International Journal of Research in Agronomy

E-ISSN: 2618-0618
P-ISSN: 2618-060X

NAAS Rating (2025): 5.20
www.agronomyjournals.com
2025; 8(12): 43-52
Received: 21-10-2025
Accepted: 23-11-2025

Yogita Bali
District Extension Specialist, KVK, Bhiwani, Haryana, India

Anurag
Department of Agriculture Meteorology, CCSHAU, Hisar, Haryana, India

Uma Devi
Department of Agronomy, CCSHAU, Hisar, Haryana, India

Renu Devi
District Extension Specialist, KVK, Sirsa, Haryana, India

Corresponding Author:
Yogita Bali
District Extension Specialist, KVK Bhiwani, Haryana, India

Climate resilience and nutritional security: Understanding abiotic stress response and mitigation strategies in pearl millet (*Pennisetum glaucum* L.)

Yogita Bali, Anurag, Uma Devi and Renu Devi

DOI: https://www.doi.org/10.33545/2618060X.2025.v8.i12a.4323

Abstract
Pearl millet (*Pennisetum glaucum* (L.) R. Br.), is a robust, drought-resistant and climatic resilient cereal that is essential for ensuring food security in semi-arid tropical regions crop, particularly in South Asia and sub-Saharan Africa, whereas other crop fails to withstand in harsh environmental conditions such as drought, high temperatures, and low nutrient status soils. Pearl millet is grown on approximately 26 million hectares globally. To feed the rapidly expanding population, pearl millet is a smart choice for modern diet and also a climatic resilient crop to meet the demand of food and nutritional security to everyone. As climate change intensifies and abiotic stress becomes more pronounced, the significance of pearl millet as a excellent food source for millions is increasingly evident. This review examines the physiological and mechanisms that enable pearl millet to withstand abiotic stresses, including heat stress, salinity and drought and explores its potential for mechanism to stand with these stresses. Key adaptive traits, such as deep rooting systems, efficient water use, and robust photosynthetic mechanisms, are highlighted as essential for its resilience. Additionally, the review discusses emerging mitigation strategies, including selective breeding, biotechnology, and improved agronomic practices aimed at enhancing yield stability and resilience under changing climatic conditions. Ultimately, understanding and leveraging the adaptive capacity of pearl millet will be essential for sustaining agricultural productivity and food security in vulnerable regions amid global climate challenges.

Keywords: Abiotic stress, heat, stress, global warming, drought, salinity, climate resilient

Introduction

The article provides a comprehensive review of the growing importance of millets in human nutrition and sustainable agriculture. Millets, which include a variety of small-seeded grasses such as finger millet, pearl millet, and foxtail millet, are gaining recognition due to their exceptional nutritional profiles and their resilience in arid environments. (Fig.-1) The major highlights, millets as rich sources of essential nutrients including proteins, dietary fibre, vitamins, and minerals, particularly calcium, iron and zinc. Their low glycaemic index makes them suitable for managing lifestyle-related disorders such as diabetes and obesity. Additionally, millets are gluten-free, making them an excellent option for individuals with celiac disease or gluten intolerance. The review underscores recent scientific studies showcasing the bioactive compounds in millets, such as phenolic acids, flavonoids, and tannins, which contribute to their antioxidant, anti-inflammatory, and antimicrobial properties. These functional benefits make millets a promising component in nutraceuticals and functional food development. The potential of millets as its contribution to food and nutritional security, particularly in the context of climate change and population growth, due to their adaptability to harsh agro-climatic conditions and low input requirements. Millets not only as nutritious food grains but also as strategic crops for sustainable agriculture and health-focused food systems. The integration of millets into mainstream diets and food industries, supported by continued research and policy initiatives, could significantly impact global nutrition and agricultural sustainability.

Pearl millet (*Pennisetum glaucum*), popularly known as bajra, bajri, kambu, kamban, and sajjalu in different Indian local languages, belongs to the family Poaceae. This ancient and versatile cereal is valued for its use as food, fodder, and feed. Renowned for its exceptional drought tolerance, pearl millet thrives even under harsh climates and nutrient-poor soils, making it an indispensable crop for millions living in arid and semi-arid regions. In the context of a rapidly growing global population, pearl millet is gaining attention as a climate-resilient grain that can contribute significantly to food and nutritional security. Due to its superior nutritional profile and adaptive resilience to climate change, pearl millet, along with other small millets, is categorized as a "nutri-cereal."

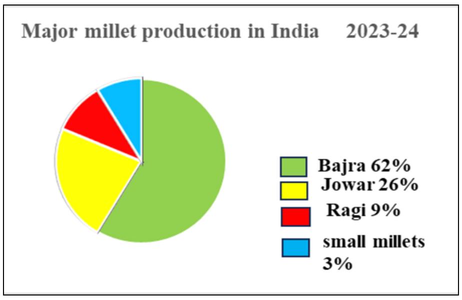


Fig 1: Major millet production in India (Source: APEDA 2023-24)

Pearl millet is widely grown in the arid and semi-arid regions of India, particularly in Northern, Central and Western India during *kharif* season (June-September), from late June to early July coinciding with the onset of the monsoon season. In India, pearl millet is ranked as the fourth most important food crop after rice, wheat, and maize (Anonymous, 2020) [2]. It thrives under conditions of high temperature and low humidity during its growing season. Being a short-day plant, it requires relatively shorter photoperiods to initiate flowering and complete its reproductive phase. Among the millets, pearl millet is regarded as the hardiest species, owing to its low water requirement and remarkable ability to withstand adverse climatic conditions. Besides serving as a staple food, it is also recognized as a valuable forage crop. This is primarily due to its lower concentration of hydrocyanic acid compared to sorghum, and the fact that its green fodder is not only safe but also nutritious, with appreciable amounts of protein, calcium, phosphorus, and other minerals, while oxalic acid levels remain within safe limits (Khairwal and Yadav, 2005) [26].

Pearl millet grain is nutritionally rich, containing about 74% carbohydrates, 13-14% protein, 5-6% fat, and 1-2% minerals, along with appreciable amounts of phosphorus and iron (Reddy *et al.*, 2016) [52]. It is also a good source of carotene, riboflavin, and niacin, making it highly suitable for both human consumption and livestock feed. Agronomically, pearl millet is well adapted to regions with limited water availability. Its deep root system enables efficient extraction of moisture from subsoil layers, while also enhancing soil structure and water infiltration. Compared to many other cereals, it requires relatively low external inputs such as fertilizers and pesticides, thereby contributing to reduced greenhouse gas emissions and aiding in carbon sequestration through photosynthetic capture of atmospheric carbon dioxide. Additionally, it provides high-quality fodder for livestock.

Globally, India is the leading producer of pearl millet, followed by Nigeria, Niger, and China; however, stabilizing yield levels remains a challenge. Major constraints include the limited availability of improved high-yielding, short-duration varieties, suboptimal agronomic management (such as cultivation on marginal lands with minimal inputs and predominance of rainfed farming), and inadequate post-harvest handling practices (Yadav *et al.*, 2016) [69]. In the broader context of foodgrain production, reliance on chemical fertilizers contributes to more than 40% of total output, highlighting the need for balanced and sustainable nutrient management strategies.

Millet is a gluten-free grain that retains its alkaline properties after cooking, making it suitable for individuals with gluten allergies or sensitivities. It has a higher content of slowly digestible starch (SDS) and resistant starch (RS), contributing to its lower glycaemic index (GI) property, which makes it an appealing option for people looking to manage their blood sugar levels. This characteristic, along with the rise in awareness around gluten-free and low-GI diets, has increased its popularity in recent times (Satyavathi *et al.*, 2020) [54]. The consumption of various millets, including pearl millet, is recognized for its protective effects against certain cancers, cardiovascular diseases, and several age-related health conditions. This has increased the popularity of pearl millet among health-conscious consumers globally (Goswami *et al.*, 2020; Kumar *et al.*, 2020d) [18, 31]. Developing fortified pearl millet varieties with enhanced iron (Fe) and zinc (Zn) content is crucial, particularly for improving the health and immune status of rural women, addressing issues like anemia. Due to its rich nutritional profile, pearl millet has been officially designated as a "Nutri-cereal" (Gazette of India, No. 133, dated 13 April 2018) and holds significant potential for combating malnutrition and securing food and nutritional security.

Being a climatic resilient crop, pearl millet is the smart choice among the other cereal and millets from the environmental and agricultural prospective. It is mainly cultivated on marginal lands under rainfed conditions and can sustain even under drought prone area that receive an average annual precipitation of <250mm (Nambiar *et al.*, 2011) [42]. Pearl millet, as a food grain with full of nutrient and also known as miracle grain, because of their ability to adapt under wide range of ecological and climatic conditions with less water requirement and ability to grow in low-nutrient status soils and also for its various health benefits, important in preventing various chronic diseases. It is a hardy crop for its drought tolerance and can thrive better in harsh climate during its growth and development period and combat the climatic change as compare to other millets.

Pearl millet in India: Current status and future prospects

In India, pearl millet is the most widely cultivated food crop after rice, wheat and maize, plays a vital role in Indian agriculture system, mainly in arid and semi-arid region where hot and dry spell remain for prolong period. India is the largest producer of pearl millet contributing to about 40% of world population. During 2023-24, pearl millet area in India was 7.36 million ha with an average production of 10.67 million tons and 1449 kg/ha productivity. (Source: DA&FW).

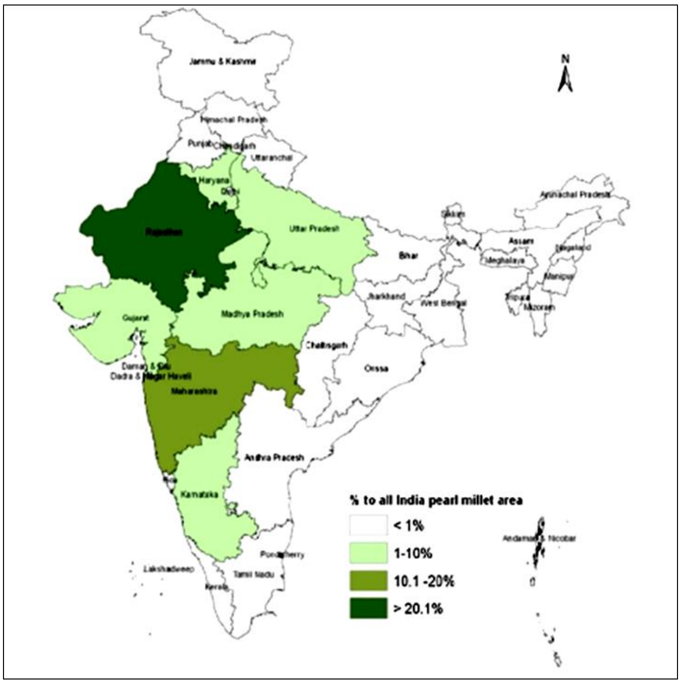


Fig 2: Area under pearl millet (Source: Agric research, 2013)

The major pearl millet-growing states in India are Rajasthan, Maharashtra, Gujarat, Uttar Pradesh, and Haryana, together accounting for more than 90% of the country's total pearl millet acreage (Fig. 2). Among these, Rajasthan holds the largest share, covering 4.32 million ha (57.10% of the national area), with a production of 4.53 million tons (41.71% of India's total production) and a productivity level of 1049 kg/ha. During the period 2010-2012, the average area under pearl millet cultivation in India was 8.5 million ha, while the average production stood at 9.4 million tons (Fig. 3) (Directorate of Millets Development, 2020) [12].

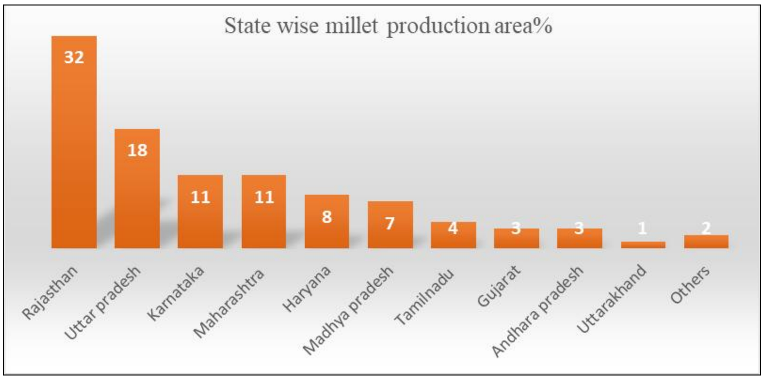


Fig 3: State wise millet production:2023-24 (Source: Directorate of Millets Development, 2020) [12]

(Source: Satyavathi *et al.*, 2013) [54]

Fig 4: Area, Production and productivity of pearl millet in India since 2000

Although it is a climatic resilient crop, pearl mill*et al*so faces wide variation in economic yield due to change in climatic pattern like heat waves, erratic rainfall and many more factors. But however, its capacity to tolerate drought make it most promising crop for rainfed agriculture zones. It is also value of its nutrition profile, consider as staple food for developing countries due to resilient and reliable crop with food and nutritional security and sustainable in nature for millions of people. Climate change with extreme weather conditions such as prolonged drought, heatwaves, rainfall distribution pattern, salinity have also affected pearl millet yield and also due to anthropogenic activities which limit its potential. (Fig.-4) Despite with all these changes pearl millet is have capability to adapt itself with harsh weather conditions.

In this direction, future prospects have been explored by numerous researchers, scientists, and breeders with a focus on developing high-yielding, disease-resistant, and climate-resilient varieties. For instance, marker-assisted selection (MAS) and genomic tools have been employed to develop hybrids capable of withstanding adverse weather conditions while simultaneously enhancing productivity and economic returns. To date, a total of 206 hybrids and 66 varieties have been identified and released for cultivation across different agroecological zones of the country. Notably, pearl millet is the first crop to establish global minimum standards for micronutrient content as a criterion for cultivar release. Since 2018, benchmark levels for iron (42 ppm) and zinc (32 ppm) have been introduced in cultivar promotion and release policies, thereby ensuring nutritional security in line with the vision of a nutritionally secure India (AICRP-PM, 2024). In recent years, pearl millet has also gained interest in the production of value-added products, gradually expanding its consumer base, particularly among health-conscious individuals owing to its nutritional superiority, millets have been promoted globally, with the year 2023 being celebrated as the "International Year of Millets." This recognition followed the declaration of 2018 as the "Year of Millets" by the Government of India and the endorsement by the FAO Committee on Agriculture (COAG) in 2021. In this context, the Government of India has undertaken several initiatives to promote millets, including their inclusion under the National Food Security Mission (NFSM) and distribution through the Public Distribution System (PDS).

Pearl millet holds immense potential in Indian agriculture due to its adaptability to marginal conditions. However, its future prospects depend on continued research, technological advancements, stable market policies, and consistent government support. Among millets, it occupies a strategic position for cultivation in arid and semi-arid regions. Being a hardy crop, it can withstand adverse weather conditions with minimal input requirements. Moreover, its low demand for external inputs makes it suitable for organic farming, while its rich nutrient profile offers significant health benefits.

It perform best in 32-40 ^{0}C temperature, but due to change in climatic trends i.e. GHG emissions, global warming, loss of carbon pool etc. several studies have been done by agriculture scientist and researcher with the objective were to study the impact of climatic change on pearl millet due to heat stress, erratic rainfall, drought, salinity, water logging (abiotic stresses) play critical role during its growth phases as well as on economic, by decrease in emergence of seedling, booting to maturity stage, on yield and yield attributes parameters.

Effect of heat stress

Pearl millet is a robust and resilient crop that performs well under conditions of heat stress and poor soil fertility. The optimum temperature during its initial growth stage is 38-42 °C, although it can tolerate temperatures up to 45 °C (Arya *et al*., 2010) [3]. However, beyond this threshold, further increases in temperature induce metabolic, physiological, and biochemical changes in plants, leading to impaired growth and a substantial decline in economic yield (Wahid *et al*., 2007) [66]. High soil temperatures exceeding 45 °C during midday are particularly detrimental, often resulting in poor seed germination and weak plant stands (Ong, 1983) [44]. Several growth stages of pearl millet, including germination, coleoptile elongation, and photosynthesis, require moderately high temperatures of up to 35 °C. However, when temperatures surpass this level, normal growth processes become inhibited (Arya *et al*., 2014) [4]. Heat stress is therefore a major environmental constraint, reducing yields by impairing growth and seed set during critical stages (Jagdish *et al*., 2021). The flowering and grain-filling stages are especially sensitive, with heat stress causing pollen sterility, poor seed set, and reduced grain size, all of which contribute to lower productivity. In addition, heat stress accelerates physiological maturity, shortens the grain formation period, reduces photosynthetic activity, limits biomass accumulation, and promotes the production of reactive oxygen species (ROS), which inflict oxidative damage to cellular membranes, proteins, and nucleic acids (Sliman *et al*., 2014; Gupta *et al*., 2015) [62, 20].

Plant growth and development also depend on efficient nutrient and water uptake, which are primarily regulated by root function and phytohormone signaling (Kong *et al*., 2012) [27]. Heat stress disrupts nutrient uptake and impairs the expression of genes involved in the regulation of amino acids, carbohydrates, and essential nutrients, including Zn, K, Mg, and B, along with macronutrients. Heat shock proteins (HSPs) serve as a protective mechanism, enhancing heat tolerance and mitigating temperature-induced stress, thereby supporting productivity and economic returns (Singh *et al*., 2015) [61]. Gupta *et al*. (2015) [20] further emphasized that heat stress during flowering and grain filling leads to reduced yield due to pollen sterility, poor seed set, smaller grain size, accelerated physiological maturity, and oxidative damage. Pearl millet (bajra), known for its hardy nature, thrives in high temperatures up to approximately 42 °C, making it suitable for cultivation in heat- and drought-prone regions. However, its resilience diminishes when temperatures exceed this threshold. Djanaguiraman *et al*. (2009) [13] reported that at temperatures above 42 °C, the crop's carbohydrate reserves—critical for growth and energy supply—begin to deplete rapidly. This depletion results in "plant starvation," wherein normal metabolic functions cannot be sustained due to inadequate energy availability. Prolonged high-temperature stress thus leads to stunted growth, reduced yield, and, in severe cases, plant mortality.

Mitigating strategies for Heat stress

Although pearl millet has been high potential to tolerate heat stress up to some extend more than other cereal crops but due to change in climatic condition like global warming, emission of GHG. Now it is important to develop genotypes to mitigate stress and which are ability to adopt the climatic change. When plant is exposed to higher temperature about 5 ^{0}C more than the threshold temperature for a short time spell, it responds to it by the mechanism of heat shock proteins, metabolite synthesis and other stress related gene (He *et al*.,2023) [21], but more studies about HSP are not available, so multilocation trail and analysis should be carried out under various field condition (Khairwal *et al., 1999*) [25]. HSP produces by pearl millet acts as molecular chaperons promoting protein and structure stability in response to environment stress due to heat stress and allow to survive under prolong period of high temperature by activating the other responsive gene to mitigate the heat stress in pearl millet including production of antioxidants, osmo-protectants and other protective molecules. Development of heat tolerant varieties is an effective way to combat heat stress during critical growth stages like flowering and grain filling stage, using molecular markers to induce desirable traits related to with stand heat stress. As Mittler *et al.*, (2012) [40] explains, this HSF-HSP system is an essential for helping plants cope with and survive under heat stress by maintaining protein integrity and protecting cellular functions under extreme temperatures. During heat stress, plants have evolved defence mechanisms to protect themselves. The production of heat stress factors (HSFs), which play a critical role in regulating heat shock proteins (HSPs). HSPs act as molecular chaperones that help in refold damaged proteins, prevent protein aggregation, Assist in the degradation of irreparable damaged proteins. Pearl millet, have a capability to cope with heat stress, maintaining cellular function and survival during extreme conditions. As stated by (Mukesh Sankar *et al*., 2021) [41]. The production of these stress proteins is vital for enhancing the plant's ability to tolerate heat, especially in regions where temperatures can rise sharply. This stress response contributes to pearl millet's resilience, making it a valuable crop in hot, arid environments by adaptation of these mechanisms. Adjusting sowing time to avoid peak heat period during sensitive stage and exogenous application of plant growth regulator such as salicylic acid help to mitigate heat stress and developing tolerance (*Yadav et al., 2012)* [67]

Therefore, the growing of pearl millet as irrigated summer season (February-June) crop in parts of Gujarat, Rajasthan and Uttar Pradesh where high temperatures (42 ^{0}C) are of common occurrence during flowering. As high air temperatures coinciding with flowering in this region can cause spikelet sterility, leading to drastic reductions in grain yield

Salinity stress

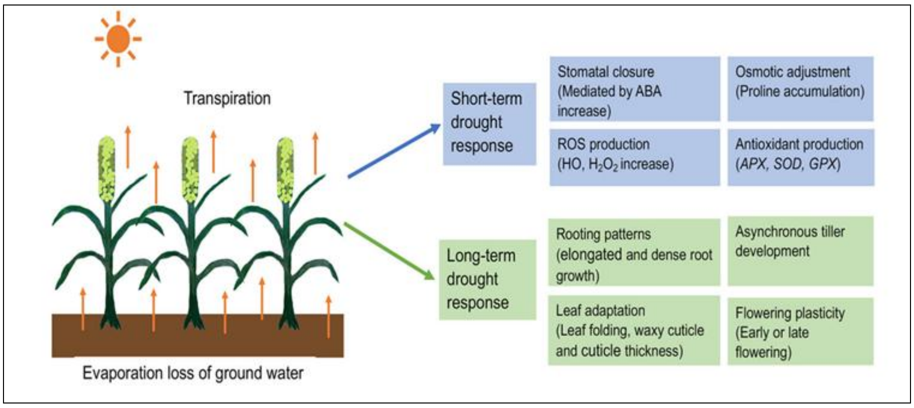
Pearl millet (*Pennisetum glaucum* L.) is a versatile and dual-purpose crop known for both its grain and fodder uses. It stands out due to its short duration and quick growth, making it highly suitable for regions with limited growing seasons. In particular, pearl millet possesses good salinity tolerance, giving it an edge over other fodder crops in salt-affected areas. According to (Kulkarni *et al*., 2006) [28] and (Patel *et al*., 2008) [47], pearl millet has demonstrated significant resilience to both salinity and drought. This makes it a crucial crop for ensuring high-quality fodder in arid and semi-arid regions, its ability to thrive under harsh conditions ensures a reliable food source for livestock, even in environments where other crops may fail due soil salinization or water scarcity. Reduction in grain yield by increasing salinity of irrigation water may be due to more negative water potential of soil solution causing reduction in water and nutrient uptake result into lower leaf area development in turn reduced net assimilates. Shani and Dudley (2001) [55] explored the impact of salinity on crop yield, under saline conditions there is reduction in Photosynthesis, Salinity stress limits the plant's ability to carry out photosynthesis efficiently. The accumulation of salts in the soil can interfere with water uptake, leading to stomatal closure in plants. Under saline conditions, high energy and carbohydrate expenditure in osmoregulation, to maintain cellular water balance and ion homeostasis, Excessive salt concentrations can disrupt normal cellular functions, including enzyme activity, protein synthesis, and membrane stability. Thus limiting its ability to grow and produce high yields. Meena *et al.*, (2012) [38] reported similar findings regarding the impact of salinity on grain yield reduction in pearl millet. It showed that salinity stress significantly decreased in grain yields due to Impaired Photosynthesis, expenditure of energy in Osmoregulation and Cellular Disruptions. Kumar *et al*. (2016) [29] suggest that the reduction in relative water content (RWC) observed in plants under salinity stress is likely related to a decline in the plants' overall vigor by decreased plant growth result reduce photosynthesis. High salt concentrations in the root zone induce osmotic stress, which restricts water absorption by plants and leads to cellular dehydration, primarily resulting in a decrease in relative water content (RWC) (Greenway and Munns, 1980) [19]. These findings are consistent with the observations made by Netondo *et al*., (2004) [43] in sorghum and Vijayalakshmi *et al*. (2012) [65] in pearl millet. In addition to the osmotic effects of salts in the soil solution, the excessive concentration and absorption of individual ions, such as Na^+, can be toxic to plants. This is particularly relevant when considering the impact of saline water irrigation on root and shoot Na^+ content in dual-purpose pearl millet varieties. Research by Makarana *et al*. (2019) [37] indicates that leaching excess salts from the root zone is effective up to irrigation water with electrical conductivity (EC) of 6.0 dS/m. Among the varieties studied, AVKB-19 exhibited significantly higher dry matter (DM) yield in both the first cut (5.67 t/ha) and the second cut (5.09 t/ha) compared to ICMV-15111. The use of good-quality irrigation water notably enhanced the uptake of macro and micronutrients by the plants, which ultimately improved dry matter yield due to its positive effects on photosynthetic efficiency. Conversely, high salinity levels restricted root growth, limiting nutrient uptake and resulting in leaf chlorosis, which further reduced the photosynthetic potential of the crops and led to lower dry matter yields. Similar findings regarding reduced dry matter yield due to the lack of essential plant nutrients have been reported by Qadir *et al*., (2008) [49] and Yadav *et al*. (2004) [68].

Mitigating strategies for salinity

The accumulation of compatible solutes, such as soluble sugars and proline—key osmolytes involved in osmotic adjustment—plays a crucial role in enabling plants to maintain cellular functions under stress. These solutes allow plants to tolerate high intracellular concentrations without toxicity, facilitating additional water uptake from the environment and supporting both turgor pressure and cellular stability (Sairam *et al*., 2002; Misra & Gupta, 2005) [53, 39]. Under extreme salinity, sugars serve not only as a vital source of energy and carbon but also as critical contributors to adaptive and defensive responses. Elevated sugar levels act as a protective mechanism against salt-induced damage, a phenomenon widely reported in several halophytic species, where carbohydrate changes are largely regulated by K^+ and Cl^- ions (Prado *et al*., 2000; Ashraf & Harris, 2004; Kumar *et al*., 2016, 2017) [48, 5, 29, 30]. Proline functions as a potent osmoregulatory molecule, mitigating the harmful effects of toxic salt ions stored in vacuoles. It stabilizes membranes, protects cellular structures from NaCl-induced damage, and supports enzyme activity under stress. In comparative studies, the pearl millet variety AVKB-19 exhibited significantly higher proline content than ICMV-15111, suggesting superior stress adaptation. Similarly, the accumulation of total soluble proteins under stress may act as a nitrogen reserve, later mobilized during recovery, while also contributing to osmotic adjustment. AVKB-19 consistently showed slightly higher levels of soluble proteins than ICMV-15111 across different observations, further indicating its tolerance potential. In addition to osmolyte accumulation, epicuticular wax deposition on leaves plays an important role in stress avoidance. Under abiotic stress, increased wax deposition reduces cuticular permeability, thereby minimizing transpirational water loss when stomata close (Blum, 1988) [7]. Kumar *et al*. (2016) [29] also reported enhanced epicuticular wax loads under salt and sodic stress in halophytic species, highlighting its significance in adaptation. Collectively, these mechanisms—osmolyte buildup, protein accumulation, and wax deposition—contribute to the resilience of pearl millet under saline and drought-prone environments.

Drought stress

Drought is one of the major limiting factors in agricultural production, substantially reducing crop yields. As a critical constraint on plant growth and development, drought disrupts key physiological processes, including respiration, photosynthesis, and stomatal activity, ultimately impairing overall plant performance. To cope with water scarcity, plants adopt diverse drought adaptation strategies such as structural and morphological modifications, activation of drought-resistance genes, hormone synthesis, and production of osmotic regulators. Under drought conditions, plants perceive water-deficit signals and initiate a cascade of responses through signaling molecules such as abscisic acid (ABA), calcium ions (Ca^{2+}), inositol-1,4,5-triphosphate (IP_3), cyclic adenosine diphosphate ribose (cADPR), and nitric oxide (NO). These molecules participate in signal transduction, directly or indirectly regulating structural and physiological adjustments that enhance stress adaptation. Such signaling pathways also activate downstream drought-responsive genes, whose products—such as proline, glycine betaine (GB), soluble sugars (SS), and late embryogenesis abundant (LEA) proteins, and aquaporins (AQP) — play crucial roles in maintaining osmotic balance, protecting cellular structures, and conserving water. Collectively, these metabolites enable plants to stabilize cellular functions and withstand drought stress. In pearl millet, drought-related research has primarily focused on three critical growth stages: vegetative, panicle development, and grain filling (Shivhare *et al*., 2020a) [60]. These studies have highlighted several adaptive mechanisms, including drought avoidance, tolerance, escape, and recovery, which can be further categorized into short-term and long-term responses (Figure 5). As a C4 grass, pearl millet exhibits inherent physiological advantages for water-use efficiency (Pardo & VanBuren, 2021) [45]. It follows the NADP-dependent malic enzyme (NADP-ME) pathway, wherein CO_2 is initially fixed in mesophyll cells into a four-carbon compound, subsequently transported to bundle sheath cells, and released for entry into the Rubisco-mediated C3 pathway to synthesize glucose. In this system, the light reactions of photosynthesis primarily occur in mesophyll cells, spatially separating oxygen evolution from carbon fixation. This minimizes photorespiration and reduces competition between oxygen and carbon dioxide for enzymatic binding sites. Consequently, stomatal closure is less prolonged, lowering water loss compared to C3 crops such as wheat and rice. These physiological features, coupled with genetic and biochemical responses, position pearl millet as one of the most drought-resilient cereals for arid and semi-arid regions.



Source: Shrestha *et al*, 2023

Fig 5: Short-term and long-term responses of pearl millet to adapt drought stress

Short term responses

1. Stomatal conductance

Stomata are essential structures in plants that facilitate the exchange of gases and water by playing a crucial role in the processes of photosynthesis and transpiration. They are small openings located on the surface of leaves and stems, allowing carbon dioxide (CO_2) to enter the plant while enabling oxygen (O_2) and water vapor to exit. During photosynthesis, plants take in CO_2 through the stomata, which is necessary for converting light energy into chemical energy in the form of glucose. At the same time, stomata help regulate water loss through transpiration, the process by which water evaporates from the plant's surface. This not only aids in nutrient transport and cooling the plant but also maintains the necessary pressure for water uptake from the roots. Therefore, the proper functioning of stomata is vital for plant health and overall growth, as it directly influences both photosynthesis and water management (Li *et al*., 2017) [34].

2. Osmotic adjustment

Osmotic adjustment is a crucial physiological mechanism that enables plants to withstand drought by sustaining cell turgor, maintaining relative water content, supporting cell expansion, facilitating photosynthesis, and preserving stomatal conductance. This process involves the accumulation of solutes that lower osmotic potential, thereby enhancing the cell's ability to retain water and function efficiently under water-deficit conditions. Consequently, osmotic adjustment plays a central role in ensuring plant survival and productivity during drought stress. Plants achieve this by accumulating both organic and inorganic osmolytes. Under field conditions, pearl millet has demonstrated effective osmotic adjustment in response to water limitation (Henson *et al.*, 1982) [22], a response comparable to that observed in other drought-tolerant C3 and C4 grasses such as upland rice (Lum *et al.*, 2014) [35], diverse wheat genotypes (Hong-Bo *et al.*, 2006) [23], and sorghum (Blum and Ebercon, 1976) [8].

Reactive oxygen species (ROS), including singlet oxygen ($^1O_2$), superoxide radicals (O_2^-), hydroxyl radicals (HO•), and hydrogen peroxide (H_2O_2), are commonly produced during both biotic and abiotic stress (Dudhate *et al.*, 2018) [14]. In response, plants rapidly generate ROS while simultaneously activating scavenging systems to maintain a balance between their roles in defence signalling and their potential toxicity (Qi *et al.*, 2017) [50]. However, excessive ROS accumulation leads to oxidative stress, which causes lipid peroxidation, protein denaturation, and severe cellular damage (Anjum *et al.*, 2017) [1]. Several studies have explored the expression of antioxidant genes in pearl millet under drought stress. Experiments using polyethylene glycol (PEG) to simulate drought at both early and late seedling stages revealed a marked increase in the expression of genes encoding antioxidant enzymes such as ascorbate peroxidase (APX), glutamyl-tRNA reductase (GlutR), and superoxide dismutase (SOD) in drought-tolerant pearl millet genotypes (Shivhare and Lata, 2017) [58]. These findings support the role of antioxidant gene expression in mitigating oxidative stress, highlighting their critical function in scavenging ROS under drought conditions (Shivhare and Lata, 2019) [59].

Long term responses

1. Rooting patterns

The development of long, deep roots enables plants to access water from deeper soil horizons, allowing them to maintain a higher leaf water potential under drought stress. In pearl millet, the embryonic root system is characterized by a primary root that exhibits the most rapid growth during the first week after germination. During this period, the primary root elongates at an accelerated rate of 9.1 cm per day, which is significantly faster than that of maize and wheat (2.7 cm per day) (Passot *et al.*, 2016) [46]. This fast elongation allows the root to quickly reach deeper, moisture-retentive soil layers. After approximately one week, lateral roots emerge from the primary root, followed by the formation of adventitious crown roots at the shoot base. The primary root is identified by the presence of a large metaxylem vessel, whereas crown roots are thicker and possess a larger stele containing multiple metaxylem vessels. The rate of primary root elongation and lateral root density varies across genotypes (Passot *et al.*, 2016) [46], suggesting the potential for breeding programs aimed at improving root elongation during early seedling growth. Additionally, genetic variation in lateral root types among genotypes offers further opportunities for developing dense root systems capable of maximizing soil moisture utilization (Passot *et al.*, 2016) [46].

Mitigating strategies for drought

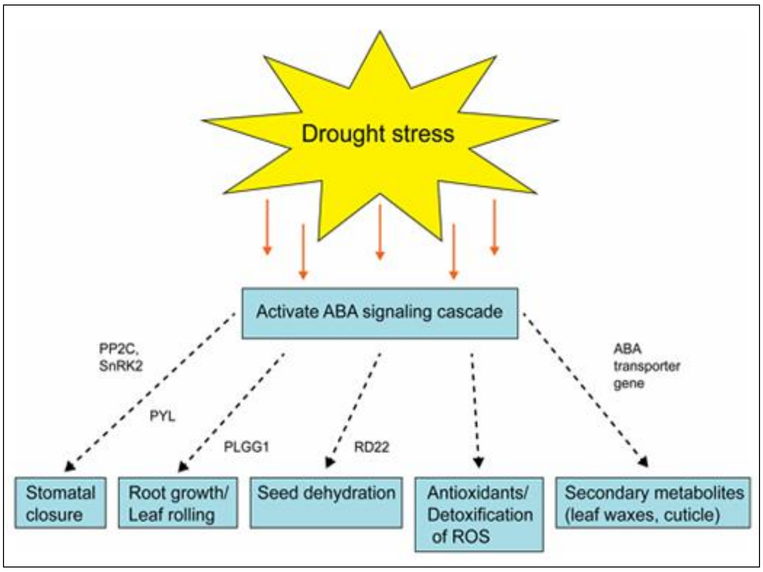


Fig 6: Mitigating strategies for drought (Source: Shrestha *et al*, 2023)

Under drought conditions, pearl millet develops both elongated and dense root systems. Studies have shown that when drought stress occurs in the topsoil, pearl millet responds by increasing lateral root density, thereby enhancing its ability to extract water from deeper, moister soil layers (Zegada-Lizarazu and Iijima, 2005) [71]. Compared with other millet species, drought-resistant pearl millet genotypes exhibit greater water uptake, larger leaf area, and increased shoot biomass under topsoil drought (Zegada-Lizarazu and Iijima, 2005) [71]. Moreover, the deep roots of pearl millet are capable of penetrating compacted soil layers under water-limited conditions. Interestingly, genotypes with lower osmotic adjustment were found to possess longer root lengths under drought stress (Kusaka *et al.*, 2005a) [33]. While root architecture and plasticity are vital for crop performance in drought-prone environments, research on root development remains limited. Developing predictive models for root length density in crops such as pearl millet and maize has been suggested as an important step for advancing knowledge in this area (Das *et al.*, 2015; Faye *et al.*, 2019; Shao *et al.*, 2021) [10, 16, 56]. In addition to root traits, structural adaptations also contribute to drought resistance. Pearl millet exhibits a waxy cuticle that plays a protective role against water loss (Bi *et al.*, 2017) [6]. Several genes involved in the biosynthesis of cutin, flavonoids, suberin, and wax have been identified (Varshney *et al.*, 2017) [64]. Similarly, Debieu *et al.* (2017) [11] reported an expanded family of ABA transporter genes, which are linked to the transport of secondary metabolites associated with cuticle components. Asynchronous tillering is another important adaptive trait, enabling pearl millet to recover from drought by producing tillers that flower once the dry spell has passed (Craufurd and Bidinger, 1988) [9]. When mid-season drought ends before or around flowering, tiller development is strongly promoted (Mahalakshmi *et al*., 1987) [36]. Further research is needed on asynchronous tiller development, as these tillers may substantially influence yield recovery under drought stress. Quantitative trait locus (QTL) analyses have identified associations between stover and biomass yield with tiller number and growth vigour (Yadav *et al*., 2019) [70]. Pearl millet is typically classified as a short-day plant; however, considerable genotypic variation in photoperiodic flowering requirements exists among varieties, influenced by their latitude of adaptation. About 54.4% of cultivated pearl millet germplasm flowers irrespective of day length, while most varieties exhibit facultative photoperiod sensitivity, displaying delayed flowering under extended day lengths (Rai *et al*., 1999) [51]. Early flowering serves as a vital drought escape strategy, as observed in wheat, where a shortened vegetative phase facilitates avoidance of terminal stress (Shavrukov *et al*., 2017) [57]. In pearl millet, Vadez *et al*. (2012) [63] suggested that delayed floral initiation helps escape early to mid-season droughts, whereas early initiation is beneficial for evading late-season droughts. Varieties are frequently adapted to flower toward the rainy season’s end, allowing maturation using residual soil moisture. Nonetheless, climate change and altered rainfall patterns may disrupt this alignment with local environments, potentially affecting flowering times and overall adaptation. Molecular research offers further understanding of drought responses. Shivhare *et al*. (2020a) [60] studied terminal drought stress in both drought-tolerant and drought-sensitive pearl millet lines during the reproductive phase. They discovered that most differentially expressed genes (DEGs) in tolerant genotypes were linked to secondary metabolite pathways, including mevalonate, shikimate, and biosynthesis of alkaloids, phenolics, flavonoids, lignin, and wax, along with phytohormones such as abscisic acid (ABA), ethylene, gibberellic acid, jasmonic acid, and salicylic acid. Additionally, several DEGs associated with Photosystems I and II were upregulated in tolerant genotypes, implying possible drought effects on electron transport. Further studies at vegetative (25 days post-sowing) and reproductive (40 days post-sowing) stages revealed more pronounced secondary metabolite production during the reproductive stage, indicating that pearl millet preferentially protects reproductive tissues under drought by allocating greater resources to these compounds.

Conclusion

The morphological, physiological, and genetic mechanisms of drought resistance in pearl millet is essential for aiding farmers in marginalized regions who depend on this crop for their livelihoods. The insights gained from pearl millet can also benefit the improvement of other cereal crops facing increasing drought stress due to climate change.

The review vividly illustrates how pearl millet stands out among cereal crops for its remarkable resilience to abiotic stresses exacerbated by climate change, such as extreme heat, drought, and salinity. Climate-induced stressors like increased temperature, erratic rainfall, and soil salinization adversely affect the crop’s physiological processes-most notably photosynthesis, nutrient uptake, and reproductive development-ultimately impacting yield and quality. However, pearl millet’s inherent adaptive mechanisms, including deep rooting systems, efficient osmotic regulation, and the production of heat shock proteins and antioxidants, help mitigate these effects. Research findings indicate that short-term responses such as stomatal regulation and long-term traits like robust root architecture and asynchronous tillering significantly contribute to stress adaptation. Furthermore, the development of climate-resilient and nutrient-enriched varieties through marker-assisted breeding and genomics underscores the crop's potential in combating food insecurity under climate stress. Thus, the studies reviewed affirm that pearl millet is not just a viable option but a strategic necessity for sustainable agriculture in the face of escalating climate challenges.

References

1. Anjum SA, Ashraf U, Imran K, Tanveer M, Shahid M, Shakoor A. Phyto-toxicity of chromium in maize: oxidative damage, osmolyte accumulation, antioxidative defence and chromium uptake. Pedosphere. 2017;27:262-273. doi:10.1016/S1002-0160(17)60315-1
2. Anonymous. Estimated of area, production and yield of kharif cereals. Directorate Economics and Statistics, Department of Agriculture Cooperation and Farmers Welfare, Government of India. 2020.
3. Arya RK, Yadav HP, Yadav AK, Singh MK. Effect of environment on yield and its contributing traits in pearl millet. Forage Res. 2010;36:176-180.
4. Arya RK, Singh MK, Yadav AK, Kumar A, Kumar S. Advances in pearl millet to mitigate adverse environment conditions emerged due to global warming. Forage Res. 2014;40(2):57-70.
5. Ashraf MP, Harris PJC. Potential biochemical indicators of salinity tolerance in plants. Plant Sci. 2004;166(1):3-16.
6. Bi H, Kovalchuk N, Langridge P, Tricker PJ, Lopato S, Borisjuk N. The impact of drought on wheat leaf cuticle properties. BMC Plant Biol. 2017;17:1-13. doi:10.1186/s12870-017-1033-3
7. Blum A. Plant Breeding for Stress Environments. Boca Raton, Florida, USA: CRC Press; 1988. p. 1-223.
8. Blum A, Ebercon A. Genotypic responses in sorghum to drought stress. III. Free proline accumulation and drought resistance. Crop Sci. 1976;16:428-431. doi:10.2135/cropsci1976.0011183X001600030030x
9. Craufurd P, Bidinger F. Effect of the duration of the vegetative phase on crop growth, development and yield in two contrasting pearl millet hybrids. J Agric Sci. 1988;110:71-79. doi:10.1017/S0021859600079715
10. Das A, Schneider H, Burridge J, Ascanio AKM, Wojciechowski T, Topp CN. Digital imaging of root traits (DIRT): a high-throughput computing and collaboration platform for field-based root phenomics. Plant Methods. 2015;11:1-12. doi:10.1186/s13007-015-0093-3
11. Debieu M, Kanfany G, Laplaze L. Pearl millet genome: Lessons from a tough crop. Trends Plant Sci. 2017;22:911-913. doi:10.1016/j.tplants.2017.09.00
12. Directorate of Millets Development. Department of Agriculture, Cooperation & Farmers Welfare, Ministry of Agriculture & Farmers Welfare, Government of India. 2020.
13. Djanaguiraman M, Sheeba JA, Devi DD, Bangarusamy U. Cotton leaf senescence can be delayed by nitrophenolate spray through enhanced antioxidant defense system. J Agron Crop Sci. 2009;195:213-224. doi:10.1111/j.1439-037X.2009.00360.x
14. Dudhate A, Shinde H, Tsugama D, Liu S, Takano T. Transcriptomic analysis reveals the differentially expressed genes and pathways involved in drought tolerance in pearl millet [*Pennisetum glaucum* (L.) r. br]. PLoS One. 2018;13:e0195908. doi:10.1371/journal.pone.0195908
15. Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib

A. Crop production under drought and heat stress: plant responses and management options. Front Plant Sci. 2017;8:1147. doi:10.3389/fpls.2017.01147
16. Faye A, Sine B, Chopart JL, Grondin A, Lucas M, Diedhiou AG. Development of a model estimating root length density from root impacts on a soil profile in pearl millet (*Pennisetum glaucum* (L.) r. br): application to measure root system response to water stress in field conditions. PLoS One. 2019;14:e0214182. doi:10.1371/journal.pone.0214182
17. Freschert GT, Violle C, Malo Y, Bourget M, Florian F. Allocation, morphology, physiology, architecture: the multiple facets of plant above-and belowground responses to resource stress. New Phytol. 2018;219:1338-1352. doi:10.1111/nph.15225
18. Goswami S, Asrani P, Ansheef Ali TP, Kumar RD, Vinutha T, Veda K. Rancidity matrix: development of biochemical indicators for analysing the keeping quality of pearl millet flour. Food Anal Methods. 2020;13:2147-2164. doi:10.1007/s12161-020-01831-2
19. Greenway H, Munns R. Mechanisms of salt tolerance in nonhalophytes. Annu Rev Plant Physiol. 1980;31:149-190.
20. Gupta SK, Rai KN, Singh P, Ajeigbe HA. Impact of heat stress on flowering and grain filling in pearl millet. Front Plant Sci. 2015;6:862.
21. He Y, Guan H, Li B, Zhang S, Xu Y, Yao Y. Transcriptome analysis reveals the dynamic and rapid transcriptional reprogramming involved in heat stress and identification of heat response genes in rice. Int J Mol Sci. 2023;24:14802. doi:10.3390/ijms241914802
22. Henson I, Mahalakshmi V, Bidinger F, Alagarswamy G. Osmotic adjustment to water stress in pearl millet (*Pennisetum americanum* [L.] leeke) under field conditions. Plant Cell Environ. 1982;5:147-154. doi:10.1111/1365-3040.ep11571559
23. Hong-Bo S, Xiao-Yan C, Li-Ye C, Xi-Ning Z, Gang W, Yong-Bing Y. Investigation on the relationship of proline with wheat anti-drought under soil water deficits. Colloids Surf B Biointerfaces. 2006;53:113-119. doi:10.1016/j.colsurfb.2006.08.008
24. Jagadish SV, Way KDA, Sharkey TD. Plant heat stress: concepts directing future research. Plant Cell Environ. 2021;44:1992-2005. doi:10.1111/pce.14050
25. Khairwal IS, Singh S. Quantitative and qualitative traits. In: Khairwal IS, Rai KN, Andrews DJ, Harinarayana G, editors. Pearl millet breeding. New Delhi: Oxford and IBH Publishing Co. Pvt. Ltd.; 1999. p. 119-155.
26. Khairwal IS, Yadav OP. Pearl millet (*Pennisetum glaucum* L.) improvement in India, retrospect and prospects. Indian J Agric Sci. 2005;75:183-191.
27. Kong X, Luo Z, Dong H, Eneji AE, Li W. Effects of nonuniform root zone salinity on water use, Na+ recirculation, and Na+ and H+ flux in cotton. J Exp Bot. 2012;63:2105-2116.
28. Kulkarni VN, Rai KN, Dakheel AJ, Ibrahim M, Hebbara M, Vadez V. Pearl millet germplasm adapted to saline conditions. Int Sorghum Millet Newsl. 2006;47:103-106.
29. Kumar A, Krishnamurthy SL, Lata C, Kumar P, Devi R, Kulshrestha N, Yadav RK, Sharma SK. Effect of dual stress (salinity and drought) on gas exchange attributes and chlorophyll fluorescence characteristics in rice. Indian J Agric Sci. 2016;86(6):19-27.
30. Kumar A, Lata C, Krishnamurthy SL, Kumar A, Prasad KRK, Kulshreshtha N. Physiological and biochemical characterization of rice varieties under salt and drought stresses. J Soil Salinity Water Qual. 2017;9(2):167-177.
31. Kumar RR, Rai GK, Goswami S, Singh SP, Satyavathi CT, Praveen S. Millets: the orphan crop for uncertain future. New Delhi: Scientific International Pvt. Ltd.; 2020. p. 194.
32. Kumar Y, Tiwari KN, Singh T, Raliya R. Nano fertilizers and their role in sustainable agriculture. Ann Plant Soil Res. 2021;23(3):238-255.
33. Kusaka M, Lalusin AG, Fujimura T. The maintenance of growth and turgor in pearl millet (*Pennisetum glaucum* [L.] leeke) cultivars with different root structures and osmoregulation under drought stress. Plant Sci. 2005;168:1-14. doi:10.1016/j.plantsci.2004.06.021
34. Li Y, Li H, Li Y, Zhang S. Improving water-use efficiency by decreasing stomatal conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant wheat. Crop J. 2017;5:231-239. doi:10.1016/j.cj.2017.01.001
35. Lum M, Hanafi M, Rafii Y, Akmar A. Effect of drought stress on growth, proline and antioxidant enzyme activities of upland rice. J Anim Plant Sci. 2014;24:1487-1493.
36. Mahalakshmi V, Bidinger F, Raju D. Effect of timing of water deficit on pearl millet (*Pennisetum americanum*). Field Crops Res. 1987;15:327-339. doi:10.1016/0378-4290(87)90020-7
37. Makarana G, Kumar A, Yadav RK, Soni PG, Lata C, Sheoran P. Effect of saline water irrigations on physiological, biochemical and yield attributes of dual-purpose pearl millet (*Pennisetum glaucum*) varieties. Indian J Agric Sci. 2019;89(4):624-633.
38. Meena HN, Bhalodia PK, Jat RS, Vekaria LC. Prospects of using saline water for irrigation in groundnut (*Arachis hypogaea*), pearl millet (*Pennisetum glaucum*) cropping system in saline black soils of Saurashtra. Indian J Agron. 2012;57(2):122-126.
39. Misra N, Gupta AK. Effect of salt stress on proline metabolism in two high yielding genotypes of green gram. Plant Sci. 2005;169:331-339.
40. Mittler R, Finka A, Goloubinoff P. How do plants feel the heat. Trends Biochem Sci. 2012;37:118-125. doi:10.1016/j.tibs.2011.11.007
41. Mukesh Sankar S, Satyavathi CT, Barthakur S, Singh SP, Bharadwaj C. Differential modulation of heat-inducible genes across diverse genotypes and molecular cloning of a sHSP from pearl millet (*Pennisetum glaucum* (L.) R. Br.). Front Plant Sci. 2021;12:659893. doi:10.3389/fpls.2021.659893
42. Nambiar VS, Dhaduk JJ, Sareen N, Shahu T, Desai R. Potential functional implications of pearl millet (*Pennisetum glaucum*) in health and disease. J Appl Pharm Sci. 2011;1:62-67.
43. Netondo GW, Onyango JC, Beck E. Sorghum and salinity: I. Response of growth, water relations, and ion accumulation to NaCl salinity. Crop Sci. 2004;44(3):797-805.
44. Ong CK. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.): II. Reproductive development. J Exp Bot. 1983;34:337-348. doi:10.1093/jxb/34.3.337
45. Pardo J, VanBuren R. Evolutionary innovations driving abiotic stress tolerance in C4 grasses and cereals. Plant Cell. 2021;33:3391-3401. doi:10.1093/plcell/koab205
46. Passot S, Gnacko F, Moukouanga D, Lucas M, Guyomarc'h S, Ortega BM. Characterization of pearl millet root architecture and anatomy reveals three types of lateral roots.

Front Plant Sci. 2016;7:829. doi:10.3389/fpls.2016.00829
47. Patel MR, Sadhu AC, Patel RM, Parmar HP, Kher HR. Cutting management in different genotypes of forage bajra during summer season. Res Crops. 2008;9(2):325-327.
48. Prado FE, Boem C, Gallardo M, Gonzalez HJA. Effect of NaCl on germination, growth and soluble sugar content in Chenopodium quinoa wild seeds. Bot Acad Sci. 2000;41:27-34.
49. Qadir M, Tubeileh A, Akhtar J, Larbi A, Minhas PS, Khan MA. Productivity enhancement of salt-affected environments through crop diversification. Land Degrad Dev. 2008;19(4):429-453.
50. Qi J, Wang J, Gong Z, Zhou JM. Apoplastic ROS signalling in plant immunity. Curr Opin Plant Biol. 2017;38:92-100. doi:10.1016/j.pbi.2017.04.022
51. Rai K, Murty D, Andrews D, Bramel-Cox P. Genetic enhancement of pearl millet and sorghum for the semi-arid tropics of Asia and Africa. Genome. 1999;42:617-628. doi:10.1139/g99-040
52. Reddy SBP, Nagamadhurai KV, Venenkaiah, Prathima T. Effect of nitrogen and potassium on yield and quality of pearl millet (*Pennisetum glaucum* L.). Int J Agric Innov Res. 2016;4:678-681.
53. Sairam RK, Veerabhadra RK, Srivastava GC. Differential responses of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. Plant Sci. 2002;163:1037-1047.
54. Satyavathi CT, Khandelwal V, Supriya A, Beniwal BR, Sushila B, Mahesh CK. Pearl millet-hybrids and varieties-2020. Jodhpur: ICAR-All India Coordinated Research Project on Pearl Millet; 2020.
55. Shani U, Dudley LM. Field studies of crop response to water and salt stress. Soil Sci Soc Am J. 2001;65:1522-1528.
56. Shao MR, Jiang N, Li M, Howard A, Lehner K, Mullen J. Complementary phenotyping of maize root system architecture by root pulling force and X-ray imaging. Plant Phenomics. 2021;2021:9859254. doi:10.34133/2021/9859254
57. Shavrukov Y, Kurishbayev A, Jatayev S, Shvidchenko V, Zotova L, Koekemoer F. Early flowering as a drought escape mechanism in plants: how can it aid wheat production? Front Plant Sci. 2017;8:1950. doi:10.3389/fpls.2017.01950
58. Shivhare R, Lata C. Exploration of genetic and genomic resources for abiotic and biotic stress tolerance in pearl millet. Front Plant Sci. 2017;7:2069. doi:10.3389/fpls.2016.02069
59. Shivhare R, Lata C. Assessment of pearl millet genotypes for drought stress tolerance at early and late seedling stages. Acta Physiol Plant. 2019;41:1-10. doi:10.1007/s11738-019-2831-z
60. Shivhare R, Asif MH, Lata C. Comparative transcriptome analysis reveals the genes and pathways involved in terminal drought tolerance in pearl millet. Plant Mol Biol. 2020;103:639-652. doi:10.1007/s11103-020-01015-w
61. Singh J, Reddy PS, Reddy S, Reddy M. Molecular cloning and characterization of salt inducible dehydrin gene from the C4 plant *Pennisetum glaucum*. Plant Gene. 2015;4:55-63. doi:10.1016/j.plgene.2015.08.002
62. Sliman B, Najar MT, Ghram A, Dabbebi H, Mrad MB, Manef A. Reactive oxygen species, heat stress and oxidative-induced mitochondrial damage: a review of hyperthermia. Int J Hyperthermia. 2014;30:513-523. doi:10.3109/02656736.2014.971446
63. Vadez V, Hash T, Kholova J. II. 1.5 Phenotyping pearl millet for adaptation to drought. Front Physiol. 2012;3:386. doi:10.3389/fphys.2012.00386
64. Varshney RK, Shi C, Thudi M, Mariac C, Wallace J, Qi P. Pearl millet genome sequence provides a resource to improve agronomic traits in arid environments. Nat Biotechnol. 2017;35:969-976. doi:10.1038/nbt.3943
65. Vijayalakshmi T, Varalaxmi Y, Jainender S, Yadav SK, Vanaja M, Jyothilakshmi N, *et al*. Physiological and biochemical basis of water-deficit stress tolerance in pearl millet hybrid and parents. Am J Plant Sci. 2012;3(12):1730.
66. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. Environ Exp Bot. 2007;61:199-223.
67. Yadav OP, Bidinger FR, Gupta SK. Mitigating heat stress in pearl millet. J Agron Crop Sci. 2012;198(5):360-373.
68. Yadav RK, Kumar A, Lal D, Batra L. Yield responses of winter (rabi) forage crops to irrigation with saline drainage water. Exp Agric. 2004;40:65-75.
69. Yadav SK, Babalad H, Sharma S, Choudhary R. Studies on nutrient management through organics in summer mungbean (*Vigna radiata* L. Wilczek). The Bioscan. 2016;11(4):2499-2501.
70. Yadav S, Sandhu N, Singh VK, Catolos M, Kumar A. Genotyping-by-sequencing based QTL mapping for rice grain yield under reproductive stage drought stress tolerance. Sci Rep. 2019;9:1-12. doi:10.1038/s41598-019-50880-z
71. Zegada-Lizarazu W, Iijima M. Deep root water uptake ability and water use efficiency of pearl millet in comparison to other millet species. Plant Prod Sci. 2005;8:454-460. doi:10.1626/pps.8.454