



REVIEW ARTICLE

Impact of heat stress on nutritional status of staple crop vs. millets: A review

Ponmani V¹, Kokilavani S^{1*}, Manivannan V², Arthirani B³ & Vanitha K⁴

¹Agro Climate Research Centre, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

²Department of Agronomy, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

³Agricultural Research Station, Kovilpatti 628 501, Tamil Nadu, India

⁴Department of Fruit Science, Horticultural college and Research Institute, Tamil Nadu Agricultural University, Coimbatore 641003, Tamil Nadu, India

*Correspondence email - kokilavani@tnau.ac.in

Received: 07 March 2025; Accepted: 26 July 2025; Available online: Version 1.0: 07 October 2025

Cite this article: Ponmani V, Kokilavani S, Manivannan V, Arthirani B, Vanitha K. Impact of heat stress on nutritional status of staple crop vs. millets: A review. *Plant Science Today*. 2025; 12(sp1): 1-12. <https://doi.org/10.14719/pst.8126>

Abstract

Climate change and global warming have led to increased heat stress (HS), significantly impacting agricultural productivity and nutritional security. Staple crops such as rice, wheat and maize are particularly vulnerable, with elevated temperatures disrupting key physiological processes, including seed germination, photosynthesis, pollination and grain filling. HS causes severe metabolic imbalances, oxidative stress and phytohormone disruptions, ultimately reducing crop yield and grain quality. These challenges pressurize to identify heat-tolerant crop alternatives for sustaining global food security. Millets have emerged as a strategic solution due to their inherent resilience to abiotic stresses, including HS. These C4 plants possess unique morphological, physiological and biochemical adaptations, such as deep root systems, osmoprotectant accumulation, antioxidant enzyme activity and stress-responsive gene regulation, which enhance their thermotolerance. Unlike major cereals, millets maintain productivity under extreme temperatures, making them a viable alternative in climate-smart agriculture. Genetic advancements, including molecular breeding, transcriptomics and CRISPR/Cas9-based genome editing, offer potential strategies to further improve millet varieties for enhanced heat resilience and nutritional quality. This review explores the physiological, metabolic and molecular responses of staple crops and millets to HS, highlighting the advantages of millet-based agricultural systems. By integrating advanced biotechnological tools with traditional breeding methods, millets can be optimized for improved yield and climate adaptability. Intensifying the frequency of heat waves, promoting millet cultivation can play a pivotal role in mitigating global food insecurity, ensuring sustainable agricultural production and enhancing nutritional security in the phase of climate change.

Keywords: climate change; global warming; heat stress; millets; molecular adaptation; nutritional security; physiological and metabolic impacts; resilient crop

Introduction

The world population of 805 crores is fed with 9.5 billion tonnes in 2021 as World production. Among food crops, major cereals are an energy contributor for more than half of the population. According to the Food and Agriculture Organization (FAO), 2019 report more than 820 million people in the world are still hungry today, underscoring the immense challenge of achieving the Zero Hunger target by 2030. Another disturbing fact is that about 2 billion people in the world experience moderate or severe food insecurity (1). FAO defined food security as (i) the availability of sufficient quantities of food of appropriate quality, supplied through domestic production or imports; (ii) access by individual to adequate resources (entitlements) for acquiring appropriate foods for a nutritious diet; (iii) utilization of food through adequate diet, clean water, sanitation and health care to reach a state of nutritional well-being where all physiological needs are met; and (iv) stability, because to be food secure, a population, household or individual must have access to adequate food at all times (2). Food

security can be achieved via numerous strategies. Especially in India, food security was achieved after the green revolution during the 1960s. While food security ensures adequate caloric intake, nutritional security emphasizes the quality and balance of nutrients essential for human health.

In addition to food security, achieving nutritional security is very important. Though there is sufficient food production in India at present to meet the population demand quantitatively, the qualitative food with all kinds of nutrition in adequate proportion is important (3). Lack of essential micronutrients, including all kinds of vitamins and minerals in the everyday diet, leads to malnutrition, causing serious health issues, which is simply called Hidden hunger (4). The term 'food security' does not spell out the nutritional dimension of food, adequate sanitation, health services and care, allowing for a healthy and active life. Agricultural production in general and crop production in particular, must increase substantially to meet the rising food demand of a population that is projected to expand by some 40 % over the

period from 2005 to 2050. Beyond this nutrition concern, climate change and increasing climate variability and extremes are affecting agricultural productivity, food production and natural resources, with impacts on food systems and rural livelihoods, including a decline in the number of farmers leading to major shifts in the way in which food is produced, distributed and consumed worldwide. Above all, projected insecurity in food productivity and nutritional security should be given importance in the context of changing climate with the consequence of global warming. In this changing climate, understanding the biological timing of crop development, particularly flowering, becomes pivotal to sustaining productivity.

Understanding how environmental factors trigger phenological processes like flowering is crucial for future food production, as a significant portion of food consists of grains and seeds. Changes in flowering time can impact not only the quantity of seed production but also the composition of food (5) which is seriously affecting the nutritional security, causing hidden hunger and malnutrition symptoms worldwide. Increased temperature is one of the inevitable consequences of climate change, playing a major role in the production and nutritional composition of food crops. Increased temperature for a prolonged period is typically called heat stress (HS). HS at different periods coincide with different stages of crop cause physiological, genetic and biochemical consequences. Exposure to HS severely affects physiological processes such as seed germination and vigour, root growth, leaf enlargement, reproductive development, photosynthesis, grain filling duration and rate of grain filling, which eventually reduce grain yield and quality. Metabolic impacts include membrane damage, reactive oxygen species (ROS) accumulation, photosynthesis and carbohydrate imbalance, phytohormone and biochemical imbalance. Altogether, ultimately leads to nutritional imbalance of the produce of the crop which experiences HS during its different growth stages.

Rising global temperatures due to climate change are exerting significant stress on agricultural systems, particularly affecting the growth, yield and nutritional integrity of staple crops such as rice, wheat and maize. While the impacts of heat stress are relatively well studied in these crops, there remains a significant knowledge gap in understanding how heat stress alters their nutritional composition, especially micronutrient profiles. Although millets are recognized for their climate resilience and nutritional richness, their comparative performance under heat stress remains underexplored in consolidated reviews. This hinders the development of climate-smart crop strategies aimed at ensuring food and nutritional security. Therefore, the objectives of the review are to analyse the physiological, metabolic and nutritional impact of heat stress on major staple crops (rice, wheat and maize) and millets, including both major and minor species, under similar stress conditions. To compare and contrast the resilience and nutritional retention of millets vs. staple cereals under heat stress and to identify gaps in current literature and highlight the role of millets as climate-resilient alternatives for sustainable agriculture and nutrition.

Importance of heat-stress study

The temperature of the environment is a crucial factor in deciding seasonal growth and distribution of crops. Rapidly warming climate causes HS, commonly defined as an increase in

temperature above a threshold level for a certain period, that causes irreversible damage to the growth and development of plants. The Sixth Assessment Report of the IPCC projects the impacts associated with a global average warming of 1.5 °C and higher levels of warming. Global warming has become a severe threat to agricultural productivity worldwide. IPCC also reported that for every 1 °C increase in global mean temperature, there will be a reduction in global yield of wheat by 6.0 %, rice by 3.2 % and, maize by 7.4 %, respectively. These alarming projections translate directly to physiological disruptions in crop development.

Increased temperatures lead to changes in the timing of leaf development, flowering, harvesting and fruit production, along with a shorter vernalization period and mismatches between flowering and pollinators (6). Higher temperatures also result in increased respiration rates, shorter seed formation periods, reduced biomass production and thus lower yields (7). When assessing the impact of temperature on crop yields, it's crucial to consider key stages of crop development, seasonal temperature events and day-night temperature variations on a geographical scale for better assessment. A few days of extreme temperatures during the flowering stage can significantly reduce yields in many crops. Pre- and post-anthesis heat events at 35 °C have been shown to cause substantial yield losses in wheat (6). Each crop species has an optimal temperature for vegetative growth, with growth declining as temperatures move away from this optimum. Similarly, each crop has a specific temperature range required for seed setting; outside this range, reproduction is inhibited. For example, maize cannot reproduce at temperatures above 32 °C, while soybean fails to reproduce above 38 °C (8). As a result, India's trend towards increased production of wheat and rice and decreased production of maize and millets is expected to continue. High temperatures (above 35 °C), combined with high humidity and low wind speed, can increase rice panicle temperature by up to 4 °C, leading to floret sterility (9). Identification and analysis of physiological and biochemical characteristics of plants responsive to heat stress, genes and proteins responsible for heat tolerance and molecular mechanisms under HS are essential for thermotolerance improvement. This review summarizes HS-caused morphological and physiological symptoms of staple crops and progress in elucidating molecular mechanisms underlying crop response to HS and discusses thermotolerance improvement approaches (10). To comprehensively assess crop vulnerability, it is necessary to consider stage-specific temperature thresholds for both staple and millet crops. Table 1 lists the minimum, optimum and maximum threshold temperatures of staple and millet crops. Building upon the general overview of heat stress, it is crucial to analyze how it specifically alters crop physiology at different growth stages.

Physiological impact of HS

Morpho-physiological changes and a reduction in genetic potential are the major impacts of heat stress (HS), which serve as the root causes of reproductive stage impairment and yield reduction. This may also lead to nutritional imbalance as it affects the grain filling process. Heat stress in wheat leads to reduced leaf chlorophyll content, premature senescence and shortened grain-filling duration, ultimately decreasing grain weight. HS during anthesis interferes with pollination and fertilization, while during grain filling it limits starch accumulation.

Table 1. Minimum, optimum and threshold temperature of staple and millet crops

Crop/Millet	Min (°C)	Optimum (°C)	Max threshold (°C)	Reference
Rice (<i>Oryza sativa</i>)	10-12	25-29 (vegetative stage), 21-25 (grain filling stage)	>35-38 (spikelet sterility, chalkiness)	(11)
Wheat (<i>Triticum aestivum</i>)	3.5-6.2	19.7-26.5 (stage-specific)	30-32 (anthesis/grain filling)	(12)
Maize (<i>Zea mays</i>)	~6-7	20-30	>38 (yield declines)	(13)
Pearl millet (<i>Pennisetum glaucum</i>)	12-15	30-35	~45 (seedling lethal)	(14)
Sorghum (<i>Sorghum bicolor</i>)	~7-10	26-30	>40 °C (flowering stress)	(15)
Proso millet (<i>Panicum miliaceum</i>)	~10-13	~20-30 (C4 warm-season)	~35+ (stress threshold)	(16, 17)
Little millet (<i>Panicum sumatrense</i>)	~10-15	20-30	~35-38 (assumed analogous)	(18)
Kodo millet (<i>Paspalum scrobiculatum</i>)	~12-15	25-27	~35 (heat-limited)	(19)
Barnyard millet (<i>Echinochloa</i> spp.)	~12-15	27-33	~35-38 (analogous trend)	(20)

In maize, HS causes leaf rolling, reduced stomatal conductance and disrupted tassel emergence and pollen viability. HS during silking and grain-filling phases leads to poor kernel set and reduced grain size. Elevated temperatures above 35 °C severely reduce chlorophyll fluorescence and net photosynthetic rate. Maize hybrids show variability in thermotolerance based on membrane stability and antioxidant capacity.

Germination, seedling growth, vegetative and tillering stage

Prolonged exposure to elevated temperature reduces seed germination potential and leads to a poor rate of germination and seed vigour (7). In Rice, HS of 42-45 °C at the seedling stage may cause increased dehydration, withering and yellowing of leaves, impaired seedling and root growth and even death of seedlings (21). HS at tillering stage causes morphological symptoms such as leaf wilting, leaf curling and yellowing, reduced tillering and biomass yield (22, 23). As the plant progresses into reproductive phases, its sensitivity to temperature extremes becomes even more pronounced.

Reproductive stage

At the reproductive stage, the process of panicle initiation, anthesis, pollination and fertilization are more susceptible to HS than the vegetative stage. HS impairs panicle initiation and spikelet development, which leads to deformed floral organs and reduced spikelet number and size (23, 24). In rice, spikelet number decreases by 66 % at 40 °C day temperature and 35 °C night temperature at the pre-flowering stage (25). The anther development and pollen viability are highly sensitive to elevated temperatures during pollen mother cell meiosis. Impaired nutrient supply under stress conditions can lead to pollen grain abortion (26). A decrease of pollen viability by 78.8 % and seed-setting by 48.5 % due to HS of about 40 °C day temperature and 30 °C night temperature at the pollen mother cell meiosis stage (27). Altered anther shape, diminished anther dehiscence, poor pollen viability, reduced pollen number on stigma, reduced pollen swelling, poor germination of pollen grains on the stigma, inhibited pollen tube elongation and reduced stigma length are all consequences of HS during anthesis that impair pollination and fertilization (28, 29). The occurrence of HS during the reproductive stage resulted up to 80 % reduction in spikelet fertility of rice (23). Following fertilization, the grain-filling phase is equally susceptible to heat-induced changes that ultimately determine yield and grain quality.

Grain-filling stage

The grain filling stage involves the transport and synthesis of carbohydrates, proteins and lipids in seeds in rice. HS at the grain filling stage reported to increase the grain filling rate, but the total grain filling period is reduced by 21.3-37.1 %. HS of 35 °C at the early seed development stage impaired endosperm and

embryo development (30). HS also results in altered kernel size and reduced grain weight and yield (31). Grain filling at high temperature of 38 °C day temperature and 23 °C night temperature reduces the grain weight by 24.6-39.1 % and poor rice quality, reduced palatability, undesirable grain appearance and increased grain chalkiness are the consequences of HS at the grain filling stage. HS triggers non-uniform filling and impairment of starch biosynthesis, resulting in irregular and smaller starch granules and loosely packed starch granules, thus increasing chalky/chaffy kernel formation. Amylose content is lower under HS (16.1 %) than under normal conditions (19.8 %), which shows that lower activity of amylose synthesis may be involved in chalk formation (32). Beyond physiological impact heat stress also impairs core metabolic processes, which are explored in the following section. Table 2 lists the threshold temperature of rice at different stages.

Metabolic impact of HS

Alongside visible physiological symptoms, heat stress triggers metabolic disruptions at cellular and biochemical levels that compromise crop function.

Membrane damage and lipid peroxidation

Impairment of growth and development by HS is associated with disrupted physiological as well as metabolic processes of the plant cell. In rice, physiological structures consisting of lipids and proteins, biomembranes are considered to be the most heat-sensitive component (33). Impaired structure and functions of the plasma membrane alter the ratio of saturated and unsaturated fatty acids and trigger the denaturation of protein (34).

Photosynthesis, a vital metabolic process, declines under elevated temperatures due to thylakoid membrane damage, reduced chlorophyll content and increased production of reactive oxygen species (ROS) (35, 36). Elevated photorespiration due to oxygen and CO₂ solubility changes and a change in the affinity of RuBisCO for these gases. Negative impact on meiosis, causing increased meiotic abnormalities leading to failure in cell division, impairing the development of microspores and pollen cells (10).

Table 2. Threshold temperature for rice crop at different stages (11)

Growth Stage	Threshold temperature (°C)	Symptoms
Emergence	40	Delay and decrease in emergence
Seedling	35	Poor growth of the seedling
Tillering	32	Reduced tillering and height
Booting	-	Decreased number of Pollen grains
Anthesis	37	Poor anther dehiscence and sterility
Flowering	35	Floret sterility
Grain formation	34	Yield reduction
Grain ripening	29	Reduced grain filling

ROS accumulation

When rice plants are subjected to HS of 38 °C day temperature and 30 °C night temperature at the meiosis stage, the ROS content in anthers is over three times higher than that under normal temperature of 28 °C day temperature and 22 °C night temperature (37). This intercellular accumulation of ROS content causes disturbed ROS homeostasis and oxidative damage such as cell death, growth retardance, grain chalkiness, seedling death and spikelet sterility (38). Excessive ROS further causes lipid peroxidation and protein oxidation, leading to increased intercellular malondialdehyde (MDA), which impairs the normal function of proteins and nucleic acids (39, 40). HS impairs the activities of antioxidant enzymes, especially superoxide dismutase (SOD) and catalase (CAT) (41).

Photosynthetic efficiency and chlorophyll degradation

HS results in destroyed permeability of the thylakoid membrane or even thylakoid grana disintegration and causing a decrease in chlorophyll content, resulting in a variable photosynthetic rate. Photosystem II (PSII) is the most sensitive component of the photosynthesis apparatus (42). High temperature inhibits the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), mainly as a consequence of the inactivation of RuBisCO activase (43).

Phytohormone alteration

HS causes phytohormone imbalance. It reduces the levels of active cytokinin (CTK), gibberellin (GA) and indole-3-acetic acid (IAA) in rice spikelets and developing kernels, panicle formation, reducing spikelet number, pollen fertility and kernel weight (44). HS leads to an increase in abscisic acid (ABA) in anthers and seeds, resulting in pollen abortion and inhibition of germination and seedling establishment (45).

Enzymatic and non-enzymatic antioxidant responses

The biochemical traits of plants are affected due to heat stress. For example, hardness index, wet gluten content, protein concentration and amylose content were affected due to alterations in the enzyme functions involved in grain formation (46). Dehydration of plant tissues due to HS inactivates water-related antioxidants, which causes instability in the cell membrane (9). The thermolabile photosynthetic enzyme RuBisCo is less efficient in carbon fixation (47). Antioxidant enzymes like SOD, CAT, guaiacol peroxidase (GPX) significantly increase (48). At temperatures about 32-33 °C, heat shock protein synthesis, which plays a significant role in heat resistance and protein folding (49). Increased ROS levels result in reduced photosynthetic rate and growth in the wheat plant (50). To mitigate ROS and to reduce oxidative stress, plants employ enzymatic and non-enzymatic antioxidants as a defence system (51). Heat stress interferes with the expression of ZIP and YSL transporter gene families, which are essential for Zn and Fe uptake and loading into grains. These metabolic disruptions directly influence nutrient synthesis, partitioning and storage, thereby impacting the nutritional quality of crops.

Nutritional impact

Carbohydrate metabolism and partitioning imbalance

HS disturbs carbohydrate metabolism and photo-assimilate partitioning in the plant (52). When rice plants experience HS during anthesis, the sugar content in anthers is disordered,

impairing the normal nutritional supply for pollen development (53, 54). HS at the grain filling stage led to the disruption of starch synthesis-related proteins such as granule-bound starch synthase I and branching enzymes, resulting in inhibition of starch accumulation and increased grain chalkiness (55).

HS can significantly influence seed development and decrease seed biomass in cereals. As seed filling is closely related to whole plant senescence, heat stress during grain filling leads to early senescence, thus reducing the grain filling duration and remobilizing the assimilates from source to sink. Since 65 % dry weight is accumulated by starch due to heat stress, starch accumulation decreases both in rice and wheat by altered expression of starch-related genes. Reduction in seed size due to reduction in total non-structural carbohydrates leads to changes in the proportion of soluble sugar to starch. The decrease in sugar, such as fructose, sugar nucleotides and hexose phosphate levels, is due to heat stress because the plants enhance assimilate utilization rather than production. In some cases, due to upregulation of the α -amylase enzyme increase in sugar levels was reported. But this leads to chaffy grains in rice under a heat-stress environment (56).

Storage protein

Heat stress decreased the duration and amount of protein accumulation, but the rate of accumulation was unaffected in some studies. In wheat, storage protein composition is altered under heat stress during the seed filling stage due to changes in the total nitrogen accumulation. Protein quality, such as dough quality, declined in wheat under heat stress because of a reduction in aggregation properties, caused by a decline in high molecular weight glutenins and a rise in gliadin accumulation. Moreover, the ratio of gliadins and glutenins increased while the ratio of large polymers decreased in wheat grain flour (57). A significant reduction in kernel protein content percentage was recorded under heat stress than drought stress in maize. Kernel oil content is also reduced under stressed conditions compared to the control (58).

Micronutrients

Heat stress significantly disrupts the uptake, translocation and remobilization of essential micronutrients in wheat during the grain filling stage. This is primarily attributed to impaired root function, reduced photosynthesis and altered phloem loading, which affects nutrient mobilization. For example, heat exposure reproductive stage reduces Zn remobilization efficiency, leading to lower Zn content in the final grain. Similarly, high temperature reduces Fe availability in the phloem sap, likely due to oxidative stress-mediated damage to transport proteins and vascular tissues. Altogether, when heat stress coincides with the grain-filling phase, the reduction in grain Zn and Fe concentrations ranges up to 20-40 % (59).

High temperature, as mentioned above, results in an imbalanced nutritional sink in the economic parts (grains) of the staple crop. Alterations in the nutritional status of major crops due to environmental stress ultimately led to nutritional imbalances in human diets. Inadequate nutrition because of nutritional impairment leads to increased production of staple crops by fulfilling a balanced diet. Also, with increasing population and increasing land constraints, in present situation of climate change conditions makes this context even more challenging. Unlike

staple crops, where protein and carbohydrate metabolism decline sharply under HS, studies have shown that millets maintain higher levels of soluble sugars and storage proteins due to robust stress-resilient pathways, a distinction that is rarely analyzed side-by-side. Heat tolerance mechanisms of millet crops and improved approaches are discussed further to understand the available and future perspectives of HS management practices. Considering these detrimental effects on staple crops, attention is increasingly turning to climate-resilient alternatives such as millets. Table 3 summarizes the impact of heat stress on maize. Fig. 1 illustrates the impact of heat stress on the maize crop.

Comparative evaluation of heat stress impact on nutritional quality in staples vs. millets

Although many studies have established the negative effects of heat stress on staple crops such as rice, wheat and maize, they predominantly focus on yield decline and gross physiological

Table 3. Summary heat stress (HS) impact on maize (60)

Characteristics	HS @ 36 °C	HS @ 40 °C
Chlorophyll content	-10.7 % to -16.3 %	-11.8 % to -16.6 %
Net photosynthetic rate	-9.5 % to -12.1 %	-13.6 % to -16.3 %
Intercellular CO ₂ concentration	+7.1 % to +9.7 %	+15.3 % to +15.5 %
Transpiration rate	+2.6 % to +8.1 %	-
(Early temperature rise)		
(Later temperature rise)	-4.6 % to -6.7 %	-
RuBPCase activity	-7.5 % to -12.4 %	-
PEP carboxylase activity	-13.4 % to -14.9 %	-
Electron transfer rate (ETR)	-4.4 % to -5.2 %	-14.4 % to -18.3 %
Non-photochemical quenching	-	+8.2 % to +16.3 %
Light use efficiency (LUE)	-9.2 % to -9.6 %	-11.6 % to -12.6 %
Soluble protein	-8.8 % to -17.8 %	-7.1 % to -17.8 %
Sugar content	-6.2 % to -12.0 %	-14.3 % to -17.2 %
Malondialdehyde (MDA)	+6.8 % to +10.3 %	+9.8 % to +14.8 %
ROS content	+7.2 % to +7.7 %	+9.9 % to +16.6 %
Superoxide dismutase (SOD) activity	-7.2 % to -7.7 %	-9.9 % to -16.6 %
Ascorbate peroxidase (APX)	-4.9 % to -9.4 %	-10.1 % to -13.5 %
IAA content	-9.5 % to -12.3 %	-16.0 % to -18.0 %
ABA content	+6.3 % to +12.1 %	+13.1 % to +14.5 %
Yield	-44.9 % to -50.3 %	-58.5 % to -66.6 %

damage. For instance, in wheat and rice, heat exposure during grain filling significantly reduces protein content, starch biosynthesis and micronutrient accumulation like iron and zinc. However, research on the nutritional degradation under heat stress remains fragmented, often missing a broader synthesis across both staple and climate-resilient crops.

Comparatively, millets, including pearl millet, proso millet, foxtail millet and barnyard millet, show less deterioration in nutrient content when subjected to elevated temperatures. Experimental trials demonstrate that millets maintain higher levels of protein, calcium, dietary fiber and antioxidants under stress, with minimal compromise in grain quality. This is attributed to robust antioxidant systems and efficient carbohydrate partitioning in millets.

This review integrates a focus on both the physiological and nutritional dimensions of heat stress across a wide spectrum of crops, including minor millets (like kodo and little millet), which are underrepresented in most previous reviews. Unlike earlier works that treat staple and millet crops in isolation, this manuscript offers a side-by-side analysis of nutrient dynamics such as starch, protein and phenolic compound stability under comparable stress conditions. Additionally, it compiles threshold temperature ranges and molecular responses that are only partially addressed in earlier literature.

Millets as a strategic crop under HS

Millets play a crucial role in combating global warming and climate change due to their lower carbon footprint than major cereals like rice, wheat and maize. Their ability to grow with minimal inputs and lower greenhouse gas emissions makes millets an optimal choice under sustainable agriculture (61). Additionally, millets are highly resilient to climate change as they inherently withstand abiotic stresses such as drought, heat, salinity and nutrient deficiencies (16). This adaptability ensures their cultivation even in extreme climatic conditions, providing food security for vulnerable populations as specific as nutritional security. Focusing on a few major crops to fulfill demand has led

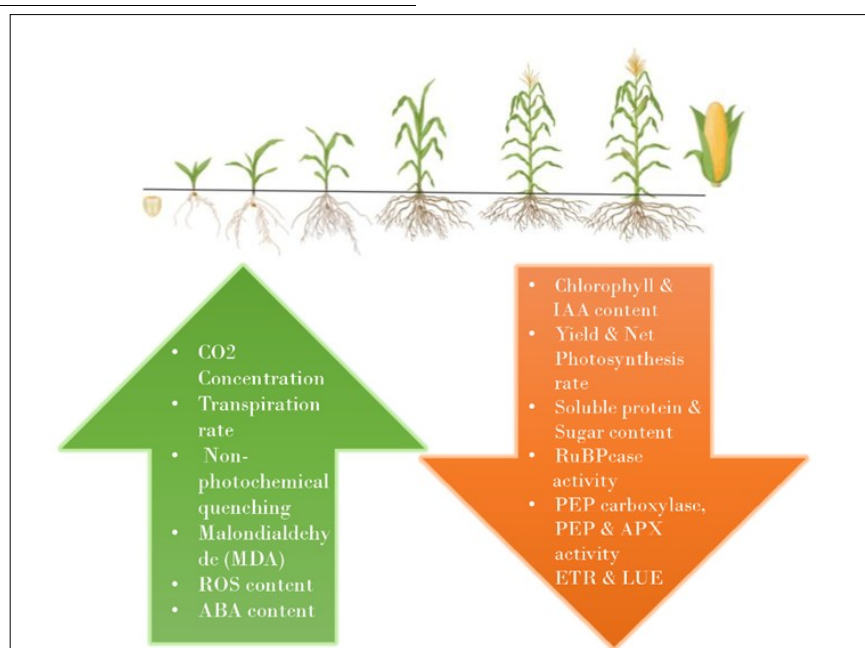


Fig. 1. Physiological effects of HS. An illustration explains the overall physiological impact of heat stress. ROS: reactive oxygen species; ABA: ascorbic acid; IAA: indole acetic acid; RuBP: ribulose-1,5-bisphosphate; PEP: phosphoenolpyruvate; APX: ascorbate peroxidase; SOD: superoxide dismutase; ETR: electron transfer rate; LUE: light use efficiency.

to genetic erosion, inadequate nutrition and an agrarian crisis in the present scenario. In this condition, cropping system or pattern diversification with climate-resilient crops like millets is essential. These naturally stress-resistant plants (NSRPs) not only offer yield stability but also contribute to global food security and agricultural sustainability in the context of climate change (62). Coupled with this, extreme environmental conditions such as high temperatures, drought and soil salinity cause the accumulation of reactive oxygen species (ROS), leading to cell damage and photosynthesis inhibition in many crops. Millets, on account of their remarkable tolerance to these stresses, make them an ideal crop for future climate-smart agriculture, is an incredible yield over staple crop. This review extends the scope of earlier literature by comparing millets and staple crops not just in stress response but also in terms of their implications for nutritional security, especially under climate-induced temperature extremes. Fig. 2 shows the area, production and yield trend since 1950.

Thermotolerance in millets

Though millet species are resistant to heat stress, physiological and molecular alterations are common responses by plants. Photosynthesis and respiration are sensitive processes that affect crop productivity drastically. Yield of any crop increases with increasing temperature up to a threshold level; after that, there will be a serious negative effect on both growth and yield. High temperature stress reduces the transport of electrons, interrupts the function of photosystem (PS) II and increases ROS accumulation. Heat stress shows desiccation of reproductive parts, which causes plant sterility, seed abortion, seed count reduction and short grain filling period (63).

The tolerance mechanism of millet involves upregulation of the antioxidant system, transcription factors, heat-shock proteins, signalling molecules, ion transporters and osmoprotectants accumulation. Plants use pathways containing antioxidants to combat ROS against various abiotic stresses, as it can induce oxidative stress (64). One of the primary reasons for millet's heat tolerance lies in its intrinsic physiological features that minimize stress-induced damage. To appreciate the resilience of millets, it is important to explore their physiological and molecular responses of millet crops to heat stress.

Physiological adaptation

Millets are short-duration crops with smaller leaf area, thickened cell walls and dense root systems, which are traits that help in resisting abiotic stresses. Being C4 plants, millets exhibit higher water use efficiency (WUE) and nitrogen use efficiency (NUE), which are approximately 1.5 to 4 times greater than those of C3 plants (15). *Panicum sumatrense* (little millet) shows an increased root length and a decreased shoot length under drought, as HS is one of the reasons for drought due to higher temperature depleting rhizosphere moisture. Foxtail millet with longer and denser root hairs, forming a large rhizosheath with more root biomass, helps penetrate deep into dry soils (65).

Pearl millet is reported to be composed of a fast-growing primary root system and a rapid colonization of deeper soil horizons. High tillering varieties having small-sized grains and small panicles minimize stress-related grain filling impairments (66). Pearl millet with varying root depths ranging from 140 cm to 300 cm, with lateral root spreading, is an important adaptation to stress to increase water uptake. Stay green is a stress tolerance trait, which is a characteristic of some genotypes where active photosynthesis is extended by delaying leaf senescence via a complex signalling network. This allows plants to continue with photosynthesis regardless of the soil water content and maintain a good grain yield under stress conditions (67). Stress-tolerant pearl millet accessions showed various morphological and physiological responses to stress, such as upright folding of leaves that reduces surface area of evaporation, greater osmotic adjustment capacity of young leaves and stems and higher accumulation of NO_3^- , K^+ , amino acids, proline, sucrose, glucose and ammonium compounds (68). Phytohormone such as auxin, cytokinin, ABA, gibberellin and ethylene plays an important role in stress adaptive responses. Stomatal closure is the foremost physiological adaptation to prevent transpiration water loss, reduced stomatal conductance, reduced photosynthetic rate and ultimately decreased CO_2 and RuBisCo activities (69). Complementing these physical traits are robust biochemical defense mechanisms, including antioxidant responses

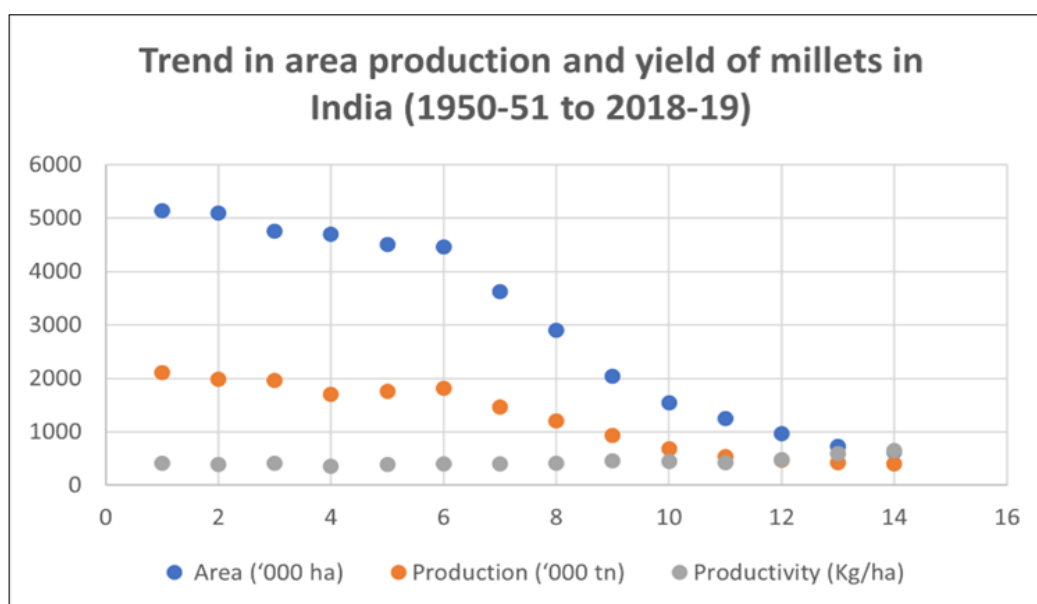


Fig. 2. Trend in area production and yield of millets in India (1950-51 to 2018-19) (19).

Biochemical adaptation and antioxidant mechanisms

An important amino acid, proline, plays a vital role as a compatible osmotic molecule and in osmotic potential adjustment, helping in improving tolerance. It also acts in antioxidative defense against oxidative damage and stress signaling (70). This consist of SOD, CAT, peroxidase (POD) and APX. Ascorbate is a water-soluble antioxidant necessary for the efficient activity of APX and plays an important role in scavenging H_2O_2 and converting it into H_2O . An increase of ascorbate of about 200 % is reported in finger millet stress-tolerant varieties, implying the importance of ascorbate in stress (71). In finger millet genotype, it was reported that the drought tolerance capacity included a lower MDA content, higher osmolyte accumulation (proline, glycine betaine and total soluble sugars) and an increased activity of antioxidant enzymes (SOD, CAT, APX and GPX) (72).

In stress-imposed pearl millet crop, an increased expression of secondary metabolite genes associated with alkaloid, terpenoid, flavanols, lignin, wax, mevalonic acid (MVA) and shikimic acid (SA) metabolic pathways was reported at the flowering stage than the vegetative stage, helping to maintain osmotic potential and membrane integrity (73). Pearl millet has expanded the gene families for waxes, suberin and cutin biosynthesis and transporters for secondary metabolites, as compared to other cereal crops has been proposed that these deposits might provide the plants with drought and heat tolerances. It was concluded that higher excised leaf water retention capacity (ELWRC), plant water relations, proline accumulation, leaf area index (LAI), total biomass (TB) and an efficient antioxidant (AOX) system contribute to the dehydration stress tolerance in pearl millet (69).

In foxtail millet, about 2474 differently expressed proteins were identified by proteomic analysis under stress up to 4 times, which are involved in processes like photosynthesis, stress and defense responses, ATP synthesis, carbon metabolism, protein biosynthesis, folding and degradation, cellular organization (74). In drought stress-tolerant foxtail millet variety, there is a moderate rate of decline in chlorophyll, increased soluble sugar and proline concentrations and a significant increase in the stress hormones ABA and JA. At various crop stages, genetic variability plays a major role in plant stress tolerance. Linoleate 9S-lipoxygenase (LOX) encodes an enzyme involved in lipid peroxidation, which is induced by water and heat stresses in foxtail millet (75). In millets, salicylic acid (SA) and jasmonic acid (JA) enhance the tolerance in plants against drought, salinity and heat stress. These phytohormones are involved in adaptive responses such as the regulation of gene expression, which help plants in the adaptation to stress. A high temperature stress-tolerant variety of foxtail millet shows low photosynthetic and stomatal conductance rates, reduced root respiration, accumulation of protective metabolites (serine, threonine, valine, fructose, glucose, maltose, isomaltose, malate and itaconate) in roots, with a better utilization of carbon and nitrogen (76). The effects of water stress and HS are reported to be key regulators of abscisic acid (ABA) biosynthesis and lead to a 7 to 8-fold increase of ABA in foxtail millet. High levels of osmotic adjustment and transpiration were found in resistant races of millet to drought stress. Osmotic adjustment is greater in millet races with smaller plants having small organs and cells; hence, having smaller plants in these races is a drought-adaptive trait. Supporting these adaptations at the molecular level are gene regulatory networks that modulate stress responses in millet species.

Molecular and genetic adaptation

Millets demonstrate exceptional adaptability to diverse abiotic stresses through intricate molecular, biochemical and physiological mechanisms. These adaptations include gene upregulation, stress-signaling pathways and the accumulation of protective metabolites (77).

In pearl millet, the PgPAP18 gene, which belongs to the purple acid phosphatase (PAP) family, acts as a ROS scavenger and crosstalks in stress signalling pathway, shows 2-to-3-fold upregulation under heat as well as drought, salt and metal stresses (78). In finger millet, EhHSP17.8, a heat shock protein gene induced by heat, shows upregulation up to 40-fold under especially in root tissues. Abiotic stress-inducible promoters in pearl millet, for example PgHsc70 (Heat shock cognate) with its chaperone activity, ensure proper protein folding and translocation of newly synthesised protein under heat temperature. The pgWRKY genes were identified with 127 cis-regulatory elements for biotic and abiotic stresses in pearl millet (79). General abiotic stress cascade, including heat stress, highlights stress signal recognition by cell membrane receptors (GPCR, ELR), calcium channels and ion transporters. Secondary messengers such as Ca^{2+} , ROS etc., activate kinase cascade (CDPK, MAPK) and phytohormone pathways (ABA, ET, SA, JA) (80). Activation/upregulation of transcription factors (TFs) like SiAREB1, SiAREB2, SiMYB42, EcNAC1, EcbZIP60, etc., under multiple abiotic stresses including heat. Leads to the expression of protective genes such as heat shock proteins, antioxidants (APX, SOD, GlutR), osmoregulators, increased wax content, membrane integrity, root traits and WUE (80). Table 4 lists the genes and sources involved in drought. These combined mechanisms make millets a superior choice for cultivation under climate stress when compared to staple cereals.

Millets are an advantageous crop over staple crops

Significant yield loss due to heat has already been reported in many crops and the annual increase in temperature due to climate change threatens food security. As estimated by statistical modeling, climate change and global warming are likely to severely affect cereal production in Africa and Asia (81).

Nearly all millet crops have innate mechanisms to cope with certain environmental stresses such as heat, drought, lodging and waterlogging. Yet, these stresses threaten millet production with the increasing impact of climate change. Millet crops have vital nutritional benefits as compared to other cereals. As demonstrated in the previous study (82), millets not only withstand abiotic stresses like heat more effectively than staple crops but also retain their nutritional value under such conditions. Their superior C4 photosynthesis, shorter life cycles and robust stress-response genes like DREB2, LEA14 and ARDP make them ideal candidates for climate-resilient agriculture. Compared to rice and wheat, which exhibit significant declines in protein and micronutrient content under heat stress, millets show higher stability of essential nutrients and antioxidants, reinforcing their role in sustainable nutritional security (82). For example, pearl millet has higher protein content (10.9 g) compared to rice (07.9 g) and wheat (10.6 g). Also, the iron content in pearl millet (6.4 mg) is higher than rice (0.6 mg) and wheat (3.9 mg) (83). Table 5 nutritional value of major cereals and millets (per 100 g) (84) (85, 86). It shows that the millets have a higher protein (7.3-12.5 g/100 g) proportion compared to rice

Table 4. List of genes and sources involved in drought stress

Gene	Source	Function
SiLEA14	Foxtail millet	Transgenic Arabidopsis, transgenic foxtail millet - overexpression enhances tolerance to salt and drought stresses
EcNAC1 (NAM, ATAF1/2 and CUC2) transcription factor	Finger millet	Increased tolerance to various abiotic stresses, such as osmotic stress and salinity stress
Plasma membrane proteolipid genes (PgPmp3-1 and PgPmp3-2)	Pearl millet	Drought and salt stresses and provided abiotic stress tolerance to plants by encoding hydrophobic proteins and maintaining cellular ion homeostasis
Lipid transfer gene (SiLTP)	Foxtail millet	Drought and salt tolerance in this species by increasing the proline and total soluble sugar contents
SiMYB42 (myeloblastosis) transcription factor	Foxtail millet	Under low nitrogen, salt and drought stresses, it regulated the expression of nitrate transporter genes, which enhanced the plant tolerance to low nitrogen conditions
Calcium-dependent protein kinases (CDPK)	Foxtail millet	Signalling pathways and enhance drought resistance in the plant and transgenic Arabidopsis
NAC (NAM, ATAF and CUC)	Foxtail millet	Enhance the gene expression in Arabidopsis for proline biosynthesis, Na ⁺ /K ⁺ transport and aqueous transport proteins
NF-Y (nuclear factor Y) genes, SiNF-YA1 and SiNF-YB8	Foxtail millet	Activates stress related genes, RWC, chlorophyll contents and SOD, POD and CAT, thus enhancing the antioxidant system
Autophagy-related gene SiATG8a	Foxtail millet	Localized in the membrane and cytoplasm - in plant responses to nitrogen starvation and drought stress, as higher nitrogen content showed higher drought tolerance
Antioxidant genes, i.e., APX, glutathione reductase (GluR) and SOD	Pearl millet	During polyethylene glycol (PEG)-induced drought stress conditions, resulting in a higher osmotic stress tolerance in the seedlings

Table 5. Nutritional value of major cereals and millets (per 100 g) (84-86)

Crop	Protein (g)	Carbohydrate (g)	Fat (g)	Crude (g)	Ca (mg)	P (mg)	Fe (mg)	Zn (mg)
Rice	4.99	82.86	1.90	1.63	0.12	0.52	1.25	0.5
Wheat	13.78	69.88	2.81	1.77	43.41	357.74	54.24	2.9
Maize	8.84	71.84	4.57	2.15	10	348	2.3	-
Pearl millet	11.6	67.5	5.0	1.2	42	296	10.3	3.10
Sorghum	10.4	72.6	1.9	1.6	25	222	5.29	3.05
Finger millet	7.3	72.0	1.3	3.6	344	283	4.27	36.6
Proso millet	12.5	70.4	1.1	2.2	14	206	2.2	4.3
Foxtail millet	12.3	60.9	4.3	8.0	31	290	3.5	60.6
Kodo millet	8.3	65.9	1.4	9.0	27	188	3.17	32.7
Little millet	8.7	75.7	5.3	8.6	17	220	9.3	3.5
Barnyard millet	11.6	74.3	5.8	14.7	14	121	17.47	57.45

Source: National Academy of Agricultural Sciences, New Delhi (2018). (4.99 g/100 g) and a higher carbohydrate (72.6-75.7 g/100 g) content compared to maize (71.84 g/100 g). Similarly, millets have higher calcium (14-42 mg/100 g) content compared to rice (0.12 mg/100 g) and maize (10 mg/100 g) and iron content is higher in millets (3.5-17.47 mg/100 g) compared to rice (1.25 mg/100 g) and maize (2.3 mg/100 g). Zinc content is higher in millets (3.05-60.6 mg/100 g) compared to rice (0.5 mg/100 g) and wheat (2.9 mg/100 g).

Millets, including pearl millet, sorghum and minor millets, have been traditionally cultivated across India, but they have been in a decreasing trend since the 1980s. A substantial increase in crop area under millets, along with major staple crops, improves the nutritional security (84). Farmers in dry areas can prefer short-duration, high tillering varieties of pearl millet, which ensures better yield and fodder value as it can escape stress by short flowering time. This approach can provide economic relief to farmers during drought years or periods of extreme heat stress, as these millet varieties offer reliable yields and fodder even under adverse conditions. Innate mechanisms of tolerance in millets play a role against nutritional impairment, which can help to sustain nutritional security.

Conclusion

Millets are emerging as strategic crops in the phase of climate change due to their resilience to HS and other abiotic challenges. Key stress-tolerance mechanisms in millets include morphological adaptations such as deep root systems and smaller leaf areas, along with biochemical and molecular responses like the upregulation of antioxidant enzymes, heat-shock proteins and osmoprotectants. Genetic variability and stress-responsive genes, such as those regulating proline accumulation, phytohormone signaling and antioxidant activity, contribute to the heat and drought resilience of millet varieties. Modern breeding techniques, including genomic and transcriptomic studies, have identified critical genes and transcription factors that enhance millet's thermotolerance. Integrating advanced technologies like CRISPR/Cas9 and PGPRs offers promising opportunities to enhance these traits further, ensuring higher productivity under extreme weather conditions. Given the rising global temperatures and the urgent need for sustainable food systems, millets hold immense potential as climate-resilient crops. Their capacity to withstand heat, drought and other environmental stresses makes them ideal for regions facing water scarcity and erratic climatic conditions. In addition to their environmental resilience, millets offer significant nutritional benefits, supporting both food and nutritional security. Future research focusing on the molecular and biochemical basis

of heat tolerance, along with the development of stress-tolerant genotypes, will be crucial to fully harnessing the potential of millets as staple crops in the fight against climate change and global food insecurity. Thus, incorporating millets into cropping systems offers a dual advantage such as resilience to thermal stress and sustained nutritional output, making them a vital component of climate-smart agriculture. While current findings highlight the promise of millets, further exploration is needed to fully leverage their potential in heat-stressed environments.

Future perspective

Though there are numerous research and concepts available for abiotic stresses (drought, salt stress) tolerance in millets, there are very less papers on HS or high temperature impact. A detailed study on the tolerance of millet crops, especially under HS impact on molecular, physiological and biochemical basis and its effect on the nutritional status of produce is needed. Identifying key adaptive traits and genes under HS at different treatments as stress at different stages of crop, different lengths of heat stress period and stress at different levels of elevated temperature, would help to choose millets as a strategic crop under a changing climate. Weather extremes these days pave the way to adopt treatments, as such extremes are used to study various crops and identify traits and components of interest against weather variabilities. Techniques such as PGPRs and CRISPR/Cas9 are being used in other crops to lessen the impact of abiotic stresses, as well as to improve the productivity of crops. Some candidate genes that can be targeted for manipulation by the CRISPR/Cas9 system to improve the growth and yield of millet crops have been suggested. In the context of climate change and global warming, this knowledge lays the foundation for further studies on metabolic engineering and selecting crops resilient to high temperatures. Genomics, transcriptomics, metabolomics, proteomics and other fields of study will also complement the alternative strategy we put forward. Improvement of millets has lagged behind that of major food crops and deserves increased attention from geneticists, biotechnologists, breeders, germplasm conservationists, etc., to improve global food security amidst climate change that is increasingly affecting the productivity of staple crops.

Acknowledgements

We would like to thank the Department of Agro Climate Research Centre, TNAU, Coimbatore, for their kind cooperation and guidance for collection of literature and critical writing of our review on heat stress impact study. I would also want to thank my advisory committee members, the professor and head, the faculty and my friends for their advice and assistance with this experiment.

Authors' contributions

Supervised the overall study, provided critical feedback on manuscript collection and interpretation, writing review. Authors contributed to finalization of review topic and related topics under study based on current scenario on climate change in a critical approach. And contributed to collection of

literature and related data on climate change, agronomical, crop physiology and biochemical (nutritional) aspects. Also ensured adherence to research standards and approved the final version for submission. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

References

- Schmidhuber J, Tubiello FN. Global food security under climate change. *Proceedings of the National Academy of Sciences*. 2007;104(50):19703-8. <https://doi.org/10.1073/pnas.0701976104>
- Lin H-I, Yu Y-Y, Wen F-I, Liu P-T. Status of food security in East and Southeast Asia and challenges of climate change. *Climate*. 2022;10(3):40. <https://doi.org/10.3390/cli10030040>
- Alam M, Lou G, Abbas W, Osti R, Ahmad A, Bista S, et al. Improving rice grain quality through ecotype breeding for enhancing food and nutritional security in Asia-Pacific region. *Rice*. 2024;17(1):47. <https://doi.org/10.1186/s12284-024-00647-x>
- Bhandari S, Banjara MR. Micronutrients deficiency, a hidden hunger in Nepal: prevalence, causes, consequences and solutions. *International Scholarly Research Notices*. 2015;2015:276469. <https://doi.org/10.1155/2015/276469>
- Noor JJ, Vinayan M, Umar S, Devi P, Iqbal M, Seetharam K, et al. Morpho-physiological traits associated with heat stress tolerance in tropical maize (*Zea mays* L.) at reproductive stage. *Australian Journal of Crop Science*. 2019;13(4):536-45. <https://doi.org/10.21475/ajcs.19.13.04.p1448>
- York LM. Functional phenomics: an emerging field integrating high-throughput phenotyping, physiology and bioinformatics. *Journal of Experimental Botany*. 2019;70(2):379-86. <https://doi.org/10.1093/jxb/ery417>
- Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, et al. Crop production under drought and heat stress: plant responses and management options. *Frontiers in Plant Science*. 2017;8:1147. <https://doi.org/10.3389/fpls.2017.01147>
- Hoffman A, Kemanian A, Forest C. The response of maize, sorghum and soybean yield to growing-phase climate revealed with machine learning. *Environmental Research Letters*. 2020;15(9):094013. <https://doi.org/10.1088/1748-9326/ab8e49>
- Farhad M, Kumar U, Tomar V, Bhati PK, Krishnan JN, Barek V, et al. Heat stress in wheat: a global challenge to feed billions in the current era of the changing climate. *Frontiers in Sustainable Food Systems*. 2023;7:1203721. <https://doi.org/10.3389/fsufs.2023.1203721>
- Kaur V, Singh S, Behl RK. Heat and drought tolerance in wheat: integration of physiological and genetic platforms for better performance under stress. *Ekin Journal of Crop Breeding and Genetics*. 2016;2(1):1-14.
- Fahad S, Adnan M, Hassan S, Saud S, Hussain S, Wu C, et al. Rice responses and tolerance to high temperature. In: *Advances in rice research for abiotic stress tolerance*. Elsevier; 2019. p. 201-24.
- Kumar SV, Kumar D, Shivay Y, Anand A, Sharma D, Sharma V, et al. Growth and productivity of wheat (*Triticum aestivum*) as influenced by potassium application. *Indian Journal of Agronomy*. 2019;64(3):341-7. <https://doi.org/10.59797/ija.v6i3.5281>

13. Kumar R, Bhardwaj A, Singh LP, Singh G. Environmental and economical assessment of maize cultivation in Northern India. *Process Integration and Optimization for Sustainability*. 2024;8(1):165-79. <https://doi.org/10.1007/s41660-023-00358-3>
14. Serba DD, Yadav RS, Varshney RK, Gupta S, Mahalingam G, Srivastava RK, et al. Genomic designing of pearl millet: a resilient crop for arid and semi-arid environments. In: *Genomic designing of climate-smart cereal crops*. Springer, Cham.; 2020. p. 221-86. https://doi.org/10.1007/978-3-319-93381-8_6
15. Lenka B, Kulkarni G, Moharana A, Singh AP, Pradhan GS, Muduli L. Millets: promising crops for climate-smart agriculture. *Int J Curr Microbiol App Sci*. 2020;9(11):656-68. <https://doi.org/10.20546/ijcmas.2020.911.081>
16. Tadele Z. Drought adaptation in millets. InTech; 2016.
17. Numan M, Serba DD, Ligaba-Osena A. Alternative strategies for multi-stress tolerance and yield improvement in millets. *Genes*. 2021;12(5):739. <https://doi.org/10.3390/genes12050739>
18. Vijayalakshmi D, Raveendran M. Physiological analysis of C3 rice [*Oryza sativa* (L.)] and C4 millet [*Setaria italica* (L.)] to identify photosynthetically efficient plants. *Indian Journal of Plant Physiology*. 2018;23:193-200. <https://doi.org/10.1007/s40502-018-0373-9>
19. Kumar A, Tripathi MK, Joshi D, Kumar V. Millets and millet technology. Springer; 2021.
20. Satyavathi CT, Solanki R, Kakani R, Bharadwaj C, Singhal T, Padaria J, et al. Genomics assisted breeding for abiotic stress tolerance in millets. In: *Genomics assisted breeding of crops for abiotic stress tolerance*. Vol. II. Springer, Cham.; 2019. p. 241-55. https://doi.org/10.1007/978-3-319-99573-1_13
21. Liu JP, Sun XJ, Xu FY, Zhang YJ, Zhang Q, Miao R, et al. Suppression of *OsMDHAR4* enhances heat tolerance by mediating H₂O₂-induced stomatal closure in rice plants. *Rice*. 2018;11:38. <https://doi.org/10.1186/s12284-018-0230-5>
22. Xu J, Henry A, Sreenivasulu N. Rice yield formation under high day and night temperatures-a prerequisite to ensure future food security. *Plant, Cell & Environment*. 2020;43(7):1595-608. <https://doi.org/10.1111/pce.13825>
23. Xu Y, Zhang L, Ou S, Wang R, Wang Y, Chu C, et al. Natural variations of *SLG1* confer high-temperature tolerance in indica rice. *Nature Communications*. 2020;11(1):5441. <https://doi.org/10.1038/s41467-020-19168-x>
24. Arshad MS, Farooq M, Asch F, Krishna JS, Prasad PV, Siddique KH. Thermal stress impacts reproductive development and grain yield in rice. *Plant Physiology and Biochemistry*. 2017;115:57-72. <https://doi.org/10.1016/j.plaphy.2017.03.024>
25. Soda N, Gupta BK, Anwar K, Sharan A, Govindjee, Singla-Pareek SL, et al. Rice intermediate filament, *OsIF*, stabilizes photosynthetic machinery and yield under salinity and heat stress. *Scientific Reports*. 2018;8(1):4072. <https://doi.org/10.1038/s41598-018-22461-2>
26. Liu G, Zha Z, Cai H, Qin D, Jia H, Liu C, et al. Dynamic transcriptome analysis of anther response to heat stress during anthesis in thermotolerant rice (*Oryza sativa* L.). *International Journal of Molecular Sciences*. 2020;21(3):1155. <https://doi.org/10.3390/ijms21031155>
27. Endo M, Tsuchiya T, Hamada K, Kawamura S, Yano K, Ohshima M, et al. High temperatures cause male sterility in rice plants with transcriptional alterations during pollen development. *Plant and Cell Physiology*. 2009;50(11):1911-22. <https://doi.org/10.1093/pcp/pcp132>
28. Zhao L, Lei J, Huang Y, Zhu S, Chen H, Huang R, et al. Mapping quantitative trait loci for heat tolerance at anthesis in rice using chromosomal segment substitution lines. *Breeding Science*. 2016;66(3):358-66. <https://doi.org/10.1270/jsbbs-16009>
29. Shi W, Li X, Schmidt RC, Struik PC, Yin X, Jagadish SK. Pollen germination and *in vivo* fertilization in response to high-temperature during flowering in hybrid and inbred rice. *Plant, Cell & Environment*. 2018;41(6):1287-97. <https://doi.org/10.1111/pce.13203>
30. Begcy K, Sandhu J, Walia H. Transient heat stress during early seed development primes germination and seedling establishment in rice. *Frontiers in Plant Science*. 2018;9:1768. <https://doi.org/10.3389/fpls.2018.01768>
31. Folsom JJ, Begcy K, Hao X, Wang D, Walia H. Rice *Fertilization-Independent Endosperm1* regulates seed size under heat stress by controlling early endosperm development. *Plant Physiology*. 2014;165(1):238-48. <https://doi.org/10.1104/pp.113.232413>
32. Ishimaru T, Parween S, Saito Y, Shigemitsu T, Yamakawa H, Nakazono M, et al. Laser microdissection-based tissue-specific transcriptome analysis reveals a novel regulatory network of genes involved in heat-induced grain chalk in rice endosperm. *Plant and Cell Physiology*. 2019;60(3):626-42. <https://doi.org/10.1093/pcp/pcy234>
33. Sita K, Sehgal A, HanumanthaRao B, Nair RM, Vara Prasad P, Kumar S, et al. Food legumes and rising temperatures: effects, adaptive functional mechanisms specific to reproductive growth stage and strategies to improve heat tolerance. *Frontiers in Plant Science*. 2017;8:1658. <https://doi.org/10.3389/fpls.2017.01658>
34. Niu Y, Xiang Y. An overview of biomembrane functions in plant responses to high-temperature stress. *Frontiers in Plant Science*. 2018;9:915. <https://doi.org/10.3389/fpls.2018.00915>
35. Coast O, Posch BC, Rognoni BG, Bramley H, Gaju O, Mackenzie J, et al. Wheat photosystem II heat tolerance: evidence for genotype -by-environment interactions. *The Plant Journal*. 2022;111(5):1368-82. <https://doi.org/10.1111/tpj.15857>
36. Lal MK, Tiwari RK, Gahlaut V, Mangal V, Kumar A, Singh MP, et al. Physiological and molecular insights on wheat responses to heat stress. *Plant Cell Reports*. 2021;40:1955-72. <https://doi.org/10.1007/s00299-021-02752-x>
37. Zhao Q, Zhou L, Liu J, Cao Z, Du X, Huang F, et al. Involvement of CAT in the detoxification of HT-induced ROS burst in rice anther and its relation to pollen fertility. *Plant Cell Reports*. 2018;37:741-57. <https://doi.org/10.1007/s00299-018-2264-6>
38. Qiao B, Zhang Q, Liu D, Wang H, Yin J, Wang R, et al. A calcium-binding protein, rice annexin *OsANN1*, enhances heat stress tolerance by modulating the production of H₂O₂. *Journal of Experimental Botany*. 2015;66(19):5853-66. <https://doi.org/10.1093/jxb/erv295>
39. Chakraborty A, Bhattacharjee S. Differential competence of redox -regulatory mechanism under extremes of temperature determines growth performances and cross tolerance in two indica rice cultivars. *Journal of Plant Physiology*. 2015;176:65-77. <https://doi.org/10.1016/j.jplph.2014.11.013>
40. Bahuguna RN, Jha J, Pal M, Shah D, Lawas LM, Khetarpal S, et al. Physiological and biochemical characterization of NERICA-L-44: a novel source of heat tolerance at the vegetative and reproductive stages in rice. *Physiologia Plantarum*. 2015;154(4):543-59. <https://doi.org/10.1111/ppl.12297>
41. Sailaja B, Subrahmanyam D, Neelamraju S, Vishnukiran T, Rao YV, Vijayalakshmi P, et al. Integrated physiological, biochemical and molecular analysis identifies important traits and mechanisms associated with differential response of rice genotypes to elevated temperature. *Frontiers in Plant Science*. 2015;6:1044. <https://doi.org/10.3389/fpls.2015.01044>
42. Wang X, Xu C, Cai X, Wang Q, Dai S. Heat-responsive photosynthetic and signaling pathways in plants: insight from proteomics. *International Journal of Molecular Sciences*. 2017;18(10):2191. <https://doi.org/10.3390/ijms18102191>
43. Perdomo JA, Capó-Bauçà S, Carmo-Silva E, Galmés J. 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*. 2017;8:490. <https://doi.org/10.3389/fpls.2017.00490>
44. Wu C, Cui K, Wang W, Li Q, Fahad S, Hu Q, et al. Heat-induced phytohormone changes are associated with disrupted early reproductive development and reduced yield in rice. *Scientific Reports*. 2016;6:34978. <https://doi.org/10.1038/srep34978>
 45. Liu J, Hasanuzzaman M, Wen H, Zhang J, Peng T, Sun H, et al. High temperature and drought stress cause abscisic acid and reactive oxygen species accumulation and suppress seed germination growth in rice. *Protoplasma*. 2019;256:1217-27. <https://doi.org/10.1007/s00709-019-01357-y>
 46. Ullah A, Nadeem F, Nawaz A, Siddique KH, Farooq M. Heat stress effects on the reproductive physiology and yield of wheat. *Journal of Agronomy and Crop Science*. 2022;208(1):1-17. <https://doi.org/10.1111/jac.12527>
 47. Wang W, Li Y, Dang P, Zhao S, Lai D, Zhou L. Rice secondary metabolites: structures, roles, biosynthesis and metabolic regulation. *Molecules*. 2018;23(12):3098. <https://doi.org/10.3390/molecules23123098>
 48. Gupta V, Jatav PK, Verma R, Kothari SL, Kachhwaha S. Nickel accumulation and its effect on growth, physiological and biochemical parameters in millets and oats. *Environmental Science and Pollution Research*. 2017;24:23915-25. <https://doi.org/10.1007/s11356-017-0042-y>
 49. Kumar A, Sharma S, Chunduri V, Kaur A, Kaur S, Malhotra N, et al. Genome-wide identification and characterization of heat shock protein family reveals role in development and stress conditions in *Triticum aestivum* L. *Scientific Reports*. 2020;10(1):7858. <https://doi.org/10.1038/s41598-020-64748-0>
 50. Lee MH, Kim K-M, Sang W-G, Kang C-S, Choi C. Comparison of gene expression changes in three wheat varieties with different susceptibilities to heat stress using RNA-Seq analysis. *International Journal of Molecular Sciences*. 2022;23(18):10734. <https://doi.org/10.3390/ijms231810734>
 51. Mohi-Ud-Din M, Siddiqui MN, Rahman MM, Jagadish K, Ahmed JU, Islam T. Heat-induced oxidative damage is ameliorated by enhanced antioxidants activity in the tolerant wheat variety. *Authorea Preprints*. 2022. <https://doi.org/10.22541/au.164864297.72130596/v1>
 52. Bahuguna RN, Solis CA, Shi W, Jagadish KS. Post-flowering night respiration and altered sink activity account for high night temperature-induced grain yield and quality loss in rice (*Oryza sativa* L.). *Physiologia Plantarum*. 2017;159(1):59-73. <https://doi.org/10.1111/ppl.12485>
 53. Rezaul IM, Baohua F, Tingting C, Weimeng F, Caixia Z, Longxing T, et al. Absciscic acid prevents pollen abortion under high-temperature stress by mediating sugar metabolism in rice spikelets. *Physiologia Plantarum*. 2019;165(3):644-63. <https://doi.org/10.1111/ppl.12763>
 54. De Storme N, Geelen D. The impact of environmental stress on male reproductive development in plants: biological processes and molecular mechanisms. *Plant, Cell & Environment*. 2014;37(1):1-18. <https://doi.org/10.1111/pce.12142>
 55. Yamakawa H, Hirose T, Kuroda M, Yamaguchi T. Comprehensive expression profiling of rice grain filling-related genes under high temperature using DNA microarray. *Plant Physiology*. 2007;144(1):258-77. <https://doi.org/10.1104/pp.107.098665>
 56. Asthir B, Koundal A, Bains N. Putrescine modulates antioxidant defense response in wheat under high temperature stress. *Biologia Plantarum*. 2012;56:757-61. <https://doi.org/10.1007/s10535-012-0140-5>
 57. Panozzo JF, Eagles HA, Cultivar and environmental effects on quality characters. *Australian Journal of Agricultural Research*. 2000;51:629-36. <https://doi.org/10.1071/AR99137>
 58. Yousaf MI, Riaz MW, Jiang Y, Yasir M, Aslam MZ, Hussain S, et al. Concurrent effects of drought and heat stresses on physiochemical attributes, antioxidant status and kernel quality traits in maize (*Zea mays* L.) hybrids. *Frontiers in Plant Science*. 2022;13:898823. <https://doi.org/10.3389/fpls.2022.898823>
 59. Mishra S, Spaccarotella K, Gido J, Samanta I, Chowdhary G. Effects of heat stress on plant-nutrient relations: an update on nutrient uptake, transport and assimilation. *International Journal of Molecular Sciences*. 2023;24(21):15670. <https://doi.org/10.3390/ijms242115670>
 60. Qu L, Gu X, Li J, Guo J, Lu D. Leaf photosynthetic characteristics of waxy maize in response to different degrees of heat stress during grain filling. *BMC Plant Biology*. 2023;23(1):469. <https://doi.org/10.1186/s12870-023-04457-3>
 61. Patil D. Agrobiodiversity and advances in the development of millets in changing environment. In: *Sustainable agriculture in the era of climate change*. Springer, Cham.; 2020. p. 643-73. https://doi.org/10.1007/978-3-030-45669-6_27
 62. Zhang H, Li Y, Zhu J-K. Developing naturally stress-resistant crops for a sustainable agriculture. *Nature Plants*. 2018;4(12):989-96. <https://doi.org/10.1038/s41477-018-0309-4>
 63. Asthir B. Mechanisms of heat tolerance in crop plants. *Biologia Plantarum*. 2015;59:620-8. <https://doi.org/10.1007/s10535-015-0539-5>
 64. Gupta N, Agarwal S, Agarwal V, Nathawat N, Gupta S, Singh G. Effect of short-term heat stress on growth, physiology and antioxidative defence system in wheat seedlings. *Acta Physiologiae Plantarum*. 2013;35:1837-42. <https://doi.org/10.1007/s11738-013-1221-1>
 65. Liu TY, Ye N, Song T, Cao Y, Gao B, Zhang D, et al. Rhizosheath formation and involvement in foxtail millet (*Setaria italica*) root growth under drought stress. *Journal of Integrative Plant Biology*. 2019;61(4):449-62. <https://doi.org/10.1111/jipb.12716>
 66. Aparna K, Hash C, Yadav RS, Vadez V. Seed number and 100-seed weight of pearl millet (*Pennisetum glaucum* L.) respond differently to low soil moisture in genotypes contrasting for drought tolerance. *Journal of Agronomy and Crop Science*. 2014;200(2):119-31. <https://doi.org/10.1111/jac.12052>
 67. Serba DD, Yadav RS. Genomic tools in pearl millet breeding for drought tolerance: status and prospects. *Frontiers in Plant Science*. 2016;7:1724. <https://doi.org/10.3389/fpls.2016.01724>
 68. Kusaka M, Ohta M, Fujimura T. Contribution of inorganic components to osmotic adjustment and leaf folding for drought tolerance in pearl millet. *Physiologia Plantarum*. 2005;125(4):474-89. <https://doi.org/10.1111/j.1399-3054.2005.00578.x>
 69. Vijayalakshmi T, Varalaxmi Y, Jainender S, Yadav S, Vanaja M, Jyothilakshmi N, et al. Physiological and biochemical basis of water-deficit stress tolerance in pearl millet hybrid and parents. *Scientific Research*. 2012;3(12). <https://doi.org/10.4236/ajps.2012.312211>
 70. Shivhare R, Lata C. Assessment of pearl millet genotypes for drought stress tolerance at early and late seedling stages. *Acta Physiologiae Plantarum*. 2019;41(3):39. <https://doi.org/10.1007/s11738-019-2831-z>
 71. Bartwal A, Pande A, Sharma P, Arora S. Intervarietal variations in various oxidative stress markers and antioxidant potential of finger millet (*Eleusine coracana*) subjected to drought stress. *Journal of Environmental Biology*. 2016;37(4):517.
 72. Mundada P, Nikam T, Kumar SA, Umdale S, Ahire M. Morpho-physiological and biochemical responses of finger millet (*Eleusine coracana* (L.) Gaertn.) genotypes to PEG-induced osmotic stress. *Biocatalysis and Agricultural Biotechnology*. 2020;23:101488. <https://doi.org/10.1016/j.bcab.2019.101488>
 73. Shivhare R, Asif MH, Lata C. Comparative transcriptome analysis reveals the genes and pathways involved in terminal drought tolerance in pearl millet. *Plant Molecular Biology*. 2020;103(6):639-52. <https://doi.org/10.1007/s11103-020-01015-w>

74. Pan J, Li Z, Wang Q, Garrell AK, Liu M, Guan Y, et al. Comparative proteomic investigation of drought responses in foxtail millet. *BMC Plant Biology*. 2018;18:1-19. <https://doi.org/10.1186/s12870-018-1533-9>
75. Saha P, Sade N, Arzani A, Wilhelmi MdMR, Coe KM, Li B, et al. Effects of abiotic stress on physiological plasticity and water use of *Setaria viridis* (L.). *Plant Science*. 2016;251:128-38. <https://doi.org/10.1016/j.plantsci.2016.06.011>
76. Aidoo MK, Bdolach E, Fait A, Lazarovitch N, Rachmilevitch S. Tolerance to high soil temperature in foxtail millet (*Setaria italica* L.) is related to shoot and root growth and metabolism. *Plant Physiology and Biochemistry*. 2016;106:73-81. <https://doi.org/10.1016/j.plaphy.2016.04.038>
77. Saleem S, Mushtaq NU, Shah WH, Rasool A, Hakeem KR, Rehman RU. Morpho-physiological, biochemical and molecular adaptation of millets to abiotic stresses: A review. *Phyton*. 2021;90(5):1363. <https://doi.org/10.32604/phyton.2021.014826>
78. Chanwala J, Satpati S, Dixit A, Parida A, Giri MK, Dey N. Genome-wide identification and expression analysis of WRKY transcription factors in pearl millet (*Pennisetum glaucum*) under dehydration and salinity stress. *BMC Genomics*. 2020;21:1-16. <https://doi.org/10.1186/s12864-020-6622-0>
79. Parvathi M, Nataraja KN, Reddy YN, Naika MB, Gowda MC. Transcriptome analysis of finger millet (*Eleusine coracana* (L.) Gaertn.) reveals unique drought responsive genes. *Journal of Genetics*. 2019;98(2):46. <https://doi.org/10.1007/s12041-019-1087-0>
80. Li C, Yue J, Wu X, Xu C, Yu J. An ABA-responsive DRE-binding protein gene from *Setaria italica*, SiARDP, the target gene of SiAREB, plays a critical role under drought stress. *Journal of Experimental Botany*. 2014;65(18):5415-27. <https://doi.org/10.1093/jxb/eru302>
81. Lipiec J, Doussan C, Nosalewicz A, Kondracka K. Effect of drought and heat stresses on plant growth and yield: a review. *International Agrophysics*. 2013;27(4). <https://doi.org/10.2478/intag-2013-0017>
82. Bandyopadhyay T, Muthamilarasan M, Prasad M. Millets for next generation climate-smart agriculture. *Frontiers in Plant Science*. 2017;8:1266. <https://doi.org/10.3389/fpls.2017.01266>
83. Satyavathi CT, Ambawat S, Khandelwal V, Srivastava RK. Pearl millet: a climate-resilient nutricereal for mitigating hidden hunger and provide nutritional security. *Frontiers in Plant Science*. 2021;12:659938. <https://doi.org/10.3389/fpls.2021.659938>
84. Louhar G, Bana R, Kumar V, Kumar H. Nutrient management technologies of millets for higher productivity and nutritional security. *Indian Journal of Agricultural Sciences*. 2020;90(12):2243-50. <https://doi.org/10.56093/ijas.v90i12.110267>
85. Kumar A, Tomer V, Kaur A, Kumar V, Gupta K. Millets: a solution to agrarian and nutritional challenges. *Agriculture & Food Security*. 2018;7(1):1-15. <https://doi.org/10.1186/s40066-018-0183-3>
86. Rouf Shah T, Prasad K, Kumar P. Maize-A potential source of human nutrition and health: a review. *Cogent Food & Agriculture*. 2016;2(1):1166995. <https://doi.org/10.1080/23311932.2016.1166995>

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonpublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonpublishing.com/journals/index.php/PST/indexing_abstracting

Copyright: © The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited (<https://creativecommons.org/licenses/by/4.0/>)

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.