Review Article

"Salinity Stress in Millets: Implications for Food Security and Climate Resilience"

ABSTRACT

Salinity stress is a major abiotic constraint limiting crop productivity, particularly in arid and semi-arid regions where altered precipitation patterns and high evapotranspiration accelerate soil salinization. Millets, including pearl millet, finger millet, and foxtail millet, are recognized as climate-resilient crops with remarkable adaptability to marginal environments. Despite their inherent tolerance, salinity adversely affects their growth, germination, physiological functions, and yield through osmotic stress, ionic toxicity, and oxidative damage. This review synthesizes current knowledge on the physiological, biochemical, and molecular mechanisms underlying salinity tolerance in millets, highlighting the role of osmolyte accumulation, antioxidant defense systems, ion homeostasis, and stress-responsive signalling pathways such as the SOS pathway. Recent advances in genomics, transcriptomics, and molecular breeding have facilitated the identification of key genes and quantitative trait loci associated with salinity tolerance. Biotechnological approaches, including transgenic strategies, gene pyramiding, and CRISPR/Cas-mediated genome editing, offer promising avenues for enhancing stress tolerance in millet crops. However, challenges such as limited genomic resources and transformation efficiency, particularly in finger millet, restrict the widespread application of these technologies. In addition to genetic improvement, agronomic interventions such as efficient irrigation, nutrient management, and the application of organic amendments (e.g., biochar, compost, and manure) play a crucial role in mitigating salinity stress and improving soil health. The integration of conventional breeding, modern biotechnological tools, and sustainable agronomic practices is essential for developing salinity-resilient millet cultivars. Overall, millets hold significant potential for ensuring food and nutritional security under saline and climate-stressed environments. Future research should focus on multi-disciplinary approaches, including high-throughput phenotyping, genome sequencing, and precision breeding, to accelerate the development of stress-tolerant and high-yielding millet varieties.

Keywords: Salinity stress, Millets, Abiotic stress tolerance and CRISPR/Cas genome editing.

Introduction

Projected climate change scenarios predominantly indicate alterations in precipitation distribution patterns rather than total rainfall volume, resulting in prolonged drought episodes interspersed with periods of waterlogging and progressive soil salinization. Among abiotic stresses, salinity stands as a principal constraint affecting plant growth, germination, and yield performance (**Sairam *et al.*, 2002**). It refers to the gradual accumulation of soluble salts within the soil profile, a phenomenon particularly prevalent in arid and semi-arid ecosystems where elevated evapotranspiration rates and insufficient rainfall hinder effective salt leaching from the rhizosphere (**Al-Hilal, 1999**). Millets, cultivated since antiquity, have recently garnered renewed scientific and agricultural interest owing to their exceptional nutritional profile and remarkable ecological adaptability. Among them, pearl millet (*Pennisetum glaucum* L.) is distinguished by its robust tolerance to multiple environmental stresses, notably its capacity to withstand high salinity levels. It is recognized as a strategically important crop for climate resilience and food security enhancement. Its agronomic advantages include dual-purpose utility (grain and fodder), rapid growth cycle, and short maturity duration, making it particularly suitable for marginal environments.

Salinity constitutes a pervasive environmental stressor in arid and coastal agroecosystems. Globally, approximately 40 million hectares of irrigated land and over 3% of total land area are adversely impacted by salinity, resulting in substantial yield limitations (**FAO, 2019; Norlyn & Epstein, 1984; Pons *et al.*, 2011**). In India, salinity has degraded nearly 5.95 million hectares of land, contributing to an estimated 6.2 million tons of productivity loss. Notably, 48% of salt-affected soils are concentrated in Haryana, Punjab, Rajasthan, Gujarat, and Andhra Pradesh (**Singh *et al.*, 2020; Mandal *et al.*, 2010**).

The deleterious effects of salinity on plant systems arise primarily through osmotic stress and ionic toxicity. Elevated salt concentrations increase the osmotic potential of the soil solution, inducing initial osmotic stress, followed by ionic toxicity due to the accumulation of harmful ions in photosynthetic tissues (**Hanin *et al.*, 2016**). Roots, being the primary interface with saline environments, are the first to perceive and respond to salt stress. This stress disrupts water and nutrient uptake, leading to cellular imbalance, reduced root elongation, impaired development, and diminished plant vigor (**Munns & Tester, 2008**).

Furthermore, saline conditions induce hyperosmotic stress, adversely influencing root physiology and associated microbial interactions (**Abbas *et al.*, 2019**). Irrigation with saline water, particularly in coastal regions, has been reported to cause irreversible physiological damage (**Zuazao *et al.*, 2004**). At the cellular level, salt stress elevates caspase activity, reactive oxygen species (ROS), hydrogen peroxide, and lipid peroxidation, all of which contribute to oxidative damage (**Striker *et al.*, 2015**).

A reduction in osmotic potential under saline conditions hampers efficient nutrient translocation within plant tissues. Two prominent physiological manifestations include:

i) reduced leaf emergence rate, and

ii) visible toxicity symptoms such as chlorosis and necrosis in mature leaves (Rahaman *et al.*, 2014).

Plant growth and productivity are intrinsically linked to successful seed germination (**Tlig *et al.*, 2008**). Early developmental stages of millets, particularly finger millet, exhibit heightened sensitivity to salinity and drought stresses (**Hema *et al.*, 2014**). Comparative studies reveal that finger millet is more susceptible to salinity stress than other cereals such as barley, sorghum, oats, and wheat (**Bray *et al.*, 2000**). Even short-term exposure to salinity can significantly impair germination, root and shoot elongation, relative water content, photosynthetic pigment levels, protein synthesis, proline accumulation, and reducing sugar content in finger millet (**Dugasa *et al.*, 2019; Kumar & Khare, 2016**). Salinity stress is particularly detrimental in arid and semi-arid regions, where soluble salts reduce soil water availability by increasing water-binding strength, thereby limiting plant uptake. Crop responses to salinity vary, but most species exhibit reduced growth rates, decreased tillering and branching, and impaired reproductive development over time.

India faces extensive salinity challenges, with over 6.7 million hectares affected, including saline, alkaline, and coastal soils. States such as Gujarat and Uttar Pradesh are disproportionately impacted, while the Indo-Gangetic plains and several peninsular regions face escalating ecological concerns due to soil salinization. Millets, often termed “Nutri-Cereals,” are nutritionally superior crops offering significant health benefits. Pearl millet is particularly rich in iron (4–8 mg/100 g), making it effective in combating anemia (**Thrupthi *et al.*, 2023**). Millets possess high protein content—approximately double that of milk—while finger millet (ragi) is exceptionally rich in calcium (364 mg/100 g), nearly three times that of milk. Their high dietary fiber content enhances digestion, prevents constipation, and supports gut health through prebiotic functions. India ranks among the leading global producers of millets, with major production centers in Madhya Pradesh, Tamil Nadu, Andhra Pradesh, and Uttarakhand, underscoring their significance in the national agricultural framework.

Salinity Management and Biomass Potential

In dryland and semi-arid regions, conventional salinity management practices such as soil reclamation and improved irrigation systems are often economically unviable, particularly in developing countries. Consequently, crop improvement strategies emerge as sustainable and cost-effective long-term solutions. Pearl millet, widely cultivated in arid zones, demonstrates significant potential for enhanced productivity under saline conditions. Simultaneously, rising global energy demands and environmental concerns associated with fossil fuels have intensified interest in renewable energy sources. Biomass represents a viable alternative, and millets—especially pearl millet—are increasingly recognized for their biofuel potential due to high cellulose and hemicellulose content (**Mallikarjuna *et al.*, 2023**).

Stress-Tolerant Millets and Their Diversity

Millets are increasingly recognized as climate-resilient, stress-tolerant cereal crops that possess remarkable adaptability to harsh agroecological conditions, including drought, salinity, and nutrient-deficient soils. Their intrinsic resilience, coupled with superior nutritional attributes, positions them as strategic crops for ensuring global food and nutritional security under changing climatic scenarios. Unlike major cereals such as rice, wheat, and maize, millets exhibit enhanced tolerance to multiple abiotic stresses, making them highly suitable for cultivation in marginal and degraded lands (**Muthamilarasan *et al.*, 2015**).

Among the diverse millet species, foxtail millet (*Setaria italica*), belonging to the genus *Setaria* under the Panicoideae subfamily, is a prominent C-4 photosynthetic crop known for its efficient carbon assimilation and stress endurance (**Chemisquy *et al.*, 2010**). It is one of the earliest domesticated millets and continues to be widely cultivated, particularly in Asia, with China contributing significantly to global production (**Hu *et al.*, 2018; Yang *et al.*, 2012**). Foxtail millet is well adapted to saline, drought-prone, and hilly environments, and is nutritionally superior due to its rich composition of proteins, essential amino acids, unsaturated fatty acids, dietary fibre, vitamins, minerals, and antioxidants (**Muthamilarasan *et al.*, 2015**). Additionally, *Setaria* species have emerged as model systems for studying grass genetics and biofuel production, owing to their short life cycle, compact genome, and ease of genetic manipulation (**Brutnell *et al.*, 2010; Panchal *et al.*, 2023**).

Another nutritionally and agronomically important millet is finger millet (*Eleusine coracana* (L.) Gaertn.), which serves as a staple food for populations in sub-Saharan Africa and South Asia, particularly in marginal environments (**Chivenge *et al.*, 2015**). It ranks third among cereals cultivated in semi-arid regions after sorghum and pearl millet (**Thilakarathna & Raizada, 2015**). Finger millet grains are exceptionally rich in essential amino acids such as methionine and tryptophan, along with high levels of calcium, iron, and phosphorus, making them a nutritionally superior alternative to conventional cereals (**Gupta *et al.*, 2017**). Its ability to thrive in resource-poor and ecologically fragile environments, coupled with its long shelf life, enhances its significance as a food security crop (**Onyango, 2016**). Furthermore, its increasing utilization in value-added food products and bioethanol production has amplified its economic importance (**Tekaligne *et al.*, 2015; Sakamma *et al.*, 2018**).

Despite its resilience, finger millet productivity is significantly constrained by abiotic stresses such as salinity, which induces osmotic imbalance, ionic toxicity, and oxidative stress, thereby impairing physiological and metabolic processes (**Hema *et al.*, 2014; Rahnama *et al.*, 2010; Shahzad *et al.*, 2021**). Excess accumulation of sodium (Na^+) and chloride (Cl^-) ions disrupts nutrient homeostasis, particularly potassium uptake, leading to reduced growth and productivity (**James *et al.*, 2011; Shah *et al.*, 2021**). Salinity stress is especially detrimental during seed germination and early seedling establishment stages, adversely affecting root and shoot growth, photosynthetic efficiency, osmolyte accumulation, and membrane stability (**Kumar & Khare, 2016; Sarabi *et al.*, 2017; Dugasa *et al.*, 2020; Mukami *et al.*, 2020**).

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is another major millet crop extensively cultivated for both grain and fodder purposes, particularly in the arid and semi-arid regions of Asia and Africa. It serves as a staple food for over 90 million people, especially smallholder farmers in resource-limited environments (**Srivastava & Kumar, 2015**). Pearl millet exhibits exceptional adaptability to extreme climatic conditions, including high temperatures, drought, and poor soil fertility, making it a vital crop where other cereals fail to produce economic yields. However, soil salinity is emerging as a major constraint, particularly in rainfed and irrigated marginal lands (**Litalien & Zeeb, 2019**).

Globally, salinity affects vast tracts of agricultural land and is projected to intensify, with over 833 million hectares already impacted and expected to expand further by 2050, posing a serious threat to food production systems (**FAO, 2021**). Salinity stress leads to cellular dehydration, ionic imbalance, osmotic stress, and oxidative damage, ultimately restricting plant growth and productivity (**Zhu, 2002**). Given these challenges, millets are increasingly viewed as climate-smart crops capable of sustaining productivity in degraded and saline-prone soils. Advancements in breeding, molecular biology, and genomic tools have facilitated the identification of key traits associated with stress tolerance in millets, particularly pearl millet. Strategies such as germplasm improvement, heterosis exploitation, marker-assisted selection, and genomic interventions are being employed to enhance salinity tolerance and yield stability under adverse conditions. These approaches hold significant promise for sustainable agricultural development and efficient utilization of marginal lands, thereby reinforcing the role of millets in future food systems.

Physiological Basis of Salt Stress Tolerance in Millets

Millets are inherently climate-resilient crops adapted to arid and semi-arid regions, capable of thriving under low rainfall and nutrient-poor soils while exhibiting substantial tolerance to abiotic stresses such as salinity. Pearl millet, predominantly cultivated in South Asia and West Africa, demonstrates notable salinity tolerance, partly attributed to its C4 photosynthetic pathway subtypes (PEP-CK, NAD-ME, and NADP-ME) (**Blummel *et al.*, 2003; Wang & Shangguan, 2010**). The C4 mechanism, supported by Kranz anatomy, enhances CO_2 concentration in bundle sheath cells, minimizes photorespiration, and improves water and nutrient use efficiency, thereby conferring resilience under stress conditions (**Sage & Zhu, 2011**).

Physiological adaptations such as low CO_2 compensation point, efficient transpiration, deep root systems, and dense leaf venation further strengthen stress tolerance. The intricate venation network facilitates efficient photosynthate transport and water distribution, enhancing overall physiological efficiency (**Govinda *et al.*, 2012; Altus & Canny, 1982**). Despite being glycophytes, pearl millet exhibits moderate salinity tolerance (~6 dS/m), making it a valuable candidate for breeding programs targeting saline environments (**Ashraf & McNeilly, 1987, 1992; Dua, 1989; Muscolo *et al.*, 2003**). Under salinity stress, plants experience oxidative damage due to reactive oxygen species (ROS) generated during metabolic processes (**Sharma *et al.*, 2013; Wang *et al.*, 2012**). To mitigate this, millets employ both enzymatic (e.g., catalase, superoxide dismutase, peroxidases) and non-enzymatic defense mechanisms, including osmotic adjustment and ion compartmentalization (**Misra & Gupta, 2005; Ashraf & Foolad, 2007**). Accumulation of compatible solutes such as proline, carbohydrates, and glycine betaine stabilizes cellular structures, scavenges ROS, and maintains osmotic balance (**Crowe *et al.*, 1987; Berjak *et al.*, 2007; Munns, 2002**).

In finger millet, salinity tolerance is reflected through minimal reductions in germination, growth, biomass, chlorophyll content, and ion homeostasis in tolerant cultivars compared to sensitive ones (**Rahman *et al.*, 2014; Taïbi *et al.*, 2016; Ishikawa & Shabala, 2019; Mukami *et al.*, 2020**). Enhanced chlorophyll retention and higher soluble sugar accumulation serve as key biochemical indicators of tolerance (**Hema *et al.*, 2014; Mahadik & Kumudini, 2020**). Additionally, proline accumulation acts as a critical Osmo protectant, preserving membrane integrity and reducing oxidative stress (**Rao *et al.*, 2013; Rasool *et al.*, 2013**). Salinity-induced osmotic stress also triggers the accumulation of osmolytes such as sugars, amino acids, and proteins, which function as ROS scavengers and structural stabilizers (**Chapman *et al.*, 2019; Singh *et al.*, 2022**). In foxtail millet, compounds like putrescine and spermidine reduce oxidative damage, while increased proline levels enhance stress tolerance (**Rathinapriya *et al.*, 2020; Sudhakar *et al.*, 2015; Qin *et al.*, 2020**). Salt-tolerant cultivars further exhibit elevated levels of organic acids, phenolics, carbohydrates, and amino acids, contributing to improved stress adaptation (Figure 1).

Molecular Response to Salinity Stress

Plants mitigate salinity-induced cellular perturbations through specialized sensors and intricate signalling cascades. The initial perception of salt stress occurs via transmembrane sensors, where elevated Na^+ levels disrupt ionic homeostasis, particularly affecting K^+ and Ca^{2+} balance (**Julkowska & Testerink, 2015**). A rapid increase in cytosolic Ca^{2+} concentration is observed within seconds of salt exposure, functioning as a primary secondary messenger in early stress signalling events (**Lynch *et al.*, 1989**). Despite limited identification of salt sensors, key components include ROS-mediated signals and Na^+/Ca^{2+} transport systems (Wu *et al.*, 2021). Plants regulate excess sodium through Na^+/H^+ antiporters located at the plasma membrane and tonoplast, facilitating either Na^+ extrusion or vacuolar sequestration. Central to this process is the well-characterized Salt Overly Sensitive (SOS) signalling pathway, which translates Ca^{2+} signals into adaptive responses under saline conditions (**Ishitani *et al.*, 2000**). The SOS pathway comprises three core components—SOS3 (Ca^{2+} sensor), SOS2 (protein kinase), and SOS1 (Na^+/H^+ antiporter)—that collectively maintain ionic homeostasis. Elevated cytosolic Ca^{2+} activates the SOS3–SOS2

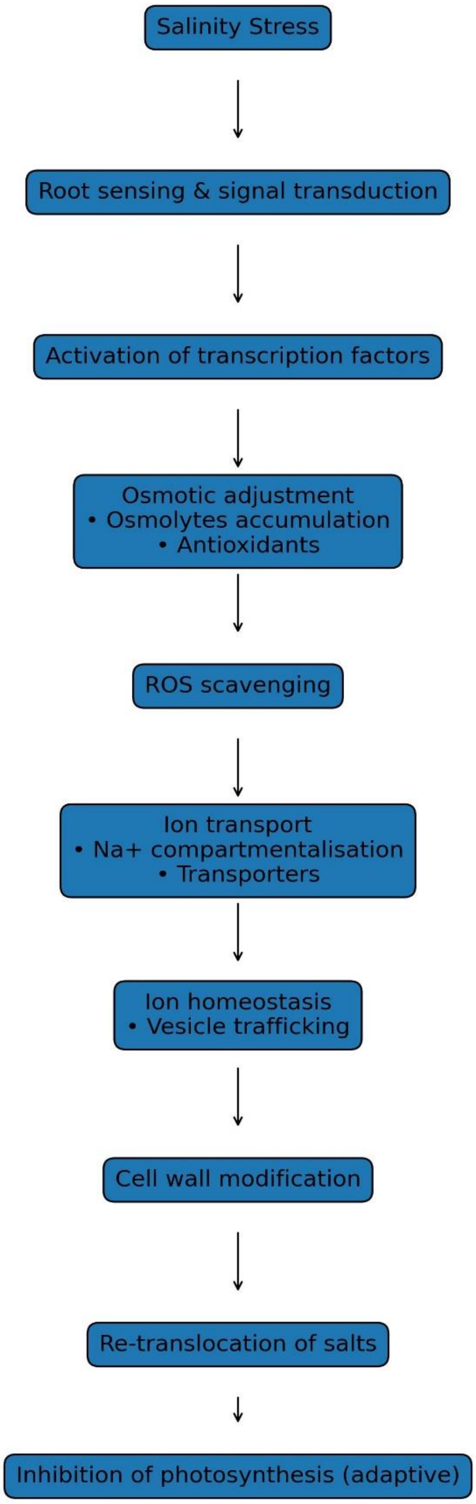

Figure 1: Summary of events that take place under salt stress in plants to confer salt tolerance

complex, which phosphorylates and stimulates SOS1 activity, thereby promoting Na^+ efflux and reducing cytotoxicity (**Guo *et al.*, 2009**). Additionally, this complex regulates vacuolar Na^+ sequestration via NHX transporters (**Qiu *et al.*, 2004**). The conservation of SOS genes across species highlights their fundamental role in salinity tolerance (**Zhu *et al.*, 1998**).

Salinity stress further induces osmotic imbalance, dehydration, and oxidative stress, severely impairing physiological processes such as stomatal conductance, photosynthesis, and chlorophyll stability (**Chaudhry *et al.*, 2020, 2021**). At the molecular level, high salt conditions restrict water and nutrient uptake, leading to extensive cellular reprogramming (**Ali *et al.*, 2021**). Concurrently, enhanced production of reactive oxygen species (ROS) serves dual roles as both damaging agents and signalling molecules, triggering adaptive transcriptional and post-transcriptional responses (table 1). Plants counteract oxidative damage through activation of stress-responsive gene networks, including those encoding ion transporters, Osmo protectants, transcription factors, and signalling molecules (**Rahman *et al.*, 2014**). ABC transporters contribute to ion homeostasis (**Kim *et al.*, 2010; Jiang *et al.*, 2010**), while aquaporins regulate cellular water balance under osmotic stress (**Horie *et al.*, 2011; Sun *et al.*, 2017; Yepes-Molina *et al.*, 2020**). Signal amplification via kinases and receptor proteins further refines stress responses through phosphorylation-mediated regulation (**Deokar & Tar'an, 2016**). Moreover, transcription factors orchestrate downstream gene expression, ensuring coordinated stress adaptation, while phytohormones such as brassinosteroids modulate growth and enhance tolerance mechanisms (**Bishop, 2003**).

Improvement for Salinity Tolerance in Millets

Salinity stress poses a significant constraint to finger millet productivity, necessitating the development of advanced and sustainable improvement strategies to ensure food security, particularly in sub-Saharan Africa and Asia (**Chivenge *et al.*, 2015**). Conventional breeding approaches, although previously employed, have shown limited success due to the complex, polygenic nature of salinity tolerance, which involves intricate genetic regulation and environmental interactions (**Manavalan *et al.*, 2009**). Modern omics-based approaches, including genomics, transcriptomics, proteomics, and metabolomics, have emerged as powerful tools for elucidating salinity tolerance mechanisms. These approaches have enabled the identification of key stress-responsive genes across crops such as soybean, rice, chickpea, cowpea, and pea (**Wang *et al.*, 2018; Das *et al.*, 2015; Vadez *et al.*, 2012; Chankaew *et al.*, 2014;**

Leonforte *et al.*, 2013). Transgenic strategies further facilitate the targeted expression of candidate genes, enhancing plant performance under saline conditions. Several genes associated with salinity tolerance, including UGT76E12, PtDRS1, MdY3IP1, AtHDG11, codA, NHX1, rstB, and GsZFP1, have been identified and functionally characterized (**Chen *et al.*, 2019; Mohammadi *et al.*, 2018; Yu *et al.*, 2018; Zheng *et al.*, 2018; Banavath *et al.*, 2018; Baloda *et al.*, 2017**).

Genetic engineering approaches have demonstrated promising outcomes in improving salinity tolerance in finger millet (table 1). Expression of genes such as mtlD has been shown to enhance growth and stress tolerance under saline conditions (Hema *et al.*, 2014), while overexpression of stress-responsive genes improves physiological attributes including proline accumulation, chlorophyll stability, and reduced oxidative damage (**Anjaneyulu *et al.*, 2014**). The availability of efficient regeneration systems and diverse stress-responsive genes further strengthens the potential for crop improvement (**Mukami *et al.*, 2018; Ngetich *et al.*, 2018; Zheng *et al.*, 2018; Chen *et al.*, 2019**). Advances in plant genomics have enabled the identification of key regulatory pathways associated with salinity tolerance, including improved ion homeostasis mechanisms and stress-responsive gene networks (**Chakraborty *et al.*, 2012**). Transgenic studies have further demonstrated enhanced tolerance through improved germination, reduced oxidative stress, and increased osmolyte accumulation.

Given the multigenic nature of salinity tolerance, reliance on single-gene strategies is often insufficient for achieving stable and durable tolerance (**Ashraf *et al.*, 2018**). Therefore, multigene pyramiding and co-expression strategies are increasingly emphasized to integrate multiple stress-responsive traits within a single genotype (**Biradar *et al.*, 2018**). Although gene transfer techniques such as Agrobacterium-mediated transformation and biolistic methods enable multigene integration, they present challenges including gene silencing, insertional complexity, and instability of inheritance (**Liu *et al.*, 2018**). Empirical evidence indicates that co-expression of multiple genes enhances salinity tolerance across several crop species (**Gupta *et al.*, 2018; Shafi *et al.*, 2017; Pehlivan *et al.*, 2016; Yan *et al.*, 2016**). In finger millet, gene stacking approaches have demonstrated improved tolerance compared to wild-type plants, highlighting their potential for long-term stress resilience (**Jayasudha *et al.*, 2014)**.

Table 1: Salinity response genes identified in finger millet (Rahman *et al.*, 2014)

Category	**Gene IDs (LOC_Os)**	**Function / Description**
Transporters	Os11g39020, Os02g32690, Os01g24010	ATP-binding cassette (ABC) transporters
ATP Synthase	Os03g14690, Os10g10500, Os04g55040	Vacuolar ATP synthase
Proteins	Os02g57720, Os03g05290, Os07g26630, Os07g26690	Aquaporin proteins (water transport)
Signalling Molecules	Os03g42130, Os06g04880, Os02g41580, Os03g46770, Os03g62180, Os07g03810, Os03g56270, Os07g35140, Os02g09740, Os01g26390	Gibberellin 20-oxidase 2; Serine/threonine kinase; Calcium/calmodulin-dependent protein kinases; RNA recognition motif protein; Lectin protein kinase; Lectin-like receptor kinase; Receptor protein kinase; Receptor-like serine/threonine kinase; STRUBBELIG receptor family; DUF26 kinases
Transcription Factors (TFs)	Os03g60080, Os08g36790, Os07g02060	NAC domain, bZIP, WRKY29
Phytohormones	Os03g16980, Os07g47700	Brassinosteroid biosynthesis
Osmo protectants	Os11g26790, Os08g32870, Os01g62900	Dehydrins; Betaine aldehyde dehydrogenase; Pyrroline-5-carboxylate synthetase (proline biosynthesis)
Carbohydrate & Osmolyte Metabolism	Os03g20120, Os01g07530, Os07g10840, Os03g59430, Os06g46340, Os08g20660	Glycosyl transferases (raffinose synthesis); Glycosyl hydrolase family 31 (melibiose hydrolysis); Sucrose phosphate synthase 1 (photosynthetic sucrose synthesis)

1. Breeding Strategies for Salt Stress Tolerance in Pearl Millets

Pearl millet and its wild relatives exhibit inherent tolerance to salinity stress, making them suitable candidates for cultivation in saline environments (**Ashraf & McNeilly, 1987**). Substantial genotypic variability has been documented in pearl millet with respect to salinity response at the whole-plant level, providing opportunities for selection and genetic improvement. Additionally, the presence of high tolerance in other Pennisetum species further expands the genetic reservoir for improving salinity tolerance through breeding and management strategies (**Muscolo *et al.*, 2003**). Salinity tolerance is a genotype-dependent trait influenced by environmental interactions, necessitating extensive germplasm screening to identify superior stress-tolerant lines. These elite genotypes serve as valuable sources for candidate gene identification and introgression into sensitive crops via conventional or transgenic approaches (**Jha, 2019**). Although germplasm screening has been widely conducted in major cereals, the identification of salinity-responsive genes remains limited due to the complex and multigenic nature of the trait (**Morton *et al.*, 2019; Jha, 2018; Lakra *et al.*, 2018**).

Extensive evaluation of pearl millet germplasm has revealed significant genetic diversity for salinity tolerance, particularly among landraces and wild relatives, which harbour adaptive traits and novel alleles (**Krishnamurthy *et al.*, 2007a, b; Toderich *et al.*, 2018; Hoang *et al.*, 2016; Quan *et al.*, 2018)**. However, despite the availability of large germplasm collections, systematic identification and utilization of superior genotypes remain limited (**Shivhare & Lata, 2017**). Recent advancements in genomics and high-throughput phenotyping (HTP) have enhanced the ability to dissect stress tolerance traits and accelerate breeding programs. Modern breeding strategies, including marker-assisted breeding, mutation breeding, exploration of wild relatives, doubled haploids, GWAS, and CRISPR-Cas9 technologies, have significantly contributed to the development of salinity-tolerant millet varieties. In pearl millet, extensive molecular marker resources such as AFLP, RFLP, RAPD, SSRs, DArTs, and SNPs have facilitated the identification of quantitative trait loci (QTLs) associated with salinity tolerance and yield improvement (**Vadez *et al.*, 2012; Singh *et al.*, 2016; Sharma *et al.*, 2014**). Linkage maps spanning approximately 700–716 cM have been constructed, enabling precise genetic dissection of stress tolerance traits (**Vadez *et al.*, 2012**).

Germplasm screening efforts have led to the development of improved breeding materials, including OPVs, hybrids, and elite parental lines with enhanced salinity tolerance (**Shivhare & Lata, 2017**). Several promising genotypes, such as ICMB series, IP lines, and region-specific accessions, have been identified and recommended for further evaluation and deployment (Sudan, Namibia, and India accessions). Notably, the variety "Hashaki I", developed in Uzbekistan, has demonstrated high forage yield under saline conditions, highlighting the potential of targeted breeding efforts (**Yadav *et al.*, 2012**). At the molecular level, functional validation of key genes and QTLs—such as VDAC, LEA genes, PgNHX1, and DT-QTLs—has provided insights into mechanisms underlying salinity tolerance (**Reddy *et al.*, 2012; Verma *et al.*, 2007; Sharma *et al.*, 2011, 2014**). However, transcriptomic and transgenic studies in pearl millet remain limited, indicating a significant research gap (**Choudhary *et al.*, 2021**). Therefore, intensified efforts toward genome sequencing, gene discovery, and transgenic validation are essential for advancing salinity tolerance breeding.

High-Throughput Approaches for Phenotyping Salt Stress Tolerance in Pearl Millet

The development of quantitative high-throughput phenotyping (HTP) systems is essential to overcome existing constraints in accurately capturing genetic gains and expediting breeding programs. HTP integrates aerial and ground-based platforms to monitor crop traits dynamically across growth stages under both abiotic and biotic stress conditions. These platforms employ advanced imaging technologies—including satellite imagery, high-resolution mobile cameras, drones, and robotic systems—along with light sensors, remote sensing tools, and mobile applications, enabling non-destructive and non-invasive data acquisition with varying degrees of automation. HTP technologies offer significant advantages, such as high-resolution data collection over extensive spatial scales, portability, operational efficiency, and reduced labor costs. However, limitations such as battery constraints, high initial investment, environmental interference, and challenges in data interpretation and image quality persist. Therefore, a comprehensive understanding of plant stress responses is critical for ensuring yield stability and sustainable agricultural productivity (**Pessarakli, 2019**). Plant phenotyping serves as a cornerstone for crop improvement by facilitating precise trait measurement and effective utilization of genetic resources. It encompasses the comprehensive evaluation of complex plant attributes, including growth, development, physiology, architecture, stress tolerance, and yield, alongside the quantification of individual parameters underlying these traits (**Li *et al.*, 2014**). Modern breeding programs require the phenotyping of large populations across multiple traits and growth stages, which is often impractical using conventional low-throughput methods due to their labour-intensive, destructive, and low-resolution nature (**Sandhu *et al.*, 2021**).

The advent of HTP has significantly addressed these limitations through the integration of automation, imaging technologies, and artificial intelligence, enabling efficient and non-destructive field-based phenotyping. HTP systems—ranging from manual to fully autonomous platforms equipped with diverse sensors—facilitate the collection of spatiotemporal data, resulting in large datasets for advanced analysis (**Kaur *et al.*, 2021; Sandhu *et al.*, 2021**). These platforms utilize a combination of imaging techniques, sensor-based measurements, and analytical indices such as NDVI, green leaf index, chlorophyll index, and stress tolerance indices to evaluate plant performance. The resulting phenotypic datasets encompass extensive physiological, morphological, and biochemical information, aiding in the identification of stress-resilient genotypes across diverse environments. Nonetheless, major challenges remain, including data integration across platforms, interpretation of spectral information, environmental variability, and cost-effective data management. Additionally, the reliability of these approaches depends on their validation under multi-locational field conditions to ensure robust and scalable crop improvement outcomes.

2. CRISPR/CAS genome editing and precision breeding for salinity stress tolerance in finger millet

The CRISPR/Cas genome editing system has emerged as a highly precise, efficient, and cost-effective tool for targeted mutagenesis and genetic improvement in plants. Its widespread application has enabled the development of crop varieties with enhanced resistance to both biotic and abiotic stresses in species such as foxtail millet, sorghum, rice, and wheat (**Cheng *et al.*, 2021; Zhang *et al.*, 2021; Liu *et al.*, 2019; Char *et al.*, 2020; Tang *et al.*, 2017; Wang *et al.*, 2017; Dong *et al.*, 2020; Liang *et al.*, 2017; Sánchez-León *et al.*, 2018**). Specifically, CRISPR/Cas-mediated editing has demonstrated significant potential in improving salinity tolerance, as evidenced by targeted modification of the OsRR22 gene in rice, resulting in enhanced tolerance in mutant lines (**Zhang *et al.*, 2019**). Similarly, manipulation of the SlARF4 gene in tomato has revealed improved physiological responses under salinity and osmotic stress (**Bouzroud *et al.*, 2020**). The CRISPR/Cas mechanism operates through RNA-guided nuclease activity, inducing site-specific double-strand breaks (DSBs), which

Table 2 HTPs platforms available for phenotyping salt tolerance in pearl millet that has been utilized in other crops under abiotic stress (adapted and modified from Gill *et al.* 2022)

HTP Platform	Crop(s)	Morpho-physiological Traits Studied	Reference
LemnaTec 3D Scanalyzer System	Rice	Salt tolerance traits	Hairmansis *et al.* (2014)
PHENOPSIS	Arabidopsis	Plant responses to water stress	Granier *et al.* (2006)
PHENODYN	Rice, Maize	Soil water status (drought), leaf elongation rate, micrometeorological variables	Sadok *et al.* (2007)
GROWSCREENFLUORO	Arabidopsis	Leaf growth and chlorophyll fluorescence (stress detection)	Jansen *et al.* (2009)
BreedVision	Wheat	Lodging, plant moisture content, biomass yield, tiller density	Busemeyer *et al.* (2013)
RhizoTubes; RADIX	Wheat, Maize	Root traits under stressed and non-stressed conditions	Jeudy *et al.* (2016)
PHENOVISION	Maize	Detection of drought stress and recovery	Asaari *et al.* (2019)

PhénoField	Wheat	Characterization of multiple abiotic stresses	Beauchêne *et al.* (2019)
PhenoImage	Wheat, Sorghum	Plant responses to water stress	Zhu *et al.* (2021)
Field Scanalyzer	Wheat	Morphological traits	Virlet *et al.* (2016)
CropQuant	Wheat	Performance-related traits	Zhou *et al.* (2017)
PhenoRoots	Cotton (*Gossypium hirsutum* L.)	Root-related traits	Martins *et al.* (2020)
Self-propelled electric HTPP platform	Wheat (*Triticum aestivum*)	Plant height	Pérez-Ruiz *et al.* (2020)

are subsequently repaired via non-homologous end joining (NHEJ) or homology-directed repair (HDR) pathways, leading to targeted genetic modifications (**Schmidt *et al.*, 2019**). Compared to earlier genome-editing tools such as mega nucleases, zinc-finger nucleases, and TALENs, CRISPR/Cas offers superior simplicity, precision, and scalability, as it eliminates the need for complex protein engineering.

Despite its transformative potential, the application of CRISPR/Cas technology in finger millet remains limited. The absence of a fully assembled and annotated reference genome has significantly constrained the design of guide RNAs (gRNAs), thereby impeding precise genome editing (**Hittalmani *et al.*, 2017; Hatakeyama *et al.*, 2018**). Furthermore, challenges such as low transformation efficiency and genotype-dependent regeneration protocols restrict its practical implementation (**Kothari *et al.*, 2004; Ignacimuthu & Ceasar, 2012; Satish *et al.*, 2017; Ngetich *et al.*, 2018**). Although off-target effects are relatively rare in plants, careful gRNA design and selection of appropriate Cas variants are essential to ensure editing accuracy (**Peterson *et al.*, 2016**). Overall, CRISPR/Cas technology holds immense promise for precision breeding and development of salinity-tolerant millet cultivars, but its full potential can only be realized through advancements in genomic resources and efficient transformation systems.

3. Agronomic approaches for salinity stress mitigation

Agronomic strategies aimed at alleviating salinity stress can be implemented at both soil and crop levels. One of the most fundamental approaches involves increasing soil moisture through efficient irrigation practices, which dilutes salt concentration to tolerable levels. However, such interventions are often economically and logistically impractical for smallholder farmers, particularly in arid and semi-arid regions where finger millet is predominantly cultivated. During critical dry periods, salinity stress intensifies, necessitating alternative management strategies. Application of calcium-based salts (e.g., calcium nitrate or calcium chloride) has been shown to enhance crop survival under saline conditions by facilitating the displacement of Na^+ ions from soil colloids, thereby promoting their leaching (**Mariani & Ferrante, 2017**). Similarly, magnesium supplementation contributes to improved soil structure and root growth. At the physiological level, chloride ions regulate sodium transport by inhibiting membrane Na^+ channels, thus reducing cytosolic Na^+ accumulation. Additionally, nitrate forms of calcium may competitively limit Na^+ uptake, although further validation is required. The use of soil amendments—both chemical and organic—

plays a pivotal role in reclaiming saline soils and improving crop performance. In pearl millet, supplementation with nutrients such as potassium, phosphorus, gypsum, silicon, and boron, along with organic inputs like manure, compost, crop residues, and biochar, has demonstrated significant improvements in growth under saline conditions. Elevated Na^+ levels in saline soils disrupt nutrient balance by reducing Ca^{2+} and K^+ availability; however, potassium fertilization mitigates these effects by enhancing stomatal regulation, osmotic balance, protein synthesis, and energy metabolism. Consequently, potassium application increases grain yield while reducing Na^+ accumulation in plant tissues (**Heidari & Jamshidi, 2011**).

Similarly, the combined application of silicon and potassium humate enhances physiological and biochemical performance under salinity stress (**Hassanein *et al.*, 2017**). Boron, an essential micronutrient, further alleviates salinity-induced damage by maintaining membrane integrity, enhancing potassium uptake, and regulating antioxidant activity, thereby improving yield (**Sezer, 2014; Salem, 2020; Riaz *et al.*, 2018**). Organic amendments represent a sustainable and effective approach to salinity management, as they improve soil physicochemical properties and nutrient dynamics. Inputs such as vermicompost, farmyard manure, and plant residues enhance soil structure, reduce salinity effects, and promote plant growth (**Diatta, 2016; Araújo *et al.*, 2022**). Among these, biochar has gained considerable attention due to its ability to improve cation exchange capacity, water retention, soil structure, and nutrient availability. It also reduces Na^+ and Cl^- uptake while enhancing potassium availability and chlorophyll synthesis (**Bamminger *et al.*, 2016; Ding *et al.*, 2022**). Overall, the incorporation of organic materials derived from agricultural and municipal by-products offers a cost-effective and environmentally sustainable strategy for mitigating salinity stress and improving soil health (**Meena *et al.*, 2018**).

Conclusion and Future Perspectives

Millets, particularly pearl millet and finger millet, are inherently climate-resilient crops with a remarkable capacity to thrive under harsh environmental conditions, including salinity. However, despite their adaptive potential, salinity stress remains a critical constraint, significantly impairing plant growth, physiological efficiency, and yield stability, thereby limiting overall productivity in affected regions. Compared to major cereals, the underexplored nature of salinity responses in millets highlights a substantial knowledge gap that warrants intensified research efforts. Future strategies should prioritize the systematic collection, characterization, and utilization of diverse germplasm resources to identify novel genetic variability associated with salinity tolerance. The development of robust and high-throughput phenotyping platforms, coupled with precise screening methodologies, will be essential for accurately dissecting stress-adaptive traits. Furthermore, whole-genome sequencing and functional genomics approaches are pivotal for elucidating the complex genetic architecture underlying salinity tolerance and for facilitating ideotype-based crop improvement.

Given the escalating global demand for food production, alongside the expanding prevalence of soil salinity due to climate change and unsustainable agricultural practices, enhancing salinity tolerance in millets has become an urgent priority. The polygenic nature of salinity tolerance, often compounded by concurrent stresses such as drought, heat, and nutrient imbalances, necessitates integrated and multidisciplinary approaches for effective crop improvement. Recent advancements in biotechnological and breeding tools, including genomic selection, high-throughput phenotyping, CRISPR/Cas-mediated genome editing, speed breeding, and synthetic biology, offer transformative potential for accelerating the development of salt-tolerant millet cultivars. The integration of these modern approaches with conventional breeding and agronomic management practices will enable the development of resilient, high-yielding, and nutritionally superior varieties. In conclusion, a holistic and synergistic framework combining genetic, physiological, and technological innovations is imperative to unlock the full potential of millets as sustainable crops for saline environments, thereby contributing to global food security and climate-resilient agriculture.

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