



REVIEW ARTICLE

Developing climate smart millets: Resilience strategies for sustainable agriculture and global nutrition security

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Received: 18 October 2025; Accepted: 27 April 2026; Available online: Version 1.0: 24 June 2026

Cite this article: Rubby S, Charupriya C, Suraj V, Sandeep KB, Tushadri S, Meenakshi A, Sunidhi T, Ashish KS. Developing climate smart millets : Resilience strategies for sustainable agriculture and global nutrition security. Plant Science Today. 13(sp2):01–11. <https://doi.org/10.14719/pst.12347>

Abstract

Millets have increasingly gained recognition as resilient, small-seeded cereal crops with immense potential for global food security and genetic improvement. These crops are of immense importance due to their ability to grow under harsh agro-climatic conditions, making them a sustainable and reliable food source. Millet requires minimal inputs, exhibits short growth cycles and provides farming communities with a stable source of income and livelihood, thereby reducing vulnerability to crop failure and market fluctuations. However, millet production faces several challenges, especially abiotic stresses like drought, salt stress and heat stress, which disrupt vital biological processes and lower productivity. Fortunately, various strategies have been successfully implemented to address these issues and improve millet yields. This review emphasises the role of millets in environmental security and sustainable agriculture and critically discusses the major abiotic stress challenges and available management and improvement strategies to ensure their sustained productivity.

Keywords: abiotic stress; food security; genetic improvement; resilient crops; sustainable agriculture

Introduction

Agriculture is a dynamic system that depends on a range of biological, chemical and physical processes to function efficiently. Among these, weather and climate are fundamental factors, as they influence essential elements such as water availability, pest and disease occurrence, topography, soil type, fertility and even the socioeconomic conditions of farming communities. All these factors are deeply interconnected and have a significant impact on agricultural production and productivity (1). Pearl millet is a vital staple crop for arid and semi-arid regions, largely due to its superior drought tolerance and nutritional value. However, even this resilient crop has its thresholds and extreme drought stress combined with poor soil fertility constitute its most significant abiotic constraints, and capping yields (2). This is particularly evident in Burkina Faso's semi-arid Sahelian and Sudano-Sahelian zones, which are marked by poor-quality soils, erratic rainfall and high temperatures. Alongside these abiotic stresses, biotic factors such as parasitic weeds like *Striga* species, bird damage, diseases like downy mildew

and pests like head miner further constrain millet production. Moreover, the reliance on low-yielding traditional varieties exacerbates these challenges (2). The effects of climate change have amplified these issues, particularly in Sub-Saharan Africa, including Burkina Faso. Climate change has led to more intense and frequent abiotic and biotic stresses, increasing the urgency for resilient crop varieties that can adapt to these changing conditions and support sustainable agricultural productivity (3).

The climate crisis has pushed humanity into a precarious position, threatening lives and livelihoods. Research shows that the frequency of natural disasters has increased fivefold over the past 50 years (4), with climate-related events such as droughts, floods, extreme temperatures and severe storms having the most direct impact on agricultural systems. This escalation has significantly disrupted crop growth, leading to food shortages and rising prices. Cereals serve as essential staple foods for billions worldwide. In the face of contemporary agricultural and climatic crises, nutritious and resilient millets emerge as strategic crops for the future. These small-grained cereals thrive in tough agricultural conditions with minimal

input. Millets are highly resilient to climate change, requiring little water and rainfall. Their efficient C_4 photosynthesis mechanism enables them to flourish even in poor soils and challenging environmental conditions (5). This makes them an excellent solution to combat climate-induced challenges both now and in the future. Millets are not just hardy; they are highly nutritious. They are rich in minerals, proteins and antioxidants. Being whole grains, they offer various forms and levels of fibre, which aid in regulating bowel movements, blood sugar and cholesterol levels. Millets also provide a healthy and nutrient-dense alternative to processed grains commonly found in international markets. Unfortunately, changing dietary preferences and the rise of alternative grains have led to a decline in millet production and demand. However, promoting millet cultivation and consumption could help reclaim their market share, offering new opportunities for small-scale farmers (6).

Among key millet species such as pearl millet, sorghum and finger millet, these grains are highly cost-effective energy sources, providing a higher proportion of digestible fibre, protein, vitamins and minerals compared to many other staples (7). For instance, the millet species sorghum alone accounts for approximately 35 % of the total calorie, protein, iron and zinc intake in regions where it dominates production and consumption (8). Beyond being a staple food, sorghum and other millets also serve as valuable sources of fodder, feed and industrial raw materials. Their ability to tolerate

high temperatures and drought makes them a reliable, climate-resilient crop. In areas like Vidarbha, which are prone to drought, promoting sorghum and other millets can significantly reduce agricultural risks. Integrating millets with pulse crops through intercropping offers a promising pathway to sustainable nutrition and financial stability. This approach achieves multiple goals: (i) increasing production, (ii) reducing cultivation costs, (iii) expanding market opportunities and (iv) building a sustainable value chain (9).

Climate change security

Rising temperatures, shifting monsoon patterns and other climate-related factors are directly affecting crop production, as well as various stages of food processing and distribution. These changes also impact the development of plants and animals, creating further challenges for agriculture (10). In this scenario, millets offer a promising solution. Known for their high content of essential nutrients such as iron, calcium and dietary fibre and their resilience to climate change, millets have the potential to provide better economic returns even under tough conditions (11). These crops are highly adaptable to diverse ecological environments, require minimal irrigation and thrive in low-nutrient soils. Millets also depend less on synthetic fertilisers and are less vulnerable to environmental stresses (12). With their climate-resilient traits, millets can play a crucial role in increasing agricultural incomes and ensuring food security while mitigating the adverse effects of climate

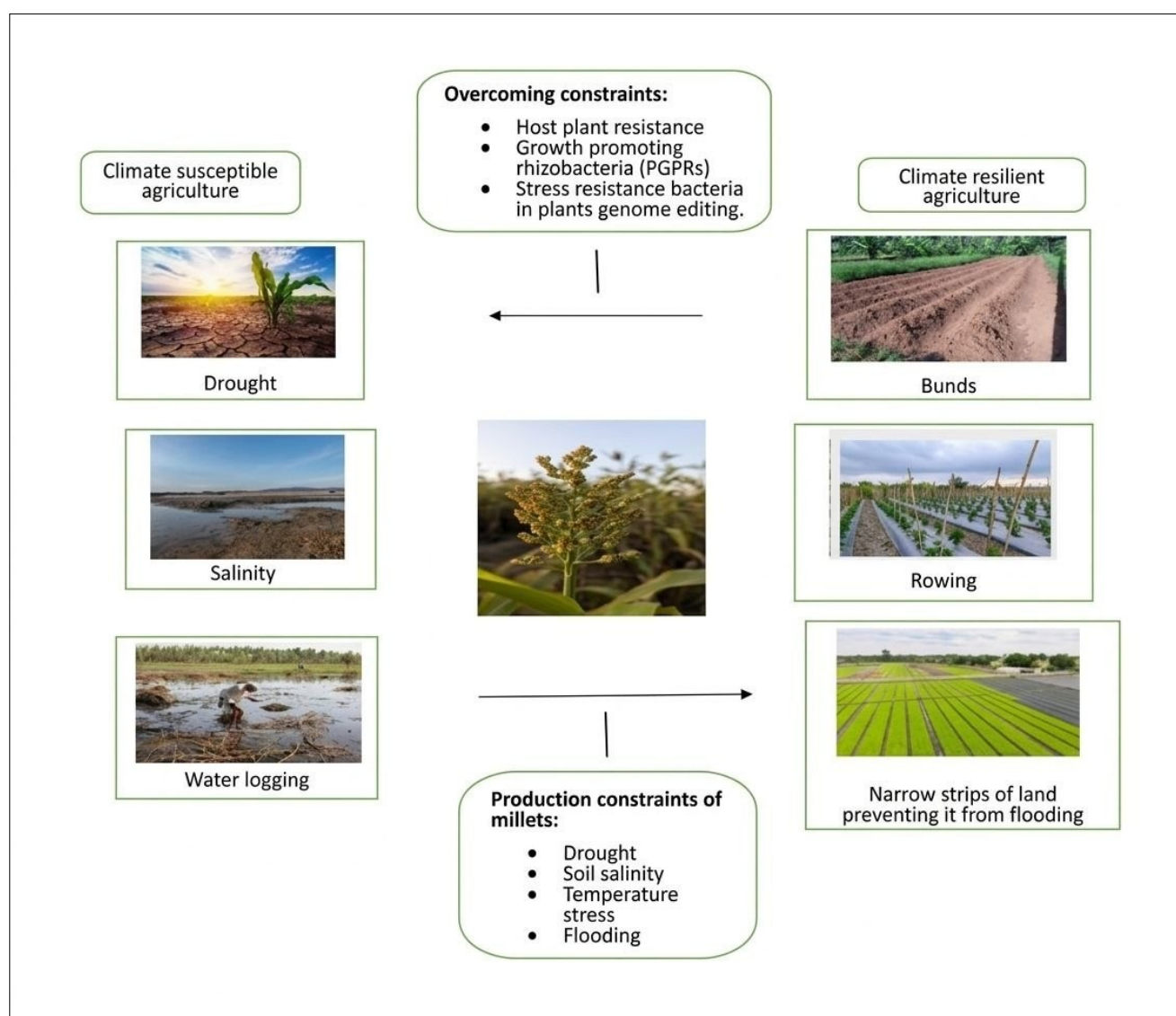


Fig. 1. Current challenges in agriculture and potential of millets to support climate-resilient farming.

change. Unlike many major staple crops whose yields are negatively impacted by changing climates, millets are uniquely equipped to thrive. Their C_4 photosynthesis system ensures high efficiency in dry matter production, shorter growing seasons and strong resistance to heat and drought. For example, some millets mature within 45 to 70 days, significantly less time than rice, which takes 120 to 140 days (10). Millets are also invaluable as a "contingent crop" during natural disasters like droughts and floods, providing a reliable option for farmers. Their high nutritional content and ability to withstand water scarcity and climate shocks make them an excellent choice for sustainable food security. By addressing key issues related to farmers' welfare, economic stability and nutrition, millets can help create climate-resilient agricultural systems (13). Fig. 1 depicts key challenges facing modern agriculture while emphasising the potential of millets in supporting climate-resilient farming.

Wheat has the highest global warming potential (GWP) among major cereal crops, producing an estimated 4 tons of CO_2 equivalent per hectare, followed by maize and rice at approximately 3.4 tons CO_2 equivalent per hectare. These crops also generate high carbon equivalent emissions (CEE), with wheat at $1000 \text{ kg C ha}^{-1}$, rice at 956 kg C ha^{-1} and maize at 935 kg C ha^{-1} . In comparison, millets have the lowest GWP at 3.2 tons CO_2 equivalent per hectare and the lowest CEE at 878 kg C ha^{-1} (10). Their low stature, limited leaf area, thicker cell walls and deep-root system allow them to withstand environmental challenges effectively. Additionally, millets benefit from their C_4 photosynthetic pathway, which enhances water use efficiency (WUE), nutrient use efficiency (NUE) and adaptability to hotter climates. These traits make millets versatile and climate-resilient crops, offering the potential for research into improving main cereal crops using knowledge gained from millet adaptation mechanisms (12). Amid global challenges such as groundwater depletion and irrigation constraints, millets stand out for their exceptional water-use efficiency. They require 70 % less water than rice and can produce a crop with as little as 400 mm of rainfall, yielding approximately 600 kg of grain per acre. For instance, foxtail millet requires only 257 g of water to produce 1 g of dry biomass,

compared to 470 g for maize and 510 g for wheat. Moreover, pearl millet demonstrates superior adaptability under osmotic stress by modifying membrane dynamics for better water permeability, along with increased root length and stronger leaf tensile strength under drought conditions (14).

Impact abiotic stress in millets

Millet production is heavily influenced by abiotic factors such as drought, heat, light stress, air drought (dry weather), high soil salinity and low soil fertility. Drought is the most significant challenge in millet-growing regions worldwide (1). Insufficient soil moisture and irregular rainfall patterns lead to drought stress, which affects millet cultivation globally. These conditions often occur during critical growth stages, such as seedling establishment, vegetative growth and grain filling (15). African countries like Eritrea, Ethiopia, Ghana, Uganda and Zimbabwe, Kenya, Namibia, Sudan, Tanzania are particularly affected. For example, in Ethiopia, soil-water deficits are common during the establishment and grain-filling stages of millet crops, while midseason moisture deficits are frequent in Uganda and Kenya (16, 17). Midseason stress is particularly damaging because it disrupts flowering, pollination and early grain set processes with high water demand that determine seed number and yield. In India, sorghum is grown during both the rainy and post-rainy seasons. However, the post-rainy season poses significant challenges due to increasing moisture stress as the season progresses. Frequent dry spells, which vary in intensity, duration and timing, result in lower sorghum yields (18).

Similarly, agriculture in West Africa heavily relies on rainfall, making it particularly vulnerable to climate change. The unpredictable nature of rainfall and temperature in the region leads to water scarcity and extreme weather events, such as droughts. These conditions significantly reduce agricultural output, threatening rural family food security (19). Despite irregular rainfall, pearl millet is not widely cultivated using supplementary irrigation in West African countries. This is primarily due to limited irrigation resources and the perception among farmers that millet is less valuable compared to other crops (20).

Impacts of abiotic stresses on millet production

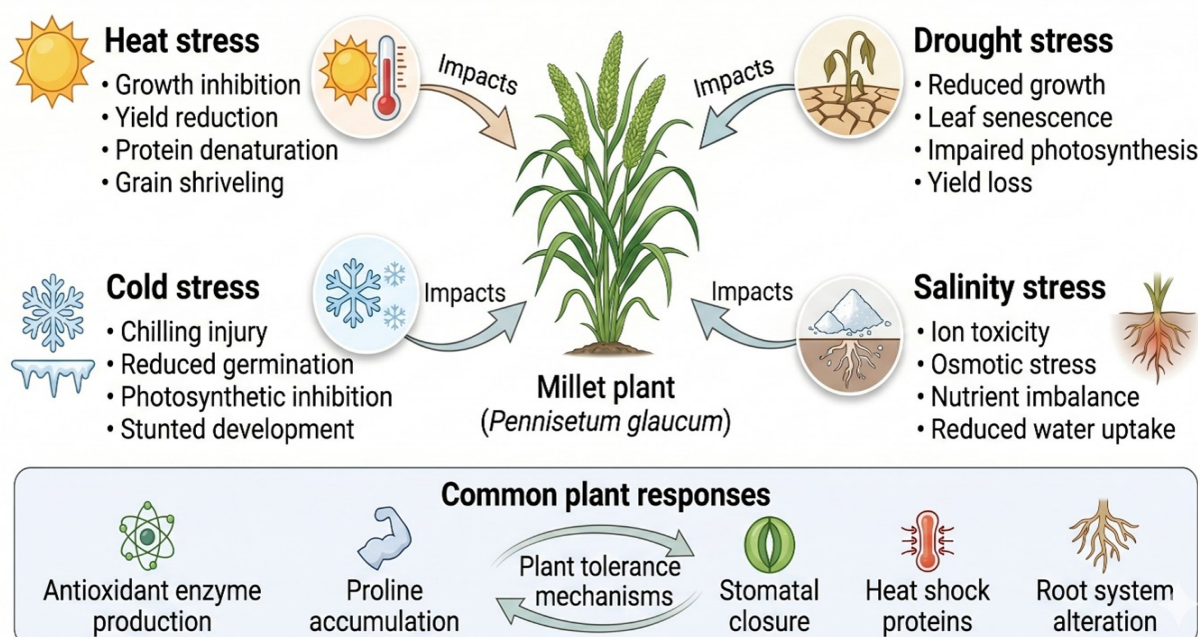


Fig. 2. Major abiotic stresses, including drought, salinity and temperature extremes, that adversely affect millet growth.

Moreover, meteorological factors such as rainfall, temperature, sunlight, wind speed and the frequency of rainy days vary greatly in semi-arid regions, leading to erratic crop establishment, reduced pollination success and substantial yield losses in millet cultivation. Major abiotic stresses affecting millet growth, including drought, salinity and temperature stress are illustrated in Fig. 2.

Low soil fertility and soil salinity

Millet is predominantly grown in sandy soils that are low in nutrients and have limited water-holding capacity. These soils often lack organic carbon, phosphorus and nitrogen, which are essential for plant growth (21). Poor nutrient content and organic carbon are major constraints in the semiarid soils of West Africa. Nutrient depletion is further exacerbated by farming practices such as continuous cropping without rotation and complete removal of crop residues, leading to soil degradation (22). The average organic matter in millet soils is about 1.4 %, with nitrogen levels of 446 mg/kg, phosphorus at 8 mg/kg and potassium at 78.2 mg/kg. These soils also struggle to retain water (21). Fertiliser usage in Africa is extremely low, averaging 16.2 kg/ha compared to the global average of 98 kg/ha. Farmers often cannot afford fertilisers due to high costs and limited availability. However, the adaptability of pearl millet to grow in challenging environments compensates for the lack of inputs, allowing it to thrive in resource-constrained conditions (23).

Salt stress effects and adaptation in millets

Salinity is a significant challenge for irrigated agricultural lands, drastically reducing crop productivity and impacting nutritional quality. Approximately 45 million hectares of irrigated land worldwide are currently affected by salinity, posing a serious threat to sustainable agriculture (24). Millets, though important crops, are classified as glycophytes and generally lack natural salt tolerance, making them vulnerable to saline conditions (25). Salt stress adversely affects foxtail millet, leading to reduced biomass, lower photosynthetic efficiency and decreased water potential, all of which limit its growth and yield (26, 27). On the other hand, finger millet exhibits a better capacity for salt tolerance, allowing it to maintain grain production even in saline environments (28). Studies on various genotypes of finger millet have demonstrated significant variation in salt tolerance, with some genotypes showing better performance under saline stress (29). However, salt stress still impairs germination and seedling development in finger millet, emphasising the need for further research and breeding initiatives to improve its resilience to salinity.

Physiological impact and plant response to salinity

Soil salinity has made many agricultural fields unproductive, posing

a significant threat to plant growth. High concentrations of sodium (Na^+) and chloride (Cl^-) ions in poor-quality water lead to osmotic stress, ion toxicity and nutritional imbalances in plants, which together contribute to salinity stress (30, 31). At present, salinity impacts approximately 33 % of irrigated agricultural land and 20 % of the world's cultivable land with projections suggesting this could rise to 50 % by 2050 (32). Salinity reduces plants' relative water content (RWC) by disrupting water absorption in roots, leading to dehydration and reduced growth (33). Finger millet, while moderately tolerant to salt stress, suffers from several adverse effects under high salinity. These include increased leaf succulence, chlorosis, tissue damage, lignification of xylem vessels, electrolyte leakage and elevated levels of hydrogen peroxide and proline. At the same time, it experiences decreases in terms of shoot dry weight, leaf number, surface area and chlorophyll content (34), finger millet has shown reduced germination rates, as well as slower root and shoot development. It also demonstrates lower leaf potassium (K^+) concentrations, along with increased salt and malondialdehyde (MDA) levels (35).

Other millet varieties, including foxtail millet and proso millet, exhibit similar responses to salinity, showing reductions in plant dry weight, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), RWC and nitrogen levels. Although foxtail millet tolerates salinity better than some other crops, it still experiences reduction in yield, growth and quality under saline conditions (36). Salinity negatively affects plant growth by inducing water stress, cytotoxic effects and nutritional imbalances due to the excessive uptake of ions like Na^+ and Cl^- . These effects often result in oxidative stress caused by the overproduction of reactive oxygen species (ROS), which further damages plant tissues (37, 38). To combat salinity, plants have evolved several mechanisms, including osmotic regulation, selective ion absorption and efficient antioxidant systems for detoxification. Osmotic stress commonly leads to the accumulation of compatible solutes such as proline, carbohydrates and proteins, which act as ROS scavengers to protect cells, maintain membrane integrity and stabilise protein structures. Both organic solutes (like sugars, amino acids and quaternary ammonium compounds) and inorganic ions are essential in developing osmotic tolerance (39, 40). The roles of key proteins contributing to salt stress tolerance in foxtail millet are presented in Table 1.

Temperature stress

Finger millet grows optimally at daytime temperatures ranging from 27–32 °C and night time temperatures around 22 °C. While the crop can withstand daytime temperatures between 18–32 °C and a night time minimum of 18 °C, any rise above 32 °C can hinder its flowering process, thereby reducing growth and productivity (41–43). This

Table 1. Role of proteins in enhancing salt stress tolerance in foxtail millet

Protein	Effect on tolerance	Relevant genes	Role	References
Late embryogenesis abundant (LEA) protein	Enhances tolerance	SiLEA14	Supports physiological responses under stress	(51)
Lipid transfer protein (LTP)	Boosts tolerance	SiLTP	It plays a role in physiological stress responses	(52)
HAK/KUP/KT Transporters (high-affinity K^+ transporters)	Promotes tolerance	SiHAK1	Contributes to physiological mechanisms	(53)
ASR Protein (Absciscic acid-, stress- and ripening-induced)	Strengthens response	SiASR1/4	Regulates gene expression and protein stability	(54, 55)
Receptor-like kinases (RLK)	Improves signalling	SiRLK35	Facilitates cellular signalling processes	(56)
WRKY Transcription factors	Enhances stress response	SiWRKY064/066/074/082	Regulates gene expression and protein	(57)

K^+ : potassium; HAK: high-affinity K^+ transporter; KUP: K^+ uptake permease.

makes temperature management critical, especially in semi-arid regions where finger millet is a vital food source for many communities (44). With global temperatures on the rise due to climate change, these regions are expected to experience even hotter conditions, potentially exacerbating challenges to the reproductive stages and yields of finger millet. The supra-optimal impacts of temperature have been investigated to comprehend how temperature affects seed germination (45). It was studied in millets that germination of seed requires 35–45 °C and at 47 °C it reduces, while at 50 °C it stops (46).

Climate projections suggest that arid and semi-arid regions will face greater vulnerability to climate change, with more extreme weather events, such as prolonged droughts and elevated temperatures, pose further threats to crop stability (47–50). Addressing these climatic challenges is crucial to protect the productivity of finger millet and ensure food security for the communities reliant on it.

Effect of temperature stress

High temperatures substantially lower crop yields by interfering with physiological processes (e.g., photosynthesis, pollen viability) and biochemical processes (e.g., enzyme denaturation, membrane lipid peroxidation). One major effect is the acceleration of crop development, which shortens the growth period and limits the time available for grain filling. Essential processes like photosynthesis and respiration are also negatively impacted, reducing their efficiency and altering the rate and duration of grain filling. Additionally, elevated temperatures decrease WUE by increasing saturation vapour pressure, which leads to greater water loss through transpiration. This added water stress further challenges plant growth and productivity. High temperatures also damage the cellular ultrastructure of plants, disrupting normal cellular functions and placing the plants under stress, ultimately reducing their overall yield and growth potential (58–61). Even modest increases in

temperature ranging from 1–4 °C above the optimal growth range can lead to a moderate reduction in crop yields. These seemingly small temperature changes can have substantial impacts on productivity (62–65). Fig. 3 illustrates the effects of temperature extremes on millets, highlighting associated physiological and genetic responses. Addressing the challenges posed by rising temperatures is crucial for maintaining crop productivity in the face of climate change. A deeper understanding of these complexities is key to developing mitigation and adaptation strategies that can reduce the negative effects of heat stress on crops.

Drought tolerance mechanisms

Millets are inherently drought-tolerant crops and extensive research has been conducted to understand how they respond to and adapt to water scarcity at different developmental stages. The impact of water stress varies depending on the growth stage of the crop. For instance, poor crop establishment can occur due to seedling death, which is often caused by water stress during germination or emergence phases (66, 67).

Exploring and understanding the drought tolerance mechanisms in different millet varieties can pave the way for developing drought-resistant crops. These mechanisms often involve specific physiological and genetic traits that allow millet plants to thrive under water-scarce conditions (68). Millets are increasingly recognised not only for their nutritional and health benefits but also for their remarkable ability to adapt to challenging environmental conditions. However, to fully harness their potential as a staple food crop, there is a pressing need to significantly improve millet productivity. Despite their adaptability, millet yields still lag behind those of major cereal crops, even under optimal growth conditions. Boosting millet yields is crucial to maximise their contribution to food security and effectively address the challenges brought about by climate change (68).

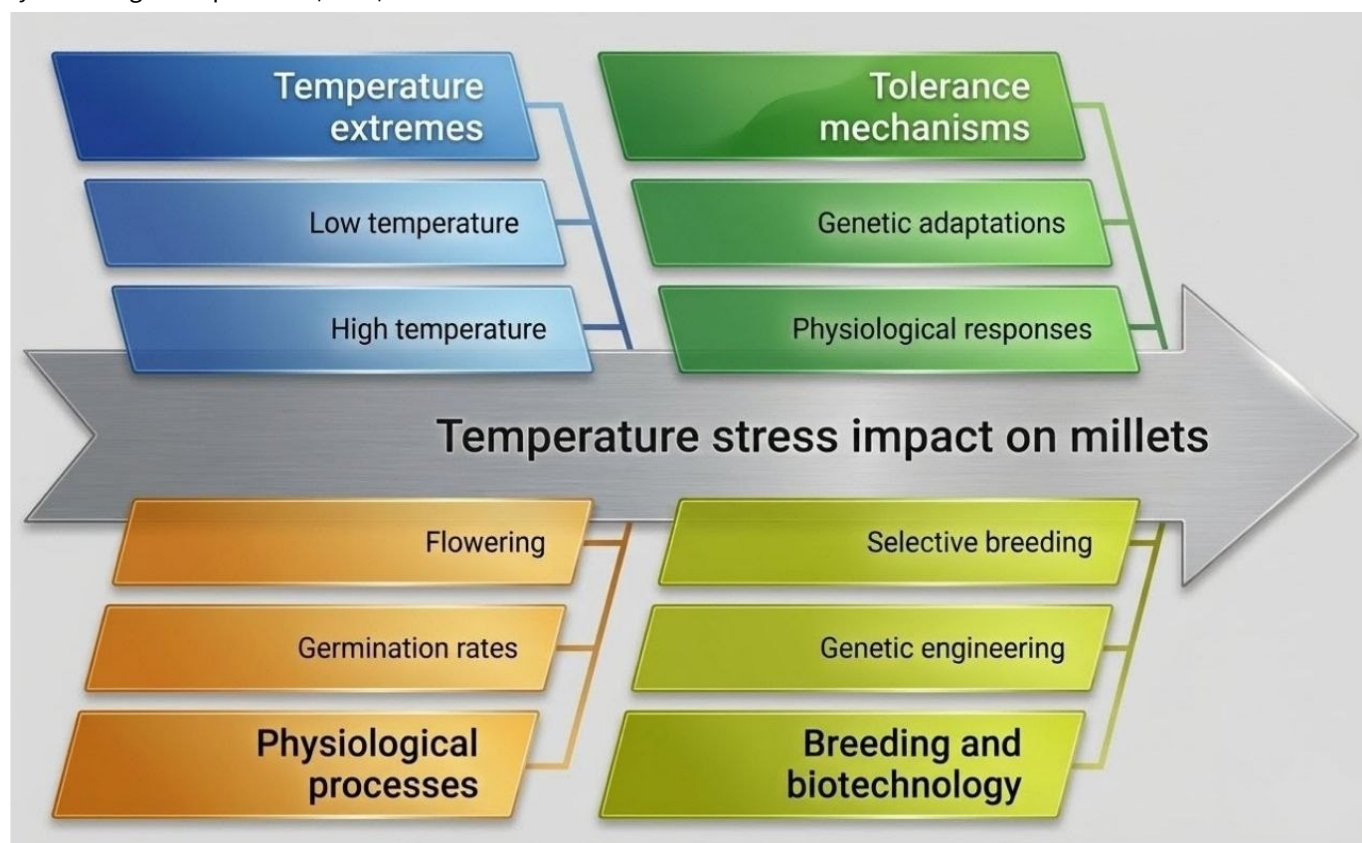


Fig. 3. Impact of temperature stress on millets, focusing on temperature extremes (low and high temperatures) and the resulting physiological and genetic mechanisms.

Physiological effect and plant response due to drought

Drought significantly affects crop productivity by creating severe water shortages. When plants experience drought, their stomata close to conserve water, which leads to an accumulation of ROS, causing oxidative stress. This stress damages key biomolecules, such as lipids and disrupts normal plant functions (69). Phytohormones like abscisic acid (ABA) and ethylene (ET) are crucial in signalling and promoting tolerance during drought stress. Furthermore, treatments with salicylic acid (SA) and jasmonic acid (JA) have been shown to enhance plant resilience to drought, salt and heat stress (70). Drought stress significantly reduces plant height, biomass, grain weight and grain number in pearl millet (71). Among finger millet varieties, the brown variety demonstrates greater resistance to water stress than the black variety, likely due to genotypic differences rather than pigment variation. Water stress in finger millet plants lowers chlorophyll content, reduces photosynthesis and decreases RWC, while increasing proline concentrations (72). Under drought conditions, finger millet also shows drooping shoots, curled leaves, elevated levels of proline and MDA and compromised membrane integrity. The oxidative stress triggers an increase in antioxidant enzyme activities, such as glutathione reductase (GR), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione peroxidase (GPX) and catalase (CAT), which help the plant combat stress (69). Drought also encourages the presence of endophyte actinobacteria in millet roots and rhizosphere soil, which may enhance the host plant's stress tolerance (73).

Strategies to mitigate abiotic stress

To tackle the challenges brought by climate change and improve millet yields, several strategies and approaches can be adopted, including:

Use of plant growth-promoting rhizobacteria (PGPRs)

Plant growth-promoting rhizobacteria (PGPRs) are beneficial soil microbes that significantly enhance plant growth and help crops withstand environmental stresses (68). These microorganisms are emerging as a promising solution for increasing millet productivity and improving their resilience under challenging growing conditions. Research has shown that PGPRs effectively boost tolerance to abiotic stresses and enhance crop yields in various economically significant crops, including rice, soybean, lettuce, tomato, maize and wheat (74–79). The PGPRs achieve these benefits through multiple mechanisms, such as producing plant growth hormones like gibberellic acid (GA) and indole-3-acetic acid (IAA), which are essential for regulating plant development. These bacteria also play a role in activating the plant's natural defence systems,

enhancing the production of defence-related compounds like jasmonic acid and salicylic acid. These compounds are crucial for strengthening plant immunity and fostering healthy growth (80). The ability of PGPRs to support plant health, improve stress tolerance and promote higher yields makes them an invaluable tool in sustainable agriculture, particularly for crops like millet that often grow under suboptimal conditions. Continued exploration of PGPRs holds the potential to revolutionise stress management and productivity in millet and other staple crops.

Stress resistance bacteria in plants

Soil microorganisms play a vital role in plant growth and stress tolerance by producing various chemical compounds during their interactions with plant roots. These compounds can be either organic or inorganic volatile gases that diffuse through soil pores, or non-volatile substances like siderophores and phytohormones (81). These chemicals are essential for both the microbial food chain and promoting plant growth and to increase plant biomass and enhance the plant's defense mechanisms against diseases through induced systemic resistance (82). When plants face multiple stressors, volatile compounds produced by microorganisms become particularly important. These stress-induced chemicals act as signalling molecules, triggering systemic effects and priming responses in the affected plants, as well as in neighbouring plants (83–85). For example, studies have shown that inoculating wheat seedlings with the AZP2 strain of *Bacillus thuringiensis* significantly boosted plant biomass and improved drought survival by five-fold. This was achieved through reduced volatile emissions and enhanced photosynthesis, illustrating the potential of bacterial inoculation to enhance plant stress resistance (86). These findings underscore the importance of beneficial microbes in supporting plant adaptation to challenging environmental conditions. Table 2 shows key stress-responsive genes and their functional roles in conferring tolerance to various abiotic stress conditions.

Genomic insights into millet improvement

Significant progress has been made in breeding various millet species in recent years. These efforts are driven by the need to improve stress resilience, enhance nutritional qualities and increase yields.

Modern breeding programs have successfully applied molecular markers such as restriction fragment length polymorphism (RFLP) amplified fragment length polymorphism (AFLP) and simple sequence repeat (SSR) for trait-linked selection, developing varieties with improved drought tolerance, pest resistance and enhanced nutritional content (92,93).

Table 2. Key stress-responsive genes and their functional roles in conferring tolerance to various abiotic stress conditions

Gene	Source	Stress	Role	Reference
<i>SiLEA14</i>	Foxtail millet	Salt/drought stress	Led to enhanced salt and drought tolerance.	(51)
<i>PgPmp3-1</i> and <i>PgPmp3-2</i>	Pearl millet	Cold/salt stress	The upregulation of <i>PgPm3</i> genes under cold and salt stress has been linked to enhanced tolerance to these stress conditions in plants.	(87)
<i>EcbZIP60</i>	Finger millet	Drought/salinity/ oxidative stress	Expression of the gene in transgenic tobacco plants led to increased tolerance to drought, salinity and oxidative stresses.	(88)
<i>WRKY1</i>	Wheat	Drought and abscisic acid stress condition	The gene <i>TaWRKY1</i> , which regulates stomatal movement and enhances leaf water retention capacity, was upregulated.	(89)
<i>GTL1</i>	Arabidopsis	Drought stress condition	It regulates various stomatal traits, including, stomatal density and water use efficiency (WUE)	(90)
<i>PcAPX</i>	Cotton	Drought stress condition	acting as ROS scavenger	(91)

Pearl millet

Known for its resilience in arid environments, pearl millet has been a primary focus of breeding efforts aimed at enhancing drought tolerance, disease resistance and nutritional quality. Marker-assisted selection (MAS) has enabled significant progress in developing varieties resistant to downy mildew, with improved drought resistance and higher levels of grain iron and zinc (94). Furthermore, several quantitative trait loci (QTLs) linked to terminal drought tolerance and grain yield have been identified and integrated into breeding programs to enhance crop performance under challenging conditions (95, 96).

Finger millet

Renowned for its exceptional calcium content, finger millet has been a target for breeding programs aimed at improving its tolerance to drought and salinity stress. Advanced genomic techniques, such as genome-wide association studies (GWAS), have played a key role in identifying genes associated with stress resilience, thus advancing the development of stress-tolerant varieties (88). These efforts are essential for ensuring the long-term sustainability of finger millet cultivation in regions affected by climate variability.

Foxtail millet

Breeding efforts in foxtail millet have concentrated on enhancing its tolerance to drought and saline conditions. Through transcriptomic studies, researchers have identified critical genes like *SILEA* and *SiWRKY*, which are instrumental in improving the crop's stress adaptation mechanisms (51, 57). These discoveries have laid the groundwork for developing robust varieties capable of thriving in marginal environments, further strengthening its role in food security.

Proso millet

Though less studied, proso millet is gaining attention in breeding programs. Efforts are now focused on identifying markers related to early maturation and drought tolerance, making it more adaptable to semi-arid environments. The integration of genomic selection (GS) and advanced phenotyping platforms, such as rain-out shelters, has enabled researchers to identify genotypes with enhanced resistance to environmental stresses has been a key focus (12). These modern techniques, when combined with traditional breeding methods, offer immense potential to increase millet production and support food security, particularly in regions vulnerable to climate change (11).

Over the past two decades, significant progress has been made in developing and utilising molecular (DNA) markers to advance genetic studies of millets at research stations globally (97). Various DNA-based markers, including RFLP, AFLP, RAPD, STSs, gSSRs, EST-SSRs, DArTs, CISP, SSCP-SNP and SNP markers, have been developed to accelerate millet breeding programs worldwide (98–101). These markers are used to assess genetic variability, analyse population structures and identify genomic regions linked to important agricultural traits. Advanced approaches such as GWAS, GS and marker-assisted breeding (MAB) have been implemented to speed up breeding programs in pearl millet. While genomics and genotyping technologies have made remarkable strides, advancements in high-throughput phenotyping have faced some practical challenges. To address these, modern plant phenomics facilities with automated systems are being set up. These platforms utilise imaging systems that capture subtle developmental changes in plants non-invasively, using technologies like hyperspectral

reflectance, visible infrared and near-infrared spectroscopy.

At International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), a specialised phenotyping platform designed for drought tolerance research has been established using a rain-out shelter. This platform allows for the study of water extraction and transpiration efficiency in plants, providing essential insights into physiological mechanisms related to terminal drought tolerance. Research has also identified several QTLs and markers associated with downy mildew resistance (95, 102). In a major breakthrough, a key QTL in the LG2 region linked to drought tolerance was validated using Near Isogenic Lines (NILs) of H 77/833–2, introgressed with QTLs from PRLT 2/89–33 (96). Another QTL on LG3, associated with higher grain iron (Fe) and zinc (Zn) content, has been a primary focus for MAB (103). This QTL, along with QTLs for downy mildew resistance, was incorporated into the genetic background of the pollen parent of the hybrid HHB 67 Improved using linked flanking markers. The resulting double QTL introgression lines were then crossed with the seed parent of HHB 67 Improved, creating hybrids that closely resemble the original. These improved hybrids and QTL introgression lines are currently being evaluated in India's national testing system (94).

Mitigating biotic threats in millet cultivation

By adopting specific strategies, farmers can create conditions that discourage the development and spread of diseases, ensuring healthier and more productive harvests. Timely sowing reduces disease risk by avoiding periods favourable for pathogen development. (104, 105). Optimum plant populations and spacing, where maintaining the right number of plants per unit area and ensuring adequate spacing allows better air circulation, reducing humidity levels that favour disease outbreaks (104, 105). Timely weeding, which prevents competition from weeds and reduces the spread of diseases by eliminating potential hosts for pathogens (106). Balanced fertiliser use, where applying fertilisers properly, especially nitrogen, minimises nutrient imbalances that could make crops more susceptible to diseases (106). Deep summer ploughing disrupts pathogen life cycles and helps manage diseases such as charcoal rot, downy mildew and smut (104, 105). Adjusting sowing dates, particularly early sowing, can help reduce the severity of diseases like blast and rust by avoiding peak disease-conducive conditions (106). Planting disease-free seeds is crucial to preventing diseases such as ergot, smut, blast, foot rot and grain mold, ensuring healthy crop growth from the start (106). Sanitation practices, which involve keeping fields clean by removing debris and infected plant material, can help prevent diseases like downy mildew, banded sheath blight, foot rot, ergot and blast (68). Roguing, the practice of removing and destroying diseased plants, is an effective way to control diseases like grain smut, head smut, ergot and grain mold (68). Eradicating alternate and collateral hosts, by eliminating plants that can harbour diseases, reduces the risk of infections such as ergot, downy mildew, rust, blast, leaf spots and bacterial and viral diseases (68). Clean cultivation practices, such as collecting smutted heads in cloth bags and treating them with boiling water, help kill pathogens and reduce inoculum for the next growing season (68). Vector management, which involves controlling insect vectors and nematodes that spread diseases, is also essential. Preventing insect damage can reduce the entry points for bacterial infections (106). By adopting these disease management practices, farmers can effectively protect their millet crops from biotic stress, leading to healthier plants and more reliable yields (68).

Host plant resistance

Using host resistance to control diseases is a cost-effective and practical approach, particularly for low-return crops like millets. Examples include GPU-28 (finger millet, resistant to blast) and hybrid HHB 67 Improved (pearl millet, resistant to downy mildew). For many farmers, especially those with limited resources, investing in additional inputs such as fungicides is often not feasible. Developing disease-resistant millet varieties is, therefore, an efficient and sustainable solution. This approach is especially beneficial for resource-poor and marginal farmers, who are the primary cultivators of millets in India (107).

Intercropping

A common farming practice in millet cultivation involves intercropping with cowpea, a method widely adopted by farmers for its numerous benefits. Typically, pearl millet and cowpea seeds are mixed and sown together in the same planting spot. Alternatively, some farmers adjust the sowing schedule by planting millet first as the main crop and then introducing cowpea or other legumes during the first weeding, about 3–4 weeks after millet sowing (108, 109). Intercropping offers several advantages, including increased yields, more efficient resource use, reduced risks of insect infestations and weed problems, enhanced crop diversity and improved farm income. Additionally, legumes like cowpea contribute residual nitrogen to the soil, which benefits subsequent crops (109). Research has also shown that intercropping pearl millet with cowpea provides both biological and economic benefits, leading to improved millet yields and overall farm productivity (110).

Integrated pest management

The parasitic weed *Striga hermonthica* (Delile) Benth. presents a significant challenge to cereal crops, especially pearl millet, in West Africa. Unlike grain sorghum (*Sorghum bicolor* (L.) Moench), which has established host plant resistance, no such resistance has been identified in cultivated pearl millet (*Pennisetum glaucum* (L.) R.Br.) (111). As a result, managing *Striga* relies primarily on cultural and agronomic practices. Infestations are worsened by factors such as low soil fertility, drought conditions and continuous cropping of susceptible crops like pearl millet (112). Traditionally, extended fallow periods have been used to reduce the soil seed bank of *Striga*, but modern strategies like crop rotation, delayed planting (113), minimal tillage, appropriate fertilisation (112, 114) and intercropping with non-host plants have proven effective in controlling *Striga* infestations (115, 116). Biological control methods offer a sustainable and eco-friendly alternative for managing *Striga* and other agricultural challenges. These strategies not only protect crops from biotic and abiotic stresses but also improve soil fertility and support sustainable farming practices. The increasing use of indigenous bio inoculants is attributed to their dual role in promoting plant growth and protecting crops in environmentally sustainable systems. Among the diseases affecting pearl millet in West Africa, downy mildew (*Sclerospora graminicola*) is the most destructive, causing yield losses of 20–30 % (117). Strategies for combating downy mildew include cultivating resistant varieties (114, 118), treating seeds with Apron Star a product combining the fungicide metalaxyl and the insecticide furathiocarb (118, 119) and manually removing infected plants from fields (120). Apron Star has been shown to increase pearl millet yields by about 30 % (119), especially benefiting the vulnerable seedling stage by reducing yield losses by up to 80 %

(Andrews, personal communication). However, its protective effects diminish after the first 35 days of crop growth (114).

Conclusion

Millets play a vital role in ensuring food security for millions of people in food-insecure regions, due to their nutritional value, climate resilience and adaptability to marginal environments. They are economically significant crops, supporting the livelihoods of small-scale and marginal farmers and providing opportunities for income diversification and risk reduction. With the potential for genetic improvement, millets hold even greater promise for contributing to global food security and resilience. Looking ahead, genomics-assisted breeding, the development of climate-resilient varieties and supportive policies and value-chain interventions will be critical to enhancing millet adoption under changing climatic conditions. More than just crops, millets represent security, adaptability and hope in a world of constant change. With scientific innovation, policy support and market integration, millets hold immense promise to contribute to global food security, nutritional well-being and ecological resilience for generations to come.

Acknowledgements

The authors express their sincere gratitude to the Department of Genetics and Plant Breeding, School of Agriculture, Lovely Professional University, which facilitated the completion of this work.

Authors' contributions

All authors made equal contributions to its writing, data verification and interpretation. All authors have read and approved the final.

Compliance with ethical standards

Conflict of interest: The authors declare no conflict of interest associated with this review article.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used Quill Bot, an AI-assisted writing tool, to reframe certain sentences to enhance the use of research-specific terminology. After utilising this tool, the authors thoroughly reviewed and edited the content as necessary and take full responsibility for the accuracy and integrity of the final publication.

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

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