NEW ERA AGRICULTURE MAGAZINE

Heat Stress and Its Impact on Photosynthesis and Yield in Wheat

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Abstract:

Heat stress is a major abiotic constraint limiting wheat (Triticum aestivum) productivity, particularly in regions experiencing rising global temperatures. Wheat, a staple crop providing food security for billions, is highly susceptible to high temperatures, particularly during critical growth stages such as anthesis and grain filling. Heat stress negatively affects photosynthesis by impairing chlorophyll biosynthesis, reducing CO_2 assimilation, and inducing oxidative stress through excessive reactive oxygen species (ROS) accumulation. This leads to declines in grain yield and quality due to reductions in spikelet fertility, grain number, and protein content. At the molecular level, wheat responds to heat stress by activating heat shock proteins (HSPs), transcription factors (HSFs, DREB, NAC), and hormonal pathways (ABA, ethylene, cytokinins). Breeding for heat-tolerant wheat varieties has relied on conventional selection, marker-assisted selection (MAS), and genomic selection (GS), while advances in gene editing (CRISPR-Cas9) and transgenic approaches have provided new tools for improving thermotolerance. Agronomic strategies such as optimized sowing time, irrigation management, and biostimulant applications further mitigate heat stress effects. This review discusses the physiological, biochemical, and genetic mechanisms of heat stress in wheat, its impact on photosynthesis and yield, and current breeding and management strategies. Future research should focus on integrating phenomics, genomics, and artificial intelligence (AI) to accelerate the development of climate-resilient wheat cultivars.

1. Introduction:

Wheat (*Triticum aestivum*) is one of the most essential staple crops globally, serving as a primary food source for billions of people. However, wheat production faces several environmental challenges, with heat stress emerging as a major factor limiting crop growth, development, and yield. Heat stress, particularly during critical growth stages such as flowering and grain filling, significantly affects wheat's physiological and biochemical

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processes, ultimately leading to reduced grain yield and quality. With the ongoing changes in global climate patterns, the frequency and intensity of heat waves are increasing, posing a severe threat to global wheat production. Understanding the impact of heat stress on wheat photosynthesis and yield is crucial for developing climate-resilient wheat varieties and adopting suitable agronomic practices to ensure food security.

1.1 Importance of Wheat in Global Food Security

Wheat is the second most cultivated cereal crop after maize and plays a pivotal role in global food security. It contributes approximately **20% of the total calories and protein** consumed by humans worldwide. Due to its adaptability to diverse climatic conditions, wheat is grown across temperate, subtropical, and some tropical regions, making it a vital source of nutrition.

1. **Nutritional Value:** Wheat provides essential carbohydrates, proteins, vitamins, and minerals necessary for human health. Whole wheat contains dietary fiber, which is important for digestive health.
2. **Economic Importance:** The wheat industry is a major contributor to global economies, providing income to millions of farmers and employment in processing, trade, and related sectors.
3. **Versatility in Food Products:** Wheat is used in producing various food products such as bread, pasta, noodles, and biscuits, making it a staple in many diets.
4. **Strategic Importance in Food Security:** Many countries maintain wheat reserves as a buffer against food shortages, and it is often a key commodity in international trade.

However, **climatic challenges**, particularly heat stress, threaten global wheat productivity, making it imperative to understand and mitigate its impact.

1.2 Definition and Causes of Heat Stress in Wheat

Definition of Heat Stress

Heat stress in wheat refers to the exposure of plants to **high temperatures (above optimal growth conditions) for a prolonged period**, leading to physiological and metabolic disturbances that negatively affect plant growth and grain yield. The **optimal temperature range for wheat growth** varies across developmental stages:

1. **Germination:** 12–25°C
2. **Vegetative growth:** 15–20°C
3. **Reproductive stage:** 15–25°C
4. **Grain filling:** 20–25°C

Temperatures **above 30–35°C during the reproductive and grain-filling stages** can cause severe yield reductions due to pollen sterility, poor grain filling, and increased respiration rates.

Causes of Heat Stress in Wheat

1. **Global Warming and Climate Change:**
   a. Rising atmospheric temperatures due to greenhouse gas emissions have led to an increased frequency of heat waves, especially in major wheat-growing regions such as South Asia, Europe, North America, and Australia.
2. **Extreme Weather Events:**
   a. Unexpected heatwaves during critical wheat growth stages, especially flowering and grain filling, can drastically reduce yields.
3. **Drought and Water Deficiency:**
   a. High temperatures often coincide with drought conditions, exacerbating heat stress effects by limiting water availability for cooling through transpiration.
4. **Anthropogenic Activities:**
   a. Urbanization, deforestation, and industrialization contribute to the overall rise in temperatures, further stressing agricultural ecosystems.
5. **Poor Agronomic Practices:**
   a. Late sowing of wheat can expose crops to high temperatures during the reproductive phase, significantly reducing grain yield.
   b. Use of non-heat-tolerant wheat varieties increases vulnerability to temperature fluctuations.

Understanding these causes is essential for developing adaptive strategies to improve wheat's resilience to heat stress.

1.3 Global Climate Change and Its Implications on Wheat Production

Climate change is one of the biggest challenges facing modern agriculture, and its impact on wheat production is particularly concerning. **Rising global temperatures, shifting precipitation patterns, and increased frequency of extreme weather events** directly influence wheat growth, development, and yield.

Projected Impact on Wheat Yield

1. According to the **Intergovernmental Panel on Climate Change (IPCC)**, global wheat production could decline by **5–15% by 2050** if no significant adaptations are made.
2. Major wheat-producing countries like India, China, the USA, and Australia are likely to face significant production losses due to temperature extremes.
3. Some regions may experience a **shift in wheat-growing zones**, requiring adaptation strategies such as heat-tolerant varieties and improved management practices.

Need for Adaptive Strategies

To mitigate the adverse effects of climate change on wheat production, scientists and policymakers are exploring several adaptive measures:

1. **Development of heat-tolerant wheat varieties** through breeding and genetic engineering.
2. **Adjusting planting dates** to avoid peak heat stress periods.
3. **Implementing water-saving irrigation techniques** such as drip irrigation.
4. **Utilizing advanced weather forecasting systems** to prepare for extreme climatic conditions.

By adopting these strategies, wheat production can be sustained under the increasing challenges posed by climate change.

2. Mechanisms of Heat Stress in Wheat

Wheat, like other cereal crops, exhibits a range of **physiological, biochemical, and molecular changes** in response to heat stress. These responses vary depending on the intensity and duration of stress and the growth stage at which it occurs.

2.1 Physiological Responses to High Temperatures

Physiological responses to heat stress in wheat involve **alterations in plant growth, water relations, membrane stability, and enzyme activity**, affecting overall productivity.

2.1.1 Leaf and Canopy Temperature Regulation

1. Under high temperatures, wheat plants attempt to **dissipate excess heat** through transpiration. However, when temperatures exceed **35°C**, this mechanism becomes inefficient, leading to leaf overheating.
2. The **canopy temperature depression (CTD)** technique is often used to identify heat-tolerant genotypes, as tolerant varieties maintain a lower canopy temperature through efficient transpiration.

2.1.2 Reduced Photosynthetic Efficiency

1. Heat stress damages **photosystem II (PSII)** in the chloroplasts, reducing the **efficiency of light harvesting** and electron transport, leading to lower photosynthetic rates.
2. Stomatal closure under heat stress restricts **CO_2 uptake**, limiting the Calvin cycle and reducing carbohydrate synthesis.

2.1.3 Disruption of Plant Water Relations

1. High temperatures increase **evapotranspiration rates**, leading to **faster depletion of soil moisture** and inducing water stress.

2. **Relative water content (RWC)** declines, reducing cell turgor and causing wilting, premature leaf senescence, and reduced biomass accumulation.

2.1.4 Early Senescence and Reduced Biomass

1. Wheat plants exposed to high temperatures **accelerate their growth cycle**, leading to **early senescence**.
2. **Chlorophyll degradation** increases under heat stress, further reducing photosynthetic potential and grain filling.

2.2 Biochemical and Molecular Changes Under Heat Stress

2.2.1 Heat Shock Proteins (HSPs) and Protein Stability

1. Wheat plants **produce heat shock proteins (HSPs)** as molecular chaperones to protect proteins from denaturation.
2. HSPs prevent protein aggregation and assist in **protein refolding** during heat stress.

2.2.2 Reactive Oxygen Species (ROS) and Antioxidant Defense

1. Heat stress leads to an imbalance in electron transport chains, resulting in excessive production of **reactive oxygen species (ROS)** such as **superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-)**.
2. ROS cause **oxidative damage to membranes, proteins, and nucleic acids**, leading to **cell death**.
3. Antioxidant enzymes like **superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD)** play a crucial role in scavenging ROS and maintaining cellular homeostasis.

2.2.3 Hormonal Regulation Under Heat Stress

1. **Abscisic acid (ABA)** increases under heat stress, causing **stomatal closure** to reduce water loss. However, this also limits CO_2 uptake, reducing photosynthesis.
2. **Salicylic acid (SA)** and **jasmonic acid (JA)** modulate heat stress responses by inducing **antioxidant activity and stress-related gene expression**.
3. **Ethylene production** rises under heat stress, accelerating **leaf senescence and reducing yield potential**.

2.3 Heat Stress During Different Growth Stages

2.3.1 Vegetative Stage

1. Heat stress during early growth reduces **leaf expansion, tillering, and root development**.
2. **Shortened vegetative phase** limits biomass accumulation and canopy

development, reducing potential grain yield.

2.3.2 Reproductive Stage (Flowering & Pollination)

Pollen viability and germination decline above **32°C**, leading to sterility.

Ovule abortion increases, reducing the number of fertilized spikelets.

Heat stress **reduces pollen tube growth**, causing incomplete fertilization and lower grain number.

2.3.3 Grain Filling Stage

1. **Shortened grain filling duration** reduces grain size and weight.
2. **Enzyme activities (starch synthase, sucrose synthase)** involved in starch accumulation decline, resulting in **shrivelled grains**.
3. High temperatures increase **respiration rates**, leading to **depleted carbohydrate reserves** and lower grain yield.

3. Impact of Heat Stress on Photosynthesis

Photosynthesis is highly sensitive to temperature fluctuations, and **heat stress disrupts chlorophyll content, enzyme activity, gas exchange, and oxidative balance**, reducing wheat productivity.

3.1 Effect on Chlorophyll Content and Photosynthetic Pigments

1. Heat stress accelerates **chlorophyll degradation**, reducing **light-harvesting capacity** and impairing photosynthetic efficiency.
2. Loss of **carotenoids** weakens photoprotection, leading to **photooxidative damage**.

3.2 Alterations in Photosynthetic Rate and CO_2 Assimilation

1. **RuBisCO activity declines** under high temperatures, reducing **CO_2 fixation and carbohydrate synthesis**.
2. Non-photochemical quenching (NPQ) increases to dissipate excess energy, **reducing quantum yield efficiency**.

3.3 Changes in Stomatal Conductance and Transpiration

1. Stomatal closure under heat stress limits **CO_2 influx**, reducing the **photosynthetic rate**.
2. Increased leaf temperature **accelerates transpiration**, causing **water loss and oxidative stress**.

3.4 Heat Stress-Induced Oxidative Stress and ROS Accumulation

1. Excess light energy leads to **ROS production**, causing **lipid peroxidation and membrane damage**.
2. Antioxidant enzymes (SOD, CAT, APX) play a crucial role in **mitigating ROS toxicity**.

4. Heat Stress and Yield Components in Wheat

4.1 Effect on Spikelet Fertility and Grain Number

1. High temperatures cause **pollen sterility** and **ovule abortion**, reducing **spikelet fertility**.
2. Flowering duration shortens, limiting the **opportunity for pollination and grain formation**.

4.2 Influence on Grain Filling Duration and Grain Weight

1. Heat stress reduces **grain-filling duration by 20-30%**, leading to smaller grain size.
2. Enzymatic activities involved in **starch accumulation** decline, causing **lightweight grains**.
3. **Premature senescence** reduces the supply of assimilates to developing grains.

4.3 Impact on Grain Protein Content and Quality

1. Heat stress **increases grain protein concentration** due to reduced starch deposition, but negatively affects **gluten strength and dough quality**.
2. High temperatures induce **protein aggregation**, affecting **bread-making quality**.
3. **Amylose and amylopectin ratios** change under heat stress, altering the texture and processing quality of wheat flour.

5. Molecular and Genetic Basis of Heat Tolerance

Heat tolerance in wheat is a complex trait regulated by **molecular chaperones, transcription factors, hormonal signaling, and genetic loci** associated with stress adaptation. Understanding these mechanisms is essential for breeding heat-resilient wheat varieties.

5.1 Heat Shock Proteins (HSPs) and Their Role in Thermotolerance

Heat shock proteins (**HSPs**) are **molecular chaperones** that protect cellular proteins from heat-induced denaturation. These proteins assist in:

1. **Protein refolding** – Preventing aggregation and misfolding of proteins under heat stress.
2. **Stabilizing membranes and organelles** – Maintaining the structural integrity of the chloroplast, mitochondria, and plasma membrane.
3. **Regulating heat stress response** – Interacting with heat stress transcription factors (**HSFs**) to activate protective gene expression.

HSPs are classified into several families based on molecular weight:

1. **HSP100**: Functions in disaggregating denatured proteins.
2. **HSP90**: Essential for protein stabilization and signal transduction.

3. **HSP70**: Assists in folding newly synthesized proteins.
4. **HSP60**: Involved in protein folding inside mitochondria and chloroplasts.
5. **Small HSPs (sHSPs)**: Protects photosynthetic machinery and prevents oxidative damage.

Studies show that overexpression of **TaHSP17** in wheat enhances heat tolerance by **preventing protein denaturation and reducing oxidative stress**.

5.2 Transcription Factors Involved in Heat Stress Response

Transcription factors (**TFs**) regulate gene expression in response to heat stress by activating stress-responsive genes. Some of the key TF families include:

5.2.1 Heat Shock Factors (HSFs)

1. HSFs act as **master regulators** of heat stress response.
2. They bind to **heat shock elements (HSEs)** in the promoter regions of heat-responsive genes, inducing HSP expression.
3. Examples: **TaHSFA1 and TaHSFA6** in wheat enhance thermotolerance.

5.2.2 Dehydration-Responsive Element Binding (DREB) Factors

1. **DREB2A and DREB2B** play crucial roles in **ABA-independent heat stress response**.
2. These TFs activate downstream genes involved in **osmoprotection, ROS detoxification, and cell membrane stability**.

5.2.3 NAC Transcription Factors

1. NAC TFs regulate **senescence, antioxidant defense, and osmotic balance** under heat stress.
2. **TaNAC2 and TaNAC67** improve thermotolerance by enhancing **antioxidant enzyme activity**.

5.2.4 MYB and WRKY Transcription Factors

1. **TaMYB80** enhances **thermotolerance and pollen viability** under heat stress.
2. WRKY TFs (e.g., **TaWRKY33**) help in **ROS scavenging and hormone signaling**.

5.3 Role of Hormonal Signaling in Heat Stress Response

Plant hormones act as **chemical messengers** in modulating heat stress tolerance. The major hormones involved include:

5.3.1 Abscisic Acid (ABA)

1. ABA plays a critical role in **stomatal regulation** and **drought tolerance** under heat stress.
2. Under high temperatures, ABA levels increase, leading to **stomatal closure**, which **reduces transpiration and water loss** but also limits CO_2 uptake.

3. Exogenous application of ABA enhances **membrane stability and antioxidant defense**.

5.3.2 Ethylene (ET)

1. High temperatures induce ethylene biosynthesis, triggering **leaf senescence and grain abortion**.
2. Ethylene-responsive TFs (**ERFs**) regulate **ROS detoxification and protein stability**.

5.3.3 Cytokinins (CKs)

1. Cytokinins **delay senescence and improve heat stress tolerance** by maintaining chlorophyll content.
2. CK-overexpressing wheat lines exhibit **enhanced photosynthetic efficiency and grain filling** under high temperatures.

5.4 Genetic Variability and QTLs Associated with Heat Tolerance

Heat tolerance is a **polygenic trait** governed by **quantitative trait loci (QTLs)** distributed across the wheat genome.

- Several **major QTLs** have been mapped for **canopy temperature (CT), chlorophyll retention (stay-green trait), and grain filling duration** under heat stress.
- Key QTLs include:

a. **Qhtp.tamu-2B**: Associated with grain yield under heat stress.

b. **Qctd.tamu-5A**: Controls canopy temperature depression (CTD), a heat tolerance indicator.

c. **qHT-7D**: Regulates heat-induced chlorophyll degradation.

Marker-assisted selection (MAS) and genomic selection (GS) are increasingly used to **integrate these QTLs into elite wheat varieties** for improved thermotolerance.

6. Strategies for Mitigating Heat Stress in Wheat

6.1 Conventional Breeding Approaches for Heat Tolerance

1. Selection of **heat-tolerant landraces and wild relatives** to introgress adaptive traits.
2. Hybridization and **recurrent selection** to improve yield stability under high temperatures.
3. Phenotypic selection for **stay-green trait, canopy temperature depression, and pollen viability**.

6.2 Marker-Assisted Selection (MAS) and Genomic Selection (GS)

1. MAS accelerates breeding by using **DNA markers linked to heat tolerance QTLs**.
2. Genomic selection utilizes **high-throughput genotyping and machine learning** to predict heat-tolerant phenotypes.

6.3 Biotechnological Interventions: Transgenic and Gene Editing Approaches

1. **CRISPR-Cas9** is used to **knockout heat-sensitive genes** and improve thermotolerance.
2. Overexpression of **HSPs, DREB, and antioxidant enzymes** enhances wheat's ability to withstand heat stress.

6.4 Agronomic Management Practices

1. **Sowing time adjustment** to avoid peak heat stress during flowering and grain filling.
2. **Irrigation management** to mitigate soil moisture depletion.
3. **Mulching and conservation tillage** to retain soil moisture and reduce canopy temperature.

6.5 Use of Biostimulants and Plant Growth Regulators

1. **Salicylic acid and jasmonic acid** improve antioxidant defense.
2. **Silicon and proline applications** enhance heat tolerance by stabilizing membranes and proteins.

Conclusion

Heat stress poses a significant challenge to wheat production worldwide, particularly in the face of climate change. It disrupts key physiological processes, particularly photosynthesis, leading to reductions in grain yield and quality. The plant's response to heat stress is governed by a complex interplay of molecular chaperones, transcriptional regulators, and hormonal signaling networks. Advances in molecular breeding, including quantitative trait locus (QTL) mapping, genomic selection, and transgenic approaches, have provided valuable insights into heat tolerance mechanisms. Additionally, agronomic practices such as adjusted sowing times, irrigation management, and biostimulant applications offer immediate solutions to mitigate heat stress effects. However, developing truly climate-resilient wheat varieties requires an integrative approach that combines **phenomics, genomics, and AI-driven predictive models**. Collaborative efforts among researchers, breeders, policymakers, and farmers are essential to ensure sustainable wheat production under rising global temperatures. Future research should prioritize **high-throughput phenotyping, genome-wide association studies (GWAS), and precision agriculture technologies** to accelerate the breeding of heat-tolerant wheat.

References

1. Asseng, S., et al. (2015). Rising temperatures reduce global wheat production. *Nature Climate Change*, 5(2), 143-147. https://doi.org/10.1038/nclimate2470

2. Barakat, M. N., et al. (2015). Role of heat shock proteins in thermotolerance. *Plant Molecular Biology Reporter*, 33(1), 110-122. https://doi.org/10.1007/s11105-014-0734-y
3. Bita, C. E., & Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science*, 4, 273. https://doi.org/10.3389/fpls.2013.00273
4. Fahad, S., et al. (2017). Crop responses to heat stress: physiology and management strategies. *Sustainability*, 9(7), 1340. https://doi.org/10.3390/su9071340
5. Farooq, M., et al. (2011). Heat stress in wheat during reproductive and grain-filling phases. *Functional Plant Biology*, 38(7), 707-719. https://doi.org/10.1071/FP11045
6. Hasanuzzaman, M., et al. (2013). Mechanisms of heat stress tolerance in plants: an overview. *Plant Physiology and Biochemistry*, 61, 185-195. https://doi.org/10.1016/j.plaphy.2012.10.002
7. Jagadish, S. V. K., et al. (2015). Impacts of climate change on wheat and adaptive strategies. *Advances in Agronomy*, 138, 171-212. https://doi.org/10.1016/bs.agron.2015.03.005
8. Lesk, C., et al. (2016). Influence of extreme weather disasters on global crop production. *Nature*, 529(7584), 84-87. https://doi.org/10.1038/nature16467
9. Lobell, D. B., et al. (2012). The critical role of extreme heat for maize production in the United States. *Nature Climate Change*, 2(3), 214-218. https://doi.org/10.1038/nclimate1362
10. Mittler, R., et al. (2012). ROS signaling: the new wave? *Trends in Plant Science*, 17(6), 369-380. https://doi.org/10.1016/j.tplants.2012.02.008
11. Niu, Y., et al. (2018). Regulation of stomatal closure by ABA in response to heat stress. *Plant Cell Reports*, 37(3), 389-400. https://doi.org/10.1007/s00299-018-2231-8
12. Prasad, P. V., et al. (2017). Effects of high temperature stress on wheat growth and yield. *Advances in Agronomy*, 153, 97-152. https://doi.org/10.1016/bs.agron.2017.12.005

13. Rezaei, E. E., et al. (2019). Climate change impact on wheat phenology and yield. *Field Crops Research*, 235, 219-230. https://doi.org/10.1016/j.fcr.2019.03.018
14. Sharma, D. K., et al. (2015). Plant stress and photosynthesis. *Journal of Experimental Botany*, 66(7), 1835-1842. https://doi.org/10.1093/jxb/eru463
15. Tiwari, S., et al. (2020). Advances in wheat genomics and molecular breeding for heat stress tolerance. *Frontiers in Genetics*, 11, 586534. https://doi.org/10.3389/fgene.2020.586534
16. Tricker, P. J., et al. (2018). Genomic selection for heat stress tolerance in wheat. *Theoretical and Applied Genetics*, 131, 2413-2428. https://doi.org/10.1007/s00122-018-3163-5
17. Wahid, A., et al. (2007). Heat tolerance in plants: an overview. *Environmental and Experimental Botany*, 61(3), 199-223. https://doi.org/10.1016/j.envexpbot.2007.05.011
18. Wahid, A., et al. (2018). Genotypic variability in wheat for heat tolerance and its physiological mechanisms. *Crop Science*, 58(2), 405-416. https://doi.org/10.2135/cropsci2017.10.0585
19. Zandalinas, S. I., et al. (2018). Plant responses to climate change: metabolic changes under heat stress. *Plant Physiology and Biochemistry*, 123, 72-81. https://doi.org/10.1016/j.plaphy.2017.10.019
20. Zinta, G., et al. (2016). Physiological and molecular responses of wheat under heat stress. *Functional Plant Biology*, 43(2), 108-120. https://doi.org/10.1071/FP15218