



Impacts and Mitigation Strategies of Terminal Heat Stress in Wheat: A Systematic Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Heat stress is a major abiotic limitation in semi-arid and subtropical climates. It causes significant production losses for wheat, a major grain crop, of about 6% for every °C that temperatures rise. Terminal heat stress is a major cause of decreased productivity when the grain-filling phase averages over 31°C. Low wheat yields are caused by excessive temperatures at this important development stage. In recent seasons, typical March and April temperatures were 2-3°C higher than normal, worsening terminal heat stress. Wheat yields dropped two to three quintals per acre. These years' rapid spike in North-West India's maximum and minimum temperatures reduced crop productivity by

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departures in March and April. This caused an early wheat harvest. Last several seasons, when March and April averaged 2-3 degrees hotter, indoor heat was worse. This reduced production by 2–3 quintals per acre. India has to stop wheat exports. Simply put, 4–6 quintals of wheat grain per acre have been lost. Many experts predict that without heat control, wheat yields will drop 16.10% and 11.10% in 2022 and 2050.

3. PLANT MECHANISMS TO COPE WITH TERMINAL HEAT STRESS

Heat tolerance, a vital adaptive trait in wheat, enables survival under high temperatures through mechanisms such as evasion, avoidance, and sustained greenness (Wahid et al., 2007; Nesar et al., 2022). Different effects of high temperature stress on rice and wheat grain development provide information about the mechanisms behind cereal heat tolerance (Impa et al., 2021). Plants withstand severe temperatures by shortening growth and filling phases and using stem reserves to boost growth and production. During heat stress, catalase and peroxidase enzyme activity correlates with grain yield. Peroxidase activity and zinc levels increased under heat stress, indicating thermo-tolerance (Narendra et al., 2021). The aleurone-to-endosperm ratio may change due to heat stress-induced grain size reduction due to zinc

concentration. Unlike optimal conditions, heat stress does not change grain iron content (Narendra et al., 2021). Plants can reduce heat stress by maintaining optimal hydration and minimising water loss through stomatal closure, trichome presence, leaf wax, leaf rolling, leaf angle changes, and leaf senescence. Plants use water more efficiently by enhancing root development and architecture. Plants can tolerate water stress by maintaining a low water potential, keeping their canopies cooler, maintaining an active photosynthetic state to support the current assimilate supply, increasing radiation efficiency, and extending growth and filling duration. Other names for this include "stay green" plant habit. Heat-sensitive genotypes decreased under stress, but heat-tolerant genotypes maintained their phenological, physiological, and biochemical balance (Kumar et al., 2023). The best phenological parameters for seed yield were days to maturity ($R^2 = 0.52$) and biological yield ($R^2 = 0.44$), demonstrating that biomass and crop duration were responsible for heat stress yield advantages. Genotypes that could handle heat better showed better assimilation, remobilization after terminal heat stress, delayed senescence, and more photosynthesis during grain filling. Heat stress causes developing wheat grains to make more ethylene, which leads to grain abortion and faster maturity in susceptible cultivars (Hays et al., 2007).

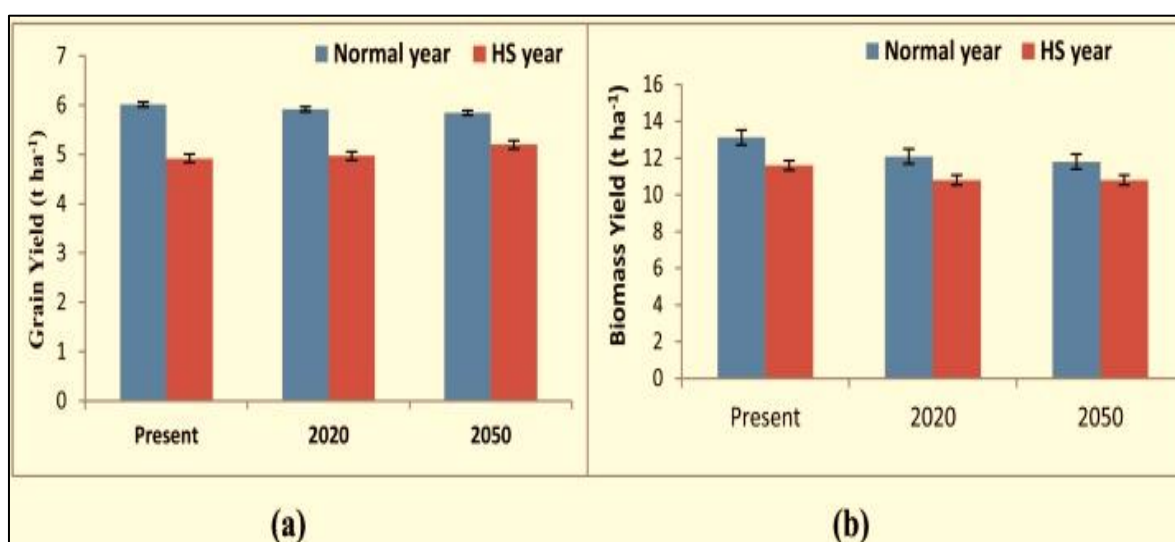


Fig. 2. Effect of terminal heat stress on wheat crop grain and biomass yield in India during a typical and favourable planting season (Dubey et al., 2020)

4. TERMINAL HEAT STRESS EFFECTS ON WHEAT

4.1 Wheat Growth and Yield

Terminal heat stress reduces wheat yield by shrinking cells, lowering internode width, biomass, and productive tiller survival, while accelerating senescence and increasing unproductive tillers (Kaur et al., 2017). Studies indicate that genotype, agronomic practices, and temperature influence the development and maintenance of wheat's PT (Pratap et al., 2025). Heat stress makes it hard for wheat to make PT and stay alive (Hasanuzzaman et al., 2013). Low soil temperatures in subtropical areas make it harder for late-planted spring wheat to germinate, produce PT, and develop early stands (Hakim et al., 2012; Hossain et al., 2013). Wheat respiration speeds up when temperatures are high during the day and at night. This shortens growth and makes spikelets with empty grains, which lowers yield. Heat stress affects the size and number of grains in different ways as they grow (Han et al., 2025). Heat stress has an impact on pollination, fertilization, and the start of spikelet growth in both males and females. Heat stress accelerates sporogenesis and spikelet initiation, causing sterile spikelets (Porter and Gawith, 1999). Heat stress ($>20^{\circ}\text{C}$) during heading and anthesis increases spike growth but decreases spikelet count (Miroslavljević et al., 2024). Heat stress during floral initiation causes complete sterility by interfering with the development of microspores and pollen cells (Anjum et al., 2008; Kaur & Behl, 2010), whereas three days of heat stress during flowering in wheat produces architecturally deformed or non-functional florets (Hedhly et al., 2009). Heat stress at $31/20^{\circ}\text{C}$ (day/night) reduces grain size by altering endosperm cell and aleurone layer architecture (Singh et al., 2024). Low assimilates availability limits photosynthetic during heat stress floret growth, limiting grain number (Shah et al., 2017). Heat stress produced aberrant anther growth and pollen viability, resulting in poor fertilisation and grain formation (Shrestha et al., 2022; Table 1). Post-fertilization grain filling is the final stage of cereal growth, and its duration and rate determine grain weight, which is the key factor impacting yield (Baillot et al., 2018). GF, which coincides with whole-plant senescence, synthesises 40% of grain dry matter from stem and sheath photo-assimilates (Yang et al., 2004).

Heat stress during GF accelerates maturity, induces early senescence, shortens grain filling duration, and reduces grain weight, which lowers grain yield (Kumar et al., 2023; Hasanuzzaman et al., 2013; Modhej et al., 2012; Bala et al., 2014). Heat stress reduces endosperm cells early in GF, and starch production stops due to insufficient photoassimilates or grain starch biosynthetic enzyme inactivation (Yin et al., 2009). Heat stress shortens wheat's life cycle because it finishes faster (Nahar et al., 2010; Alam et al., 2014; Alam et al., 2013). Prolonged suboptimal temperatures during grain filling (GF) dramatically reduce grain fill time with only a minor increase in filling rate (Sarkar et al., 2021). Grain filling duration (GFD) is three weeks shorter at $37/28^{\circ}\text{C}$ (Hurkman et al., 2003). GFD shortens and grain filling speeds up when the temperature rises above 20°C (Dias et al., 2008). When grains are exposed to heat during GF, their growth stops and their physiological maturity speeds up. For every degree Celsius above the best growing temperature of $15\text{--}20^{\circ}\text{C}$, GFD goes down by 2.8 days (Girousse, 2023; Table 1). A 5°C increase above optimal diminishes wheat GFD by 12 days (Yin et al., 2009). (Bala et al., 2014) observed that GFD falls by 0.4 days per 1°C mean temperature increases from optimal. Heat stress can reduce GFD by 3–12 days, reducing average grain weight (GW) by 36% (Vignjevic et al., 2015). Heat stress increases GF growth, but it doesn't make up for the lower GFD (Singh et al., 2021). The GF rate and duration of heat-tolerant and heat-sensitive wheat cultivars (Wardlaw and Moncur, 1995). During heat stress, tolerance cultivars have a high GF rate that makes up for the low GFD. Accelerated GF with decreased GFD might make it easier to handle heat stress. When the temperature goes up from $20/16^{\circ}\text{C}$ (day/night) to $36/31^{\circ}\text{C}$ (74), grain weight can drop by 85% from 7 days after anthesis (DPA) to maturity. Heat stress during grain filling causes winter wheat grain yield, grain number, and grain weight to drop by 78%, 63%, and 29%, respectively. Heat stress 20 days after anthesis reduces GW by 18% (Schittenhelm et al., 2020; Table 1). Late planting shortens growth, lowering yield and yield components (Din and Singh, 2005). Delaying sowing reduced GW by 33% due to heat stress (Siddique et al., 2025) reported terminal heat stress-induced grain shrinkage (Dias et al., 2008). Post-anthesis heat stress increases wheat protein and lowers glutenin/gliadin ratio, reducing flour quality (Singh et al., 2023). Late sowing reduced spike length, number of grains per spike, thousand-grain

Table 1. Effect of terminal heat stress on wheat land productivity

Sr. No.	Country	Soil Type	Agroclimatic conditions	Wheat crop productivity	References
1.	India	-	High temperature, frequent droughts, and unpredictable precipitation,	Chlorophyll and NDVI consistently increased grain production during grain filling under heat stress.	Kumar et al., 2023
2.	USA	-	Daytime maximum and minimum temperatures are 24 and 14°C, 14 h photoperiod, and ~ 70% relative humidity	Grain yield was 29 and 44% lower than the control due to significant temperature stress at the anthesis or grain-filling stage.	Djanaguiraman et al., 2020
3.	India	-	-	Terminal heat stress reduced wheat yield by 18.1%, 16.1%, and 11.1% in current, 2020, and 2050 simulations.	Dubey et al., 2020
4.	India	Loamy sand	-	Maximum wheat grain yield of 6.2 t ha ⁻¹ was recorded under ambient conditions which was 35% more than grain yield recorded under heat stress conditions.	Kaur et al., 2017
5.	India	-	-	Day (35/17°C) and day–night (35/24°C) heat stress reduces grain-filling time from 35 to 28 and 25 days, respectively.	Chunduri et al., (2021)
6.	Australia	-	-	Since anthesis and grain filling are best at 12–22°C, temperatures exceeding 30°C reduce wheat productivity.	Farooq et al., (2011)
7.	Brazil	-	-	Every degree Celsius above 15–20 degrees decrease grain weight by 1.5 milligrams per day.	Streck, 2005
8.	The Netherlands	-	-	Higher temperatures above 20°C enhanced wheat grain filling rate and reduced grain filling time by 12 days.	Yin et al., 2009
9.	Pakistan	Loamy	-	Heat treatment reduced wheat production by 53% from heading to maturity on 108 genotypes.	Qaseem et al., 2019
10.	India	-	-	The wheat crop lasts seven days less and yields 400 kg per hectare more when the mean temperature rises 1° Celsius in March and April.	Singh et al., 2011
11.	Japan	-	-	As temperatures rose over 21/16 °C, wheat grain weight at maturity dropped by about 5% every degree Celsius up to 30/25 °C.	Tashiro and Wardlaw, 1989

Table 2. Effect of terminal heat stress on wheat crop physiology

S.No.	Country/Region	Soil type	Agro-climatic conditions	Wheat crop physiology	References
1.	India (field screening / controlled)	Varied (field soils / pots)	Late sowing / controlled heat treatments during reproductive stage	Shortened grain-filling, reduced photosynthesis, induced antioxidant enzyme activity in tolerant lines	Kumar et al., 2023
2.	USA (growth-chamber)	Metro Mix 200 (potting mix)	Controlled chamber 36Å°C day / 30Å°C night applied 10 d after anthesis (high RH)	Reduced chlorophyll retention, decreased single-seed weight; genotypic differences in chlorophyll retention and seed weight	Fu et al., 2023
3.	Pakistan (Punjab)	Loam / typical Punjab field soils	Late sowing to expose reproductive stage to high temperatures	Reduced plant height, grains/spike, 1000-grain weight; lowered stomatal conductance; accelerated senescence	Rehman et al., 2021
4.	Serbia (Pannonian Plain)	Local arable loams	Field heat at anthesis and mid-grain filling; single and combined heat treatments	Increased leaf temperature, decreased SPAD and Fv/Fm; major reductions in grain yield and weight	Mirosavljević et al., 2024
5.	USA / multi-country genebank lines (greenhouse/chambers)	Pots (growth media)	16 d heat pulse after anthesis under controlled temps	Chlorophyll retention correlated with seed weight; evidence for tolerance mechanisms	Fu et al., 2023
6.	Australia / USA / Serbia (multi-site)	Potting mix / controlled soil mixes	Controlled environment screening for terminal heat tolerance	Genetic variation for chlorophyll retention, seed weight, shoot dry matter under heat	Fu et al., 2023
7.	India (multiple trials)	Alfisols / Vertisols (reported across trials)	Late-sown wheat to induce terminal heat in north-west India (semi-arid to sub-humid)	Reduced grain filling duration, lower photosynthetic rate, faster senescence, increased oxidative stress	Djanaguiraman et al., 2020
8.	Croatia / Pannonian region	Arable loams	Field heat at anthesis and/or mid-filling	Decreased Fv/Fm and chlorophyll indices; large yield penalties	Mirosavljević et al., 2024
9.	Spain / Mediterranean examples (reviewed)	Mediterranean loams / calcareous soils	Hot dry spells during grain filling (Mediterranean climate)	Accelerated senescence, reduced endosperm cell number, lower starch deposition and grain quality	Yadav et al., 2022
10.	China (controlled & field reports)	Various field soils per study	High daytime temperatures during grain filling; varying RH	Disruption of carbon assimilation and transport; reduced starch deposition and grain quality	Ullah et al., 2022
11.	USA (hard-winter wheat chambers)	Potting soil / experimental media	Short high-temperature pulses during grain fill imposed in chambers	Reduced photosynthetic capacity, accelerated leaf senescence, lower seed weight; traits linked to tolerance	Fu et al., 2023
12.	Multi-location field screenings (Pakistan/India)	Loam to sandy-loam	Late sowing / natural heat episodes during reproductive stage	Decreased stomatal conductance and photosynthesis; lower thousand-grain weight and grains per spike	Rehman et al., 2021

S.No.	Country/Region	Soil type	Agro-climatic conditions	Wheat crop physiology	References
13.	Durum wheat experiments (various)	Potting mix / experimental soil	Heat stress during grain filling in controlled experiments	Reduced spike fertility, lower photosynthetic rate, decreased spikelet fertility and grain number/weight	Mirosavljević et al., 2024
14.	Global (meta-analysis / review)	Variable across studies	Heat episodes during anthesis and grain fill across climates	Faster but shorter grain-filling rate, reduced kernel weight, pollen sterility, reduced harvest index	Yadav et al., 2022
15.	Serbia / Eastern Europe	Local arable loams	Field heat imposed at anthesis and mid-filling	Genotypic differences in leaf temperature, SPAD, Fv/Fm; some varieties maintain CI and yield	Mirosavljević et al., 2024
16.	Pakistan (breeding trials)	Agricultural loams / irrigated soils	Terminal heat by late sowing / hot spells	Negative impacts on vegetative growth and flowering; reduced grain number and weight; physio-traits for selection identified	Khan et al., 2021
17.	USA (greenhouse spectral phenotyping)	Growth media (pots)	Spectral phenotyping under controlled terminal heat	Spectral features identify heat-tolerant phenotypes; linked to maintained photosynthesis and yield	Sherstneva et al., 2024
18.	India (agronomic intervention trials)	Vertisols / Alfisols (region-specific)	Late sowing / heat episodes; trials of agronomic mitigation practices	Heat reduced assimilation and yield; mitigation (sowing timing, irrigation) improved canopy cooling and delayed senescence	Dhakar et al., 2023
19.	Experimental physiological studies (various)	Pot media or field soils (as reported)	Controlled pulses at anthesis or mid-filling	Reduced photosynthetic rate (A), higher leaf temperature, reduced Fv/Fm, increased ROS; tolerant lines show osmolyte responses	Djanaguiraman et al., 2020
20.	Global breeding/screening studies (multi-region)	Variable (field soils/pots)	--	Terminal heat shortens grain filling, reduces photosynthesis, accelerates senescence; breeding targets include stay-green and remobilization	Fu et al., 2023

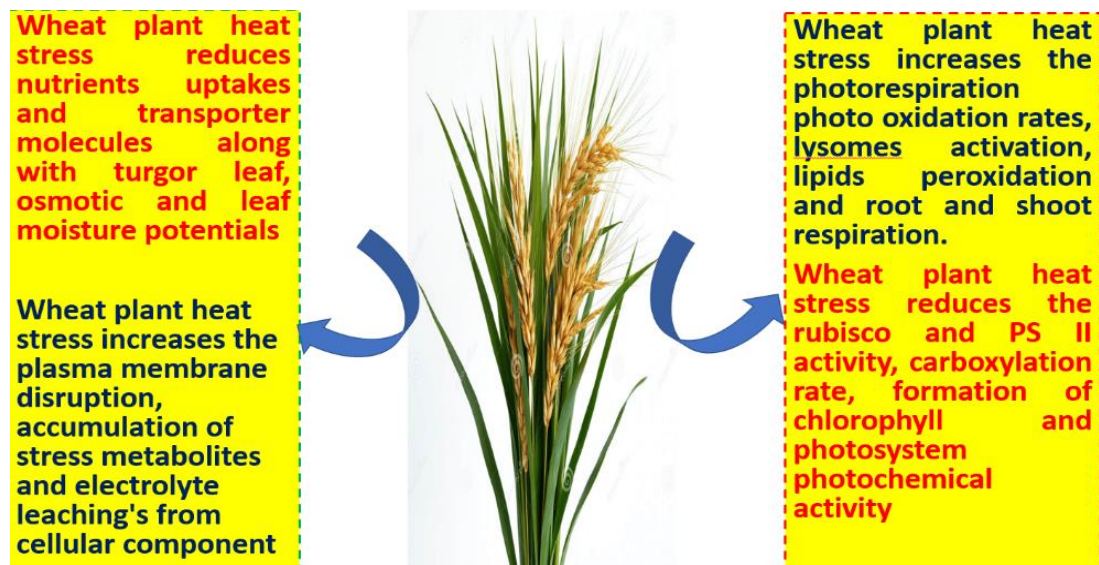


Fig. 3. Effects of heat stress on physiological and biochemical processes in wheat plant

weight, and biological yield relative to timely sowing, but the response varied by sowing condition (Rehman et al., 2021).

4.2 Crop Physiology

Later in the growth of wheat, terminal heat stress is very bad. Showed how terminal heat stress lowers yield by changing things like senescence, assimilate partitioning, heat dissipation, electrolyte conductivity, photosynthesis, and plant water status (Hasanuzzaman et al., 2013; Table 2). Heat stress at any growth stage reduces cell size and growth by reducing cell water content (Mondal et al., 2023). High evaporative demand reduces relative water content (RWC) during heat stress (Hall, 2000), speeding senescence-related

metabolic changes. Due to poor assimilate partitioning, harvest index (Wahid et al., 2007) yields (Ahmad et al., 2010a) are considerably lowered. During anthesis, temperatures shouldn't rise above 31°C to maintain plant hydration (Akter & Islam 2017). Heat stress-induced dehydration lowers osmotic potential (Ahmad et al., 2010b) and increases plasma membrane water conductivity due to aquaporin activity (Martínez-Ballesta et al., 2009). Heat stress reduces membrane stability, which impairs assimilate transport (Taiz and Zeiger, 2006; Wahid et al., 2007; Farooq et al., 2011). Heat stress causes membrane breakdown and increases EC (Hemantaranjan et al., 2014). Heat stress worsens wheat cell viability, electrolyte leakage, and membrane thermostability by 54%

(Savicka & Škute, 2010). Transpiration, stomatal conductance, and leaf RWC depend on canopy temperature (CT) (Ferris et al., 1998; Table 2). Heat stress increases CT, lowers plant hydration status, and reduces greenness (Shelake et al., 2024; Lopes and Reynolds, 2012). Wheat's thylakoid lamellae and chloroplast stroma are most affected by heat stress during photosynthesis (Zahra et al., 2023; Mathur et al., 2014). Deactivating stromal enzymes disrupts the photorespiratory electron transport cycle, slowing leaf photosynthesis and Rubisco activity (Hasanuzzaman et al., 2013; Scafaro et al., 2023). Temperatures above 40 °C damage Rubisco, Rubisco activase, and photosystem II in wheat leaves, with heat stress-induced dissociation of Rubisco activase further lowering photosynthetic efficiency (Perdomo et al., 2017). Heat stress increases respiration and mitochondrial activity. Photorespiratory injury decreases respiration once temperature increases it to a threshold point (Prasad et al., 2008). Due to photorespiration-induced carbon loss, the rhizosphere produces more ROS and less ATP (Huang et al., 2012). Heat stress greatly enhances wheat flag leaf photorespiration due to O₂ and CO₂ solubility variations and Rubisco's affinity for these gases (Kayess et al., 2024). Heat induces chloroplast death, vacuolar collapse, and plasma membrane integrity and cellular homeostasis failure, which accelerates leaf senescence (Akter & Islam, 2017; Table 2). Extreme heat stress can quickly denature or aggregate plant proteins, while chronic or moderate heat stress induces progressive senescence. Either situation can reduce plant

development or harm it (Rodríguez et al., 2005; Hasanuzzaman et al., 2013). A comprehensive field guide on wheat phenotyping, offering practical methodologies for assessing physiological traits critical to breeding for improved yield and stress adaptation (Pask et al., 2012).

5. MITIGATION STRATEGIES

Heat stress, particularly terminal heat stress intensified by climate change, severely affects wheat growth and has driven efforts to develop heat-tolerant genotypes (Fig. 4) (Dubey et al., 2020). To grow wheat in areas that are affected by heat, you need both heat-tolerant varieties and farming methods that lower heat stress (Chapman et al., 2012; Akter and Islam, 2017). Some ways to lessen the effects of terminal heat stress on wheat are to use climate-resilient cropping methods, push for climate-resilient policies, practice conservation agriculture, use water more efficiently, and change the dates for planting.

5.1 Mitigation by Chemicals

Chemical spray can reduce terminal heat stress. Foliar treatments using potassium nitrate, salicylic acid, thiourea, and sodium nitroprusside have enhanced wheat yields under suboptimal conditions (Suryavanshi and Buttar, 2016). Two sprays of 2% potassium nitrate (13:0:45) during boot leaf and anthesis can help with terminal heat stress and boost grain output. Salicylic acid

lowers the temperature of grain filling and increases wheat output when sprayed twice per acre at the boot leaf and early milk stages (15 g diluted in 450 ml of ethyl alcohol and 200 liters of water per acre). Calcium, in the form of CaCl_2 , makes it easier to handle heat. Malondialdehyde (MDA), a marker of lipid peroxidation, rises and activates catalase and superoxide dismutase. These metabolic changes boost wheat production and heat tolerance (Ali et al., 2024). Sprinkling potassium chloride may avoid a March temperature spike. Spray each acre with a solution of 200 grammes of potassium chloride and 100 litres of water. This technique should be repeated after 15 days if severe. Without potassium chloride, dissolving 200 grammes of red medicine or muriate of potash in 100 litres of water and spraying it twice at 15-day intervals works just as well. Zinc (Zn) boosts the plant's antioxidant mechanisms to regulate free radicals and reduce their negative effects during stress (Kavian et al., 2022). Silicon supports heat and drought-stressed plants' water balance, photosynthetic efficiency, leaf erectness, and xylem channel formation at high transpiration rates. Water stress increases wheat shoots and root biomass and grain productivity. (Singh et al., 2023). A study by (Kaur et al., 2017) found no effect from spraying wheat with water, salicylic acid, and calcium chloride after 108–114 days of heat stress. The duration, severity, and timing of heat stress may alter how effectively these treatments' function. Osmoprotectants, phytohormones, signalling molecules, and trace elements can be administered externally to help

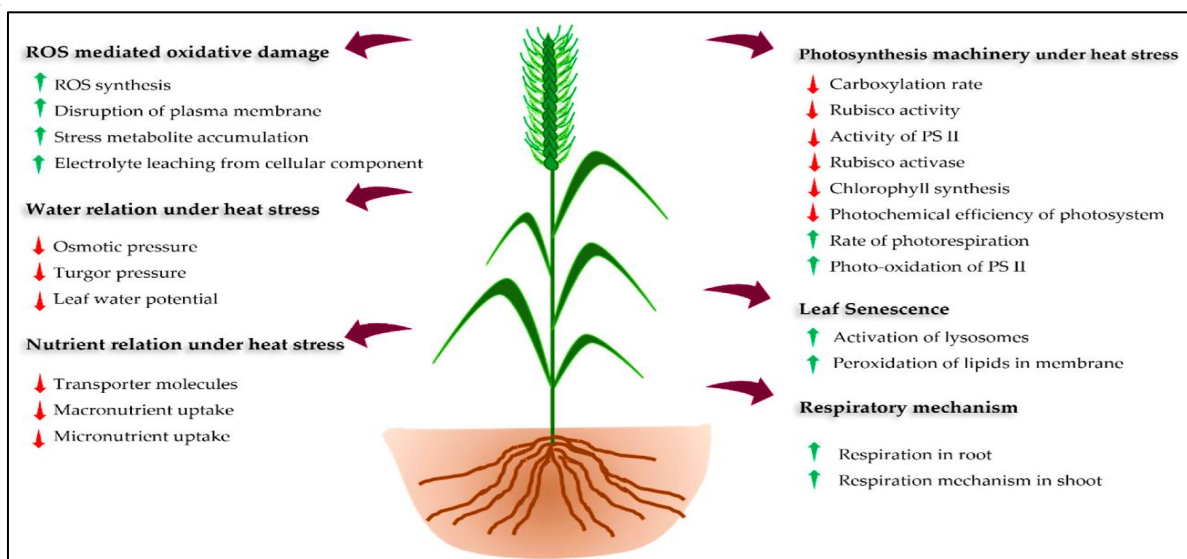


Fig. 4. A diagrammatic representation of the effects and reactions of plants to heat stress (Yadav et al., 2022)

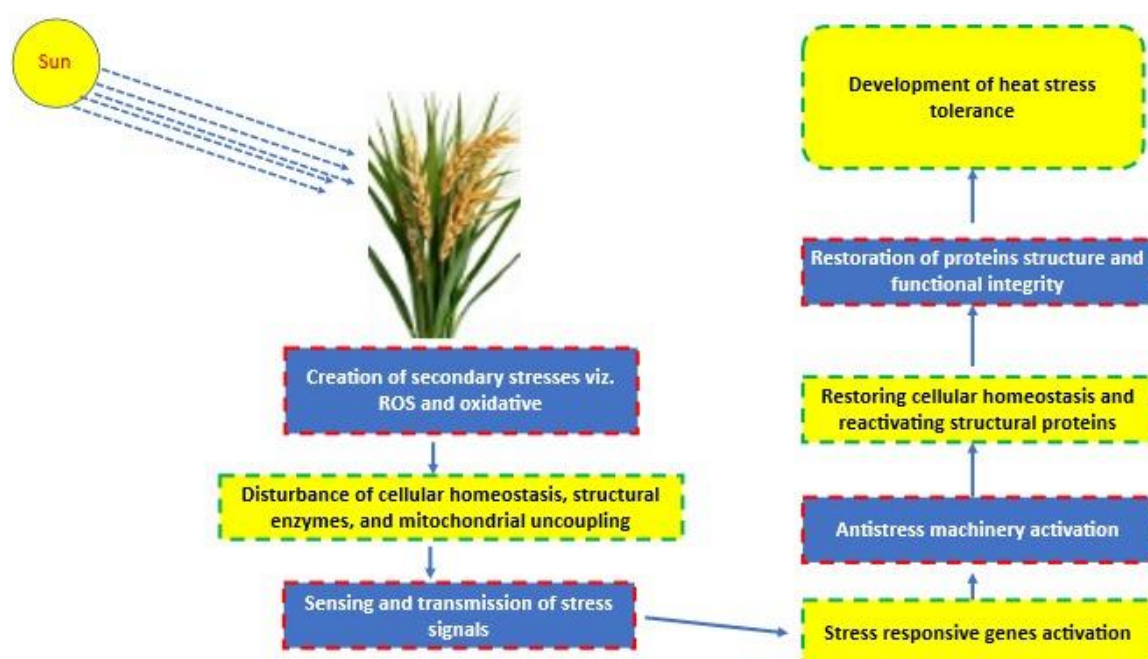


Fig. 5. Development of heat tolerance responses and mechanism under HS in wheat (Yadav et al., 2022)

plants resist heat stress. Studies suggest that plant bio-regulators enhance antioxidant defences (Sharma et al., 2012), reduce ROS (Upreti and Sharma, 2016), and promote thermo tolerance (Hemantaranjan et al., 2014), indicating their potential to improve wheat resilience against heat stress (Fig. 3 and 4) (Yadav et al., 2022; Ratnakumar et al., 2016).

5.2 Agronomic Measures

Adjusting planting dates, applying timely irrigation, and adding nitrogen fertilizer help reduce terminal heat stress, with early sowing boosting yields by allowing grain filling before high temperatures (Moghaddam et al., 2023). Early-sown crops avoid heat stress, but late-sown crops lose 20% more yield after 5–6 days of temperature rise (Kumar and Rai, 2014). Sowing wheat between October 25th and November 15th reduces terminal heat stress (Singh et al., 2023). Studies show that nitrogen fertiliser improves plant performance in high temperatures and water stress (Nunes et al., 1993).

However, (Dupont et al., 2006) found different results with 37/28 °C diurnal temperature fluctuation. The 24/17 °C temperature regime showed that nitrogen fertiliser after anthesis did not increase protein accumulation. This failure to increase protein levels under high temperatures caused early leaf senescence and lower grain

production. Life-saving irrigation during grain-filling reduces terminal heat stress yield loss (Sheng et al., 2022). Combining early sowing with timely irrigation (sprinkler, drip, or light watering during heat rise) and 30 kg ha⁻¹ nitrogen at grain filling enhances wheat yield and reduces heat stress better than individual practices (Singh et al., 2023). Water and nitrogen applied at the right time help convert absorbed starch into full grains, boosting the 1000-grain weight. Lowering the temperature of the canopy slows down leaf senescence and increases yield (Liu et al., 2024). In rice-wheat cropping systems like the Indo-Gangetic plains, early sowing may require changes to how crops are managed all year. If you can't clear the field on time, nitrogen fertilizer and irrigation can help you lose less yield and do better in the heat (Bhatt et al., 2021). These different strategies help wheat crops deal with stress from the environment and keep their yield. Straw mulch keeps the soil moist by stopping it from drying out (Chen et al., 2007). Keeping rice residue in an Indo-Gangetic Plains (IGP) rice-wheat system lowered wheat canopy temperature by 1–4°C from 138 to 153 days after sowing (DAS) (Singh et al., 2023). However, mulching is advised to prevent wheat yield loss when using low tillage (Głąb and Kulig, 2008). Studies like (Chakraborty et al., 2008) show that mulching wheat can boost output during heat stress and water shortages. Organic mulches save soil moisture and boost plant growth.

According to (Singh et al., 2011), this increases water and nitrogen use efficiency, potentially reducing. Conservation-based wheat cultivation saves time, labour, money, and other resources and prevents waterlogging during severe rains. Sow wheat with Happy Seeder, Super Seeder, or Smart Seeder after harvesting paddy to protect soil from the harsh sunlight as these interventions provides a mulch cover onto the soil surface (Bhatt et al., 2021). Through seed treatments or foliar applications of organic and inorganic substances, biocontrol agents, such as fungi (Raaijmakers et al., 2009) and plant growth-promoting rhizobacteria (Nain et al., 2010), increase wheat's resistance to heat (Yang & Zhang, 2006). According to research, inoculating wheat with plant growth-promoting rhizobacteria regularly reduces heat stress in an environmentally friendly way (Zhang et al., 2023).

6. OTHER STRATEGIES

6.1 Sowing Time

If you plant wheat at the correct time, it can withstand heat stress better. Avoid rice varieties that mature slowly because they make it difficult to sow wheat. To prevent the blossoms from becoming overheated, the seeds should be sown by October 25 and finished by November 15. Late sowing exacerbates the temperature stress, reducing grain production and quality. A higher yield is the consequence of early planting, which enhances tillering, plant height, and dry matter (Singh et al., 2023). Timely sowing is key for optimal growth under heat stress.

6.2 Irrigation Management

Transpiration is increased by high temperatures, and heat stress is exacerbated by water stress. Enough moisture is ensured by proper irrigation, which helps plants withstand high temperatures. Crops should be protected during grain development by irrigation through the end of March. On windy days, avoid irrigation to avoid lodging (Bhatt et al., 2021).

6.3 Tillage and Residue Management

Techniques used in conservation agriculture, such as mulching with rice residue, assist retain soil moisture and reduce canopy temperature. Mulching improves grain production and mitigates heat stress through transpiration cooling by lowering soil temperature and increasing water storage.

6.4 Adequate Nutrition

Under heat stress, efficient nutrient management—in particular, nitrogen optimization—helps maintain wheat output. Potassium controls nutrient transport and grain filling, phosphorus helps with grain size, and nitrogen promotes photosynthesis. Additionally, magnesium and zinc help wheat become more heat tolerant and decrease losses brought on by heat stress.

6.5 Osmoprotectants

Under heat stress, osmoprotectants such as calcium, salicylic acid, and potassium nitrate can increase wheat yield. In order to lessen the consequences of heat stress, potassium nitrate promotes photosynthesis, salicylic acid postpones senescence, and calcium sustains antioxidant activity (Singh et al., 2023). By maintaining membranes and enhancing water balance under stress, zinc and silicon provide additional protection for plants.

6.6 Microorganisms

By generating cytokines, antioxidants, and other substances that increase plant resilience, mycorrhizal fungi and plant-growth-promoting rhizobacteria (PGPR) assist plants in withstanding heat stress. These microbes aid in plants' ability to withstand extreme temperatures.

7. FUTURE SCOPE

Terminal heat stress on wheat, which lowers yields and grain quality, is becoming more common in Northwest India as grain-filling temperatures rise. Future research should integrate climate modelling, precision agriculture, and advanced breeding tools like genomics, transcriptomics, CRISPR, and marker-assisted selection to develop heat-resilient wheat cultivars. To further reduce stress, you can use climate-smart irrigation methods like deficit irrigation and alternate wetting and drying, as well as crop diversity and intercropping. Brassinosteroids and other plant growth regulators and biostimulants can help wheat resist heat better. To figure out the financial impact of terminal heat stress and to improve crop insurance plans and heat-resistant seed distribution, we need to look at the issue from a socioeconomic and policy point of view. It is important to get past the obstacles that stand in the way of climate-resilient technologies. AI-

based decision systems and IoT soil sensors can help with real-time monitoring and predictive management of heat stress in wheat. Carbon sequestration, agroforestry, and conservation agriculture are all examples of sustainable practices that can also make soil more resistant to heat stress. Another new area of study is how soil microbiomes and fungi that live on roots, like mycorrhizae, help plants take in more water and stay cool. Sustainable practices such as organic amendments and integrated nutrition management can enhance the terminal heat stress tolerance of wheat. To protect wheat production in Northwest India from climate change, we need a multidisciplinary, farmer-centered approach that includes genetic innovations, precision farming, climate adaptation, and policy support.

8. CONCLUSION

Environmental issues like terminal stress limit wheat productivity in most wheat-growing countries. A temperature spike ($>30^{\circ}\text{C}$) during anthesis and during grain development that impairs wheat grain filling is called "terminal heat stress." Although the reproductive stage is more sensitive, rising temperatures shorten the wheat crop's vegetative and reproductive stages. Several researchers have found that terminal heat stress affects wheat phenology and yield metrics in all major wheat-growing locations. To mitigate climate change, adaptation is essential. Heat-resistant wheat cultivars, sowing time, conservation agriculture (zero tillage, happy seeder, residue retention, mulching), altering sowing dates, and irrigation schedule management can reduce terminal heat stress on wheat. Osmoprotectants such potassium nitrate, salicylic acid, calcium chloride, zinc, and silicon mitigate terminal heat stress in wheat crops because they affect many physiological and biochemical processes.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declares that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could

have appeared to influence the work reported in this review paper.

REFERENCES

- Ahmad, A., Diwan, H., & Abrol, Y. P. (2010a). Global climate change, stress and plant productivity. In A. Pareek, S. K. Sopory, & G. H. J. Bohnert (Eds.), *Abiotic stress adaptation in plants: Physiological, molecular and genomic foundation* (pp. 503–521).
- Ahmad, P., Jaleel, C. A., Salem, M. A., Nabi, G., & Sharma, S. (2010b). Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. *Critical Reviews in Biotechnology*, 30(3), 161–175.
- Akter, N., & Rafiqul Islam, M. (2017). Heat stress effects and management in wheat: A review. *Agronomy for Sustainable Development*, 37, 37. <https://doi.org/10.1007/s13593-017-0443-9>
- Alam, M. N., Bodruzzaman, M., Hossain, M. M., & Sadekuzzaman, M. (2014). Growth performance of spring wheat under heat stress conditions. *International Journal of Agricultural Science*, 4(6), 91–103.
- Alam, M. N., Mannaf, M. A., Sarker, M. A. Z., & Akhter, M. M. (2013). Effect of terminal high temperature imposed by late sowing on phenological traits of wheat (*Triticum aestivum* L.). *International Journal of Agronomy and Agricultural Research*, 3(2), 6–10.
- Ali, Q., Sami, A., Haider, M. Z., Ashfaq, M., & Javed, M. A. (2024). Antioxidant production promotes defense mechanism and different gene expression levels in *Zea mays* under abiotic stress. *Scientific Reports*, 14(1), 7114. <https://doi.org/10.1038/s41598-024-57939-6>
- Anjum, F. A., Abdul Wahid, A. W., Farrukh Javed, F. J., & Muhammad Arshad, M. A. (2008). Influence of foliar applied thiourea on flag leaf gas exchange and yield parameters of bread wheat (*Triticum aestivum*) cultivars under salinity and heat stresses. *International Journal of Agriculture and Biology*, 10, 619–626.
- Baillet, N., Girousse, C., Allard, V., Piquet-Pissaloux, A., & Le Gouis, J. (2018). Different grain-filling rates explain grain-weight differences along the wheat ear. *PLoS One*, 13(12), e0209597. <https://doi.org/10.1371/journal.pone.0209597>

- Bala, S., Asthir, B., & Bains, N. S. (2014). Effect of terminal heat stress on yield and yield attributes of wheat. *Indian Journal of Applied Research*, 4(6), 1–2.
- Bhatt, R., Singh, P., Hossain, A., & Timsina, J. (2021). Rice–wheat system in the northwest Indo-Gangetic plains of South Asia: Issues and technological interventions for increasing productivity and sustainability. *Paddy and Water Environment*, 19(3), 345–365. <https://doi.org/10.1007/s10333-021-00846-7>
- Chakraborty, D., Nagarajan, S., Aggarwal, P., Gupta, V. K., Tomar, R. K., Garg, R. N., ... & Kalra, N. (2008). Effect of mulching on soil and plant water status, and the growth and yield of wheat (*Triticum aestivum* L.) in a semi-arid environment. *Agricultural Water Management*, 95(12), 1323–1334.
- Chapman, S. C., Chakraborty, S., Dreccer, M. F., & Howden, S. M. (2012). Plant adaptation to climate change—opportunities and priorities in breeding. *Crop and Pasture Science*, 63(3), 251–268.
- Chen, S. Y., Zhang, X. Y., Pei, D., Sun, H. Y., & Chen, S. L. (2007). Effects of straw mulching on soil temperature, evaporation and yield of winter wheat: Field experiments on the North China Plain. *Annals of Applied Biology*, 150(3), 261–268.
- Chunduri, V., Kaur, A., Kaur, S., Kumar, A., Sharma, S., Sharma, N., Singh, P., Kapoor, P., Kaur, S., Kumari, A., Roy, J., Kaur, J., & Garg, M. (2021). Gene expression and proteomics studies suggest an involvement of multiple pathways under day and day–night combined heat stresses during grain filling in wheat. *Frontiers in Plant Science*, 12, 660446. <https://doi.org/10.3389/fpls.2021.660446>
- Das, B., Kumar, S., Kasala, K., Nedumaran, S., Paithankar, P., Kumar, A., Jain, A., & Avinandan, V. (2025). Effects of climate change on food security and nutrition in India: A systematic review. *Current Research in Environmental Sustainability*, 9, 100286. <https://doi.org/10.1016/j.crsust.2025.100286>
- Dhakar, R., Nagar, S., Sehgal, V. K., Jha, P. K., Singh, M. P., Chakraborty, D., & Prasad, P. V. (2023). Balancing water and radiation productivity suggests a clue for improving yields in wheat under combined water deficit and terminal heat stress. *Frontiers in Plant Science*, 14, 1171479.
- Dias, A. S., Bagulho, A. S., & Lidon, F. C. (2008). Ultrastructure and biochemical traits of bread and durum wheat grains under heat stress. *Brazilian Journal of Plant Physiology*, 20, 323–333.
- Din, K., & Singh, R. M. (2005). Grain filling duration: An important trait in wheat improvement. *SAIC Newsletter*, 15(4), 4–5.
- Djanaguiraman, M., Narayanan, S., Erdayani, E., & Prasad, P. V. (2020). Effects of high temperature stress during anthesis and grain filling periods on photosynthesis, lipids and grain yield in wheat. *BMC Plant Biology*, 20(1), 268. <https://doi.org/10.1186/s12870-020-02479-0>
- Dubey, R., Pathak, H., Chakrabarti, B., Singh, S., Gupta, D. K., & Harit, R. C. (2020). Impact of terminal heat stress on wheat yield in India and options for adaptation. *Agricultural Systems*, 181, 102826. <https://doi.org/10.1016/j.agsy.2020.102826>
- Dupont, F. M., Hurkman, W. J., Vensel, W. H., Tanaka, C., Kothari, K. M., Chung, O. K., & Altenbach, S. B. (2006). Protein accumulation and composition in wheat grains: Effects of mineral nutrients and high temperature. *European Journal of Agronomy*, 25(2), 96–107.
- Farhad, M., Kumar, U., Tomar, V., Bhati, P. K., Krishnan, N. J., Mustarin, K.-E., Barek, V., Brestic, M., & Hossain, A. (2023). Heat stress in wheat: A global challenge to feed billions in the current era of the changing climate. *Frontiers in Sustainable Food Systems*. <https://doi.org/10.3389/fsufs.2023.1203721>
- Farooq, M., Bramley, H., Palta, J. A., & Siddique, K. H. (2011). Heat stress in wheat during reproductive and grain-filling phases. *Critical Reviews in Plant Sciences*, 30(6), 491–507. <https://doi.org/10.1080/07352689.2011.615687>
- Ferris, R., Ellis, R. H., Wheeler, T. R., & Hadley, P. (1998). Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. *Annals of Botany*, 82(5), 631–639.
- Fu, J., Bowden, R. L., Jagadish, S. K., & Prasad, P. V. (2023). Genetic variation for terminal heat stress tolerance in winter wheat. *Frontiers in Plant Science*, 14, 1132108. <https://doi.org/10.3389/fpls.2023.1132108>

- Girousse, C. (2023). Heat shock exposure during early wheat grain development can reduce maximum endosperm cell number but not necessarily final grain dry mass. *PLOS ONE*, 18(4), e0285218. <https://doi.org/10.1371/journal.pone.0285218>
- Głąb, T., & Kulig, B. (2008). Effect of mulch and tillage system on soil porosity under wheat (*Triticum aestivum*). *Soil and Tillage Research*, 99(2), 169–178.
- Hakim, M. A., Hossain, A., da Silva, J. A. T., Zvolinsky, V. P., & Khan, M. M. (2012). Protein and starch content of 20 wheat (*Triticum aestivum* L.) genotypes exposed to high temperature under late sowing conditions. *Journal of Scientific Research*, 4(2), 477–477.
- Hall, A. E. (2000). *Crop responses to environment*. CRC Press.
- Han, P., Wang, Y., & Sun, H. (2025). Impact of temperature stresses on wheat quality: A focus on starch and protein composition. *Foods*, 14(13), 2178. <https://doi.org/10.3390/foods14132178>
- Hasanuzzaman, M., Nahar, K., Alam, M. M., Roychowdhury, R., & Fujita, M. (2013). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International Journal of Molecular Sciences*, 14(5), 9643–9684.
- Hays, D. B., Do, J. H., Mason, R. E., Morgan, G., & Finlayson, S. A. (2007). Heat stress induced ethylene production in developing wheat grains induces kernel abortion and increased maturation in a susceptible cultivar. *Plant Science*, 172(6), 1113–1123.
- Hedhly, A., Hormaza, J. I., & Herrero, M. (2009). Global warming and sexual plant reproduction. *Trends in Plant Science*, 14(1), 30–36.
- Hemantaranjan, A., Nishant Bhanu, A., Singh, M. N., Yadav, D. K., Patel, P. K., Singh, R., & Katiyar, D. (2014). Heat stress responses and thermotolerance. *Advances in Plants and Agriculture Research*, 1(3), 00012.
- Hossain, A., Sarker, M. A. Z., Saifuzzaman, M., Teixeira da Silva, J. A., Lozovskaya, M. V., & Akhter, M. M. (2013). Evaluation of growth, yield, relative performance and heat susceptibility of eight wheat (*Triticum aestivum* L.) genotypes grown under heat stress. *International Journal of Plant Production*, 7(3), 615–636.
- Huang, B., Rachmilevitch, S., & Xu, J. (2012). Root carbon and protein metabolism associated with heat tolerance. *Journal of Experimental Botany*, 63(9), 3455–3465.
- Hurkman, W. J., McCue, K. F., Altenbach, S. B., Korn, A., Tanaka, C. K., Kothari, K. M., ... & DuPont, F. M. (2003). Effect of temperature on expression of genes encoding enzymes for starch biosynthesis in developing wheat endosperm. *Plant Science*, 164(5), 873–881.
- Impa, S. M., Raju, B., Hein, N. T., Sandhu, J., Prasad, P. V., Walia, H., & Jagadish, S. K. (2021). High night temperature effects on wheat and rice: Current status and way forward. *Plant, Cell & Environment*, 44(7), 2049–2065.
- Kaur, R., Kaur, S., & Sandhu, S. S. (2017). Effect of terminal heat stress in wheat and its management with chemicals in North-West India. *Agricultural Research Journal*, 54(1), 114–116. <https://doi.org/10.5958/2395-146X.2017.00020.5>
- Kaur, V., & Behl, R. (2010). Grain yield in wheat as affected by short periods of high temperature, drought and their interaction during pre-and post-anthesis stages. *Cereal Research Communications*, 38(4), 514–520.
- Kavian, S., Safarzadeh, S., & Yasrebi, J. (2022). Zinc improves growth and antioxidant enzyme activity in *Aloe vera* plant under salt stress. *South African Journal of Botany*, 147, 1221–1229. <https://doi.org/10.1016/j.sajb.2022.04.011>
- Kayess, M. O., Ashrafuzzaman, M., Khan, M. A. R., & Siddiqui, M. N. (2024). Functional phenomics and genomics: Unravelling heat stress responses in wheat. *Plant Stress*, 14, 100601. <https://doi.org/10.1016/j.stress.2024.100601>
- Khan, A., Ahmad, M., Ahmed, M., Gill, K. S., & Akram, Z. (2021). Association analysis for agronomic traits in wheat under terminal heat stress. *Saudi Journal of Biological Sciences*, 28(12), 7404–7415.
- Kumar, H., Chugh, V., Kumar, M., Gupta, V., Prasad, S., Kumar, S., Singh, C. M., Kumar, R., Singh, B. K., Panwar, G., & Kumar, M. (2023). Investigating the impact of terminal heat stress on contrasting wheat cultivars: A comprehensive analysis of phenological, physiological, and biochemical traits. *Frontiers in Plant Science*, 14, 1189005. <https://doi.org/10.3389/fpls.2023.1189005>
- Kumar, R. R., & Rai, R. D. (2014). Can wheat beat the heat: Understanding the

- mechanism of thermotolerance in wheat (*Triticum aestivum* L.) – A review. *Cereal Research Communications*, 42(1), 1–18.
- Kumar, S., Bhushan, B., Wakchaure, G. C., Dutta, R., Jat, B. S., Meena, K. K., Rakshit, S., & Pathak, H. (2023). Unveiling the impact of heat stress on seed biochemical composition of major cereal crops: Implications for crop resilience and nutritional value. *Plant Stress*, 9, 100183. <https://doi.org/10.1016/j.stress.2023.100183>
- Liu, J., Si, Z., Li, S., Wu, L., Zhang, Y., Wu, X., Cao, H., Gao, Y., & Duan, A. (2024). Effects of water and nitrogen rate on grain-filling characteristics under high-low seedbed cultivation in winter wheat. *Journal of Integrative Agriculture*, 23(12), 4018–4031. <https://doi.org/10.1016/j.jia.2023.12.002>
- Lopes, M. S., & Reynolds, M. P. (2012). Stay-green in spring wheat can be determined by spectral reflectance measurements (normalized difference vegetation index) independently from phenology. *Journal of Experimental Botany*, 63(10), 3789–3798.
- Martínez-Ballesta, M. C., López-Pérez, L., Muries, B., Muñoz-Azcarate, O., & Carvajal, M. (2009). Climate change and plant water balance: The role of aquaporins – A review. In Lichtfouse, E. (Ed.), *Climate change, intercropping, pest control and beneficial microorganisms*, 71–89. Springer, Netherlands.
- Mathur, S., Agrawal, D., & Jajoo, A. (2014). Photosynthesis: Response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology*, 137, 116–126.
- Mirosavljević, M., Mikić, S., Župunski, V., Abdelhakim, L., Trkulja, D., Zhou, R., ... & Ottosen, C. O. (2024). Effects of heat stress during anthesis and grain filling stages on some physiological and agronomic traits in diverse wheat genotypes. *Plants*, 13(15), 2083. <https://doi.org/10.3390/plants13152083>
- Modhej, A., Naderi, A., Emam, Y., Aynehband, A., & Normohamadi, G. (2012). Effects of post-anthesis heat stress and nitrogen levels on grain yield in wheat (*T. durum* and *T. aestivum*) genotypes. *International Journal of Plant Production*, 2(3), 257–268.
- Moghaddam, H., Oveisi, M., Keshavarz Mehr, M., Bazrafshan, J., Naeimi, M. H., Pourmorad Kaleibar, B., & Müller-Schärer, H. (2023). Earlier sowing combined with nitrogen fertilization to adapt to climate change effects on yield of winter wheat in arid environments: Results from a field and modeling study. *European Journal of Agronomy*, 146, 126825. <https://doi.org/10.1016/j.eja.2023.126825>
- Mondal, S., Karmakar, S., Panda, D., Pramanik, K., Bose, B., & Singhal, R. K. (2023). Crucial plant processes under heat stress and tolerance through heat shock proteins. *Plant Stress*, 10, 100227. <https://doi.org/10.1016/j.stress.2023.100227>
- Nahar, K., Ahamed, K. U., & Fujita, M. (2010). Phenological variation and its relation with yield in several wheat (*Triticum aestivum* L.) cultivars under normal and late sowing mediated heat stress condition. *Notulae Scientia Biologicae*, 2(3), 51–56.
- Nain, L., Rana, A., Joshi, M., Jadhav, S. D., Kumar, D., Shivay, Y. S., Paul, S., & Prasanna, R. (2010). Evaluation of synergistic effects of bacterial and cyanobacterial strains as biofertilizers for wheat. *Plant and Soil*, 331(1), 217–230.
- Narendra, M. C., Roy, C., Kumar, S., Virk, P., & De, N. (2021). Effect of terminal heat stress on physiological traits, grain zinc and iron content in wheat (*Triticum aestivum* L.). *Czech Journal of Genetics and Plant Breeding*, 57(2), 43–50.
- Nesar, N., Hameedi, A., Attri, M., Kumar, R., Bochalya, R. S., Stanikzai, R. G., & Srivastava, H. (2022). Terminal heat stress and its mitigation options through agronomic interventions in wheat crop: A review. *International Journal of Environment and Climate Change*, 12(11), 131–139.
- Nunes, M. A., Ramalho, J. C., & Dias, M. A. (1993). Effect of nitrogen supply on the photosynthetic performance of leaves from coffee plants exposed to bright light. *Journal of Experimental Botany*, 44(5), 893–899.
- Pask, A., Pietragalla, J., Mullan, D. M., & Reynolds, M. P. (Eds.). (2012). *Physiological Breeding: A field guide to wheat phenotyping* (Vol. II). CIMMYT.
- Perdomo, J. A., Capó-Bauçà, S., Carmo-Silva, E., & Galmés, J. (2017). Rubisco and Rubisco activase play an important role in the biochemical limitations of photosynthesis in rice, wheat, and maize under high temperature and water deficit. *Frontiers in Plant Science*, 8, 490. <https://doi.org/10.3389/fpls.2017.00490>

- Porter, J. R., & Gawith, M. (1999). Temperatures and the growth and development of wheat: A review. *European Journal of Agronomy*, 10(1), 23–36.
- Prasad, P. V., Staggenborg, S. A., & Ristic, Z. (2008). Impacts of drought and/or heat stress on physiological, developmental, growth, and yield processes of crop plants. In *Response of crops to limited water: Understanding and modeling water stress effects on plant growth processes* (Vol. 1, pp. 301–355).
- Pratap, A., Taylor, N. L., Pal, M., Chinnusamy, V., & Siddique, K. H. M. (2025). Heat tolerance mechanisms in bread wheat: Insights from flag leaves and spike tissues. *Plant Stress*, 16, 100876. <https://doi.org/10.1016/j.stress.2025.100876>
- Qaseem, M. F., Qureshi, R., & Shaheen, H. (2019). Effects of pre-anthesis drought, heat and their combination on the growth, yield and physiology of diverse wheat (*Triticum aestivum* L.) genotypes varying in sensitivity to heat and drought stress. *Scientific Reports*, 9, 1–12. <https://doi.org/10.1038/s41598-019-43477-z>
- Raaijmakers, J. M., Paulitz, T. C., Steinberg, C., Alabouvette, C., & Moënne-Loccoz, Y. (2009). The rhizosphere: A playground and battlefield for soilborne pathogens and beneficial microorganisms. *Plant and Soil*, 321, 341–361.
- Ratnakumar, P., Khan, M. I. R., Minhas, P. S., Farooq, M. A., Sultana, R., Per, T. S., Deokate, P. P., Khan, N. A., Singh, Y., & Rane, J. (2016). Can plant bio-regulators minimize crop productivity losses caused by drought, salinity and heat stress? An integrated review. *Journal of Applied Botany and Food Quality*, 89, 113–125.
- Rehman, H. U., Tariq, A., Ashraf, I., Ahmed, M., Muscolo, A., Basra, S. M., & Reynolds, M. (2021). Evaluation of physiological and morphological traits for improving spring wheat adaptation to terminal heat stress. *Plants*, 10(3), 455. <https://doi.org/10.3390/plants10030455>
- Rodríguez, M., Canales, E., & Borrás-Hidalgo, O. (2005). Molecular aspects of abiotic stress in plants. *Biotechnología Aplicada*, 22(1), 1–10.
- Sarkar, S., Islam, A. K. M. Aminul, Barma, N. C. D., & Ahmed, J. U. (2021). Tolerance mechanisms for breeding wheat against heat stress: A review. *South African Journal of Botany*, 138, 262–277. <https://doi.org/10.1016/j.sajb.2021.01.003>
- Savicka, M., & Škute, N. (2010). Effects of high temperature on malondialdehyde content, superoxide production and growth changes in wheat seedlings (*Triticum aestivum* L.). *Ekologija*, 56(1), 26–33.
- Scafaro, A. P., Posch, B. C., Evans, J. R., Farquhar, G. D., & Atkin, O. K. (2023). Rubisco deactivation and chloroplast electron transport rates co-limit photosynthesis above optimal leaf temperature in terrestrial plants. *Nature Communications*, 14(1), 2820. <https://doi.org/10.1038/s41467-023-38496-4>
- Schittenhelm, S., Langkamp-Wedde, T., Kraft, M., Kottmann, L., & Matschiner, K. (2020). Effect of two-week heat stress during grain filling on stem reserves, senescence, and grain yield of European winter wheat cultivars. *Journal of Agronomy and Crop Science*, 206, 722–733. <https://doi.org/10.1111/jac.12410>
- Shah, F., Ali, B. A., Usman, N., Anjum, S. A., Farooq, A., Ali, Z., Sehrish, S., Wajid, N., Adkins, S., Shah, S., Ihsan, M. Z., Alharby, H., Wu, C., Wang, D., & Huang, J. (2017). Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Science*, 8. <https://doi.org/10.3389/fpls.2017.01147>
- Sharma, P., Jha, A. B., Dubey, R. S., & Pessarakli, M. (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *Journal of Botany*, 2012(1), 217037.
- Sheng, K., Xu, L., Wang, M., Lei, H., & Duan, A. (2022). The end-use quality of wheat can be enhanced by optimal water management without incurring yield loss. *Frontiers in Plant Science*, 13, 1030763. <https://doi.org/10.3389/fpls.2022.1030763>
- Sherstneva, O., Abdullaev, F., Kior, D., Yudina, L., Gromova, E., & Vodeneev, V. (2024). Prediction of biomass accumulation and tolerance of wheat seedlings to drought and elevated temperatures using hyperspectral imaging. *Frontiers in Plant Science*, 15, 1344826.
- Shrestha, S., Mahat, J., Shrestha, J., K.C., M., & Paudel, K. (2022). Influence of high-temperature stress on rice growth and development: A review. *Heliyon*, 8(12), e12651.

- <https://doi.org/10.1016/j.heliyon.2022.e12651>
- Siddique, A. B., Shabala, S., Li, C., Chen, Z.-H., Varshney, R. K., Zhao, C., & Zhou, M. (2025). Reducing heat stress damage in cereal crops through agronomic management and breeding strategies. *Plant Stress*, 16, 100888. <https://doi.org/10.1016/j.stress.2025.100888>
- Singh, A., Singh, D., Kang, J. S., & Aggarwal, N. (2011). Management practices to mitigate the impact of high temperature on wheat: A review. *Integrative Omics and Applied Biotechnology*, 2(7), 11–22.
- Singh, C., Yadav, S., Khare, V., Gupta, V., Kamble, U. R., Gupta, O. P., Kumar, R., Saini, P., Bairwa, R. K., Khobra, R., Sheoran, S., Kumar, S., Kurhade, A. K., Mishra, C. N., Gupta, A., Tyagi, B. S., Ahlawat, O. P., Singh, G., & Tiwari, R. (2024). Unraveling the secrets of early-maturity and short-duration bread wheat in unpredictable environments. *Plants*, 13(20), 2855. <https://doi.org/10.3390/plants13202855>
- Singh, G., Salaria, A., Singh, H., & Bhatt, R. (2023). Terminal heat stress in wheat and its mitigation options through agronomic interventions. *Indian Farming*, 73(5), 15–18.
- Singh, K., Sharma, S. N., & Sharma, Y. (2011). Effect of high temperature on yield attributing traits in bread wheat. *Bangladesh Journal of Agricultural Research*, 36(3), 415–426. <https://doi.org/10.3329/bjar.v36i3.9270>
- Singh, N., Viridi, A. S., Katyal, M., Kaur, A., Kaur, D., Ahlawat, A. K., Singh, A. M., & Sharma, R. K. (2021). Evaluation of heat stress through delayed sowing on physicochemical and functional characteristics of grains, whole meals, and flours of India wheat. *Food Chemistry*, 344, 128725. <https://doi.org/10.1016/j.foodchem.2020.128725>
- Streck, N. A. (2005). Climate change and agroecosystems: The effect of elevated atmospheric CO₂ and temperature on crop growth, development and yield. *Ciencia Rural*, 35, 730–740.
- Suryavanshi, P., & Buttar, G. S. (2016). Mitigating terminal heat stress in wheat. *International Journal of Bio-resource and Stress Management*, 7(1), 142–150.
- Taiz, L., & Zeiger, E. (2006). *Plant physiology*. Sinauer Associates, Inc., Sunderland, MA.
- Tashiro, T., & Wardlaw, I. F. (1989). A comparison of the effect of high temperature on grain development in wheat and rice. *Annals of Botany*, 64, 59–65. <https://doi.org/10.1093/oxfordjournals.aob.a087808>
- Ullah, A., Nadeem, F., Nawaz, A., Siddique, K. H., & Farooq, M. (2022). Heat stress effects on the reproductive physiology and yield of wheat. *Journal of Agronomy and Crop Science*, 208(1), 1–17.
- Upreti, K. K., & Sharma, M. (2016). Role of plant growth regulators in abiotic stress tolerance. In *Abiotic stress physiology of horticultural crops* (pp. 19–46). New Delhi: Springer India.
- Vignjevic, M., Wang, X., Olesen, J. E., & Wollenweber, B. (2015). Traits in spring wheat cultivars associated with yield loss caused by a heat stress episode after anthesis. *Journal of Agronomy and Crop Science*, 201(1), 32–48.
- Wahid, A., Gelani, S., Ashraf, M., & Foolad, M. R. (2007). Heat tolerance in plants: An overview. *Environmental and Experimental Botany*, 61(3), 199–223.
- Wardlaw, I. F., & Moncur, L. J. F. P. B. (1995). The response of wheat to high temperature following anthesis. I. The rate and duration of kernel filling. *Functional Plant Biology*, 22(3), 391–397.
- Yadav, M. R., Choudhary, M., Singh, J., Lal, M. K., Jha, P. K., Udawat, P., ... & Prasad, P. V. (2022). Impacts, tolerance, adaptation, and mitigation of heat stress on wheat under changing climates. *International Journal of Molecular Sciences*, 23(5), 2838.
- Yang, J., & Zhang, J. (2006). Grain filling of cereals under soil drying. *New Phytologist*, 169(2), 223–236.
- Yang, J., Zhang, J., Wang, Z., Xu, G., & Zhu, Q. (2004). Activities of key enzymes in sucrose-to-starch conversion in wheat grains subjected to water deficit during grain filling. *Plant Physiology*, 135(3), 1621–1629.
- Yin, X., Guo, W., & Spiertz, J. H. (2009). A quantitative approach to characterize sink–source relationships during grain filling in contrasting wheat genotypes. *Field Crops Research*, 114(1), 119–126.
- Zahra, N., Hafeez, M. B., Ghaffar, A., Kausar, A., Al Zeidi, M., Siddique, K. H. M., & Farooq,

- M. (2023). Plant photosynthesis under heat stress: Effects and management. *Environmental and Experimental Botany*, 206, 105178. <https://doi.org/10.1016/j.envexpbot.2022.105178>
- Zhang, X., Yang, Z., Wang, L., Yue, Y., Wang, L., & Yang, X. (2023). The effects of plant growth-promoting rhizobacteria on plants under temperature stress: A meta-analysis. *Rhizosphere*, 28, 100788. <https://doi.org/10.1016/j.rhisph.2023.100788>
- Zhao, K., Tao, Y., Liu, M., Yang, D., Zhu, M., Ding, J., Zhu, X., Guo, W., Zhou, G., & Li, C. (2022). Does temporary heat stress or low temperature stress similarly affect yield, starch, and protein of winter wheat grain during grain filling? *Journal of Cereal Science*, 103, 103408. <https://doi.org/10.1016/j.jcs.2021.103408>

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