress; Photosynthetic efficiency; Anthesis; Reactive oxygen species; Heat shock proteins*

INTRODUCTION

The most significant task of the century is to produce sufficient food to feed India's increasing population, while also coping with decreasing amounts and quality of arable land, reducing water supplies and increasingly unpredictable weather due to climate change [1]. According to Food and Agriculture Organization (FAO) estimates, in order to meet future demand, the world will need an extra 198 million tons of wheat by 2050, meaning that developing nations' wheat production will need to rise by 77% [2]. About 30% of the world's cereal acreage is devoted to the primary, stable crop of wheat, which feeds 36% of the world's population. About 20% of the calories and proteins in a human diet come from wheat. Heat stress is estimated to have decreased global wheat productivity by as much as 5% since the 1980s [3,4]. Based on the severity of the high temperature, drought, salinity, waterlogging and mineral toxicity stresses, such an increase in world's temperature may have a major impact on productivity. High temperature-induced heat stress is defined as an increase in air temperature that lasts longer than a certain threshold and is strong enough to harm or permanently damage agricultural plants in general [5]. The issue of heat stress is made worse when soil temperature rises due to an increase in air temperature and a decrease in soil moisture. As a result, heat stress has emerged as a serious threat to worldwide crop productivity [6-9]. Wheat (*Triticum aestivum* L.) is one of the most important cereal crops in the world, providing essential nutrients to a large part of the global population. In Rajasthan, wheat occupies a significant portion of the cultivated land, contributing substantially to the state's economy and food security. However, the semi-arid climate of Rajasthan, characterized by high temperatures and low rainfall, increases the challenges of wheat production. Heat stress in particular is a significant factor that affects the growth, development and yield of wheat. The climate in Rajasthan is predominantly dry and hot, with temperatures often exceeding 40°C during the wheat growing season. The region receives an annual rainfall of approximately 250-500 mm, which is sporadic and unpredictable. These climatic conditions create a challenging environment for wheat cultivation, making the crop highly susceptible to heat stress. Heat stress affects wheat at various developmental stages, leading to a range of physiological responses. High temperatures during the germination phase can lead to reduced germination rates and poor seedling vigor. Heat stress affects the enzymatic activities essential for seed germination, resulting in delayed or uneven crop establishment. Wheat production in India had observed a quantum jump from 6.5 million tons in 1950 to 112 million tons in 2023. A 33% yield loss in late-sown wheat varieties was noted as a result of high temperatures, suggesting the necessity to produce heat-tolerant wheat cultivars in order to achieve sustainable production. The climate agency said that "the global average temperature for the past 12 months (April 2023-March 2024) is the highest recorded at 0.70°C above the 1991-2020 average and 1.58°C above the 1850-1900 pre-industrial average. The 60%-70% starch content of wheat grains steadily decreases at high temperatures. Because granule-bound starch, soluble starch and sucrose synthase are inactive during the grain filling phase, high temperatures prevent starch from building up in grains. Additionally, it reduces the synthesis of starch, translocates carbohydrates from stem reserves and modifies the structure of the seed's endosperm and aleurone layer, all of which have an impact on the growth of grains [10-13].

LITERATURE REVIEW

Physiological impact

Since photosynthesis is the physiological activity most susceptible to temperature changes, any decrease in photosynthesis has an impact on wheat growth and grain yield [14-16]. Heat stress impairs the photosynthetic efficiency of wheat plants by affecting chlorophyll content and disrupting the functioning of photosystem II [17]. The heat-induced increase in thylakoid membrane fluidity and Photosystem II's (PSII's) electron-transport dependent integrity are the main causes of PSII's vulnerability to high temperatures [18]. A notable rise in the baseline level of chlorophyll fluorescence, which is indicative of photosynthetic inhibition, is frequently used to suggest the inhibition of PSII electron transport during heat stress [19]. We must know how crops respond to elevated temperatures and how tolerance to heat can be improved in order to adapt new crop varieties to the future climate [20]. The best temperature for wheat anthesis and grain filling is between 12°C and 22°C. Exposure to temperatures higher than this can drastically reduce grain yield [21-23]. Heat stress affects grain growth because temperature variations directly affect assimilate translocation and the length and pace of grain filling. The degree of heat stress determines how much harm is caused by heat. Increased respiration rates under high temperatures lead to a depletion of carbohydrates, which adversely affects plant growth and development [24]. Wheat plants under heat stress exhibit reduced water uptake and increased transpiration rates, leading to a negative water balance [25]. Stomatal closure, a common response to heat stress, further reduces CO_2 assimilation, impacting photosynthesis and overall plant productivity (Table 1) [26].

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TABLE 1
Optimal temperature requirements of wheat at different growth stages

Stages	Optimum temperature (°C)	Minimum temperature (°C)	Maximum temperature (°C)
Root growth	17.2 ± 0.87	3.5 ± 0.73	24 ± 1.21
Shoot growth	18.5 ± 1.90	4.5 ± 0.76	20.1 ± 0.64
Leaf initiation	20.5 ± 1.25	1.5 ± 0.52	23.5 ± 0.95
Terminal spikelet	16 ± 2.3	2.5 ± 0.49	20 ± 1.6
Anthesis	23 ± 1.75	10 ± 1.12	26 ± 1.01
Grain filling duration	26 ± 1.53	13 ± 1.45	30 ± 2.13

Biochemical impact

Heat stress triggers several biochemical changes in wheat plants, including the accumulation of Reactive Oxygen Species (ROS), alterations in membrane stability and changes in protein expression. The overproduction of ROS under heat stress causes oxidative damage to cellular structures, including lipids, proteins and nucleic acids. Wheat plants activate antioxidant defense mechanisms to mitigate this damage, but the efficiency of these systems can be overwhelmed under severe stress conditions. Superoxide radicals, hydroxyl radicals and hydrogen peroxide are examples of ROS that are naturally formed in cells, but excessive amounts of these substances can be hazardous [27]. ROS are produced and accumulate as a result of heat stress [27-30]. Thus, antioxidant systems' detoxification of plants is significant for shielding them from heat stress [31,32]. Plants have both enzymatic and non-enzymatic antioxidant mechanisms as part of their antioxidant defense system. Ascorbate peroxidase, dehydroascorbate reductase, glutathione S-transferase, superoxide dismutase, catalase, guaiacol peroxidase and glutathione reductase are the components of the enzymatic antioxidant system [33]. Tocopherols, ascorbate and glutathione are examples of non-enzymatic antioxidants. High temperatures disrupt the lipid composition of cell membranes, leading to increased permeability and leakage of cellular contents. Membrane stability is a significant factor determining the extent of heat stress tolerance in wheat. Wheat plants produce Heat Shock Proteins (HSPs) in response to elevated temperatures. These proteins play a significant role in protecting cellular components from heat-induced damage and maintaining protein homeostasis. The chemical reaction to heat stress that has been investigated the most is the expression of HSPs. HSPs prevent heat-induced protein aggregation, which allows proteins to refold during the recovery phase [34-37]. According to Coles et al., the two most important factors influencing wheat grain quality are grain size and protein concentration [38]. Heat stress during the grain-filling phase reduces the amount of starch deposited in the grain, which increases protein concentration by permitting more nitrogen per unit of starch [39]. These findings have been reported by Wardlaw et al., and Gooding et al., [40 41]. A basic reaction to heat stress is the expression of HSP genes [42]. Wheat experiences a decrease in normal protein synthesis when exposed to high temperatures (>35°C), although HSPs are still generated [43].

Yield-related impact

Heat stress during significant growth stages such as anthesis and grain filling can lead to significant yield reductions. Heat stress can reduce the number of grains per spike and the individual grain weight, resulting in lower overall yield. High temperatures during the grain filling period accelerate the senescence process, limiting the duration of grain filling and reducing final grain size. Increased temperature affects both grain weight and number [44]. The developmental stage at which the elevated temperature occurs determines how temperature affects each of these grain yield components. For example, temperatures exceeding 20°C between spike initiation and anthesis may significantly limit the quantity of grains per spike [45]. Heat stress speeds up development of the spike reducing spikelet number and thus, the number of grains per spike [46]. The time between the onset of the spike and anthesis is not the most vulnerable to heat stress, though. The window of time between the emergence of double ridges on the flag leaf and shoot apex is the most important. During this time, an inverse relationship has been discovered between the number of grains per spike and the duration of heat stress [47]. This sensitivity is caused by spikelets that start to emerge in the spike-known as the double ridge stage-from tissue ridges between ridges of undifferentiated leaf primordia. Then, floret production begins on each spikelet meristem. Both the number of spikelets per spike and the number of grains per spikelet decrease with a reduction in the time between emergence and double ridge and anthesis [48]. The quality of wheat grain, including protein content and gluten strength, is also compromised under heat stress. For protein composition, high temperature stress reduces the glutenin/gliadin ratio and limits the synthesis of the larger Sodium Dodecyl Sulfate (SDS)-insoluble glutenin polymers which causes wheat dough to have weaker viscoelasticity properties [49].

DISCUSSION

According to McClung et al., heat stress interferes with a number of plant functions, causing morpho-physiological changes in wheat plants that impede their growth and ultimately result in a significant loss of production [50]. The way that plants react to heat stress varies greatly depending on the temperature, its length and the stage of growth that is being affected. Depending on the crop species, photosynthetic activities may withstand heat stress more readily and are rather stable between 30°C and 35°C. However, when temperatures rise above 40°C, photosynthesis is negatively impacted. Elevated temperatures cause O_2 and CO_2 to become less soluble; conversely, a higher concentration of CO_2 than O_2 leads to greater photorespiration and reduced photosynthesis [51]. Activities at Ribulose Bisphosphate Carboxylase Oxygenase (RUBISCO) break down in hot weather [52]. Reduced photosynthetic capacity under heat stress [53]. A significant part of leaf photosynthesis is played by photosystem II, one of the photosynthetic apparatus's components that is comparatively more resistant to heat stress than drought [54]. Furthermore, it is thought that mitochondrial respiration plays a significant role in determining a plant's ability to develop and survive [55]. Wheat morphology and seed germination are adversely affected by heat stress [56]. The symptoms of heat stress include decreased root diameter, length and quantity of roots. Because there is less carbon partitioning to the roots under heat stress during reproductive development, root growth is similarly slowed down [57]. The ideal temperature range for root growth is extremely limited when compared to other growth processes [58].

Heat stress causes fewer grains to form, which lowers the wheat harvest index [59]. The impact of heat stress on grain size and quantity however, differs depending on the developmental phases that are affected. For example, temperatures over 20°C during the period between spike initiation and anthesis accelerate spike development but decrease the amount of grains and spikelets per spike [60]. Male sterility results from heat stress's detrimental effects on pollen cells and microspores [61]. Depending on the genotype, wheat can become completely sterile even at temperatures exceeding 30°C during floret development [62]. According to Hedhly et al., wheat anther generated under three days of heat stress during anthesis was discovered to be physically aberrant and non-functional florets [63]. A daytime high temperature of 31°C/20°C may also result in grain shrinkage because of modifications to the endosperm and aleurone layer's structural makeup [64].

High temperatures have a significant impact on the wheat grain filling stage. According to Dias et al., heat stress typically shortens the grain filling time and speeds up the rate of grain filling [64]. However, in plants with varying grain weight stability, the rate and length of grain growth reduced [65]. Grain filling time in wheat can be shortened by 12 days for every 5°C increase in temperature above 20°C [66]. Compared to daytime temperature, an increase in night time temperature is more sensitive, shortens the grain filling period and lowers the grain yield. A reduction of 3 to 7 days was seen in the grain filling period by night time temperatures of 20°C to 23°C [67]. The rate of grain filling in wheat cultivars under day/night temperatures of 32°C/22°C was found to be significantly lower recently than at 25°C/15°C. Many cereals and legumes are affected by heat stress in terms of grain quality, primarily due to reduced nutrient remobilization and assimilation [68]. According to Lizana et al., heat stress has no effect on the protein concentration of wheat grain; nevertheless, Iqbal et al., found a significant link between leaf nitrogen content and grain protein [69,70].

CONCLUSION

Heat stress poses a significant challenge to wheat production in the semi-arid region of Rajasthan. Understanding the physiological responses, biochemical responses and yield related responses of wheat to heat stress is essential for developing effective mitigation strategies. The frequency of high temperatures that stress wheat is predicted to rise globally. Grain setting, length and rate are all significantly impacted by heat stress, which eventually lowers grain yield. However, the influence of heat stress on grain yield depends on its timing, duration and intensity. To address these challenges, there is a pressing need for the development of heat-tolerant wheat cultivars. Advancing our understanding of how wheat responds to elevated temperatures and enhancing its tolerance through genetic and agronomic innovations are essential steps toward ensuring sustainable wheat production. In the face of climate change, these efforts are critical to maintaining food security and supporting the livelihoods of millions, particularly in regions like Rajasthan where wheat is an important crop.

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