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Stress-resilient dryland cereals: A review on mechanisms of drought and salinity tolerance

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Abstract

Millets and sorghum, considered as dryland cereals are particularly known for their capability to grow in adverse environments. The tolerance mechanisms to major abiotic stressors remain fragmented across physiological, biochemical and molecular studies. This review aims to scrutinise and synthesise the major tolerance mechanisms that millets perform under drought and saline stress. Published evidence on stress perception, physiological adjustment, biochemical defence and molecular regulation was reviewed and integrated. Drought tolerance mechanisms are primarily associated with osmotic adjustment, root system modification, osmoprotectant accumulation and stress-responsive signalling, which includes calcium-dependent protein kinases and mitogen-activated protein kinases. Salinity tolerance involves osmotic adjustment, ion homeostasis, the salt overly sensitive (SOS) pathway and microbe-mediated stress tolerance. Stress tolerance results from the coordinated maintenance of water status through physiological, biochemical and molecular processes. Importantly, high osmotic adjustment alone does not result in high productivity, whereas root development is important for sustained growth and yield. Rhizosphere interactions further contribute to alleviating stress by modifying plant water relations and ionic balance. The increasing demand for nutrient-dense crops, coupled with climate change-induced stress factors, necessitates the promotion of naturally stress-resistant plants to ensure food security and yield stability. Millets and sorghum exhibit resilience to various abiotic stresses, yet they remain underutilised due to limited awareness and cultivation efforts. This review highlights the need for functional gene validation, physiological-omics-based approaches and an understanding of the relationship between molecular responses and yield maintenance of crops under field stress to aid the development of climate-resilient dryland cereals.

Keywords: abiotic stress, climate change, drought, millets, salinity, tolerance mechanisms

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1. Introduction

The increase in demand for nutrient rich food, complex carbohydrates and healthy phytochemicals and in addition to the challenge posed by the world's increasing population, which has been estimated to reach around 10.9 billion people on earth is increasing the need for food supplies by 50–75 % which has emerged as one of the greatest threats to food security (1, 2). Climate change has made this situation much more difficult, leading to greater carbon dioxide levels, more frequent droughts, heatwaves brought on by rising temperatures and greater precipitation (3). Human activities have contributed significantly to climate change, thereby resulting in reduced agricultural productivity and escalating the threat to food security (4). Unexpected rain, extreme heat and dry spells are a few examples of stressors that have an impact on plant growth. Certain crop varieties exhibit high tolerance to abiotic stressors and this issue can be largely resolved by utilising naturally stress-resistant plants (NSRPs), which promote stable yields, comprehensive food security and public health (5). Millets, also referred to as inherently stress-resistant crops, are small-seeded, annual grasses that utilise the C4 photosynthetic pathway and are cultivated for human and animal consumption (6). Dryland cereals, such as millets and sorghum are gaining renewed attention as climate-

resilient crops by exhibiting a remarkable resistance to a range of abiotic stressors and adapting to the poor soils which make them cultivable in arid and semi-arid environments (7). Even though millets and sorghum have a remarkable ability to tolerate abiotic stress they are neglected and considered underutilised crops (NUCs) (8–10). The Food and Agriculture Organization of the United Nations (FAO) has recognised these crops as "future smart foods" (FSFs) as they are nutritionally superior, rich in dietary fibre and have healthy bioactive components (11). Nevertheless, these crops continue to be underutilised and neglected, emphasising the need for increased scientific attention and wider cultivation (5). In this context, this review discusses different types of plant stress and highlights the tolerance mechanisms of millets against abiotic stress.

Stress

Stress is defined as an unfavourable environmental constraint in plants (12). It refers to any environmental condition that adversely affects plant growth, metabolism or productivity. Plants respond to stress through changes in gene expression, growth, yield and metabolism. Stress can also be defined as a condition that inhibits the full genetic expression of growth and development (13, 14). Biotic and abiotic stresses are the two basic groups into which plant stress is divided. Biotic stress refers to the stress factors that result from interactions between a plant and any living organisms, such as viruses, bacteria, fungi, parasites, insects, weeds, etc. and that can either cause minor injury or substantial damage (15).

Abiotic stressors affect plants and each of them affects agricultural productivity globally. Abiotic stress refers to the negative effects of non-living environmental factors on plant growth and development (13). The main abiotic stressors that affect plants are drought, salinity, temperature, heavy metals, flooding and even pollutants (16). In the agriculture sector, abiotic stress is one of the main causes of enormous production and monetary losses. Worldwide, abiotic stress factors especially hyper-salinity and drought are the main reasons for crop loss (17). Plants execute a separate tolerance mechanism for each of these abiotic stressors, in order to sustain and improve their yield. The physiological and molecular mechanisms involved in tolerance to drought and saline stress are illustrated in Fig. 1.

Drought stress

One of the most frequent environmental stressors is drought, which is defined as a prolonged period of water deficit resulting from insufficient rainfall or a momentary drop in soil moisture thereby impacting the plant water uptake (28). It is a natural phenomenon in rainfed environments and often initiates a sequence of morphological, functional, chemical and genetic changes that adversely affect plant growth, development and productivity in general (29). Global warming, the continuous rise in air temperature and atmospheric carbon dioxide (CO_2) levels, rainfall anomalies, shifts in monsoon patterns, deficient water input, loss of water from the soil by means of evaporation, determined by high-temperature events and light intensity, dry breezes are the major causes of drought stress (30).

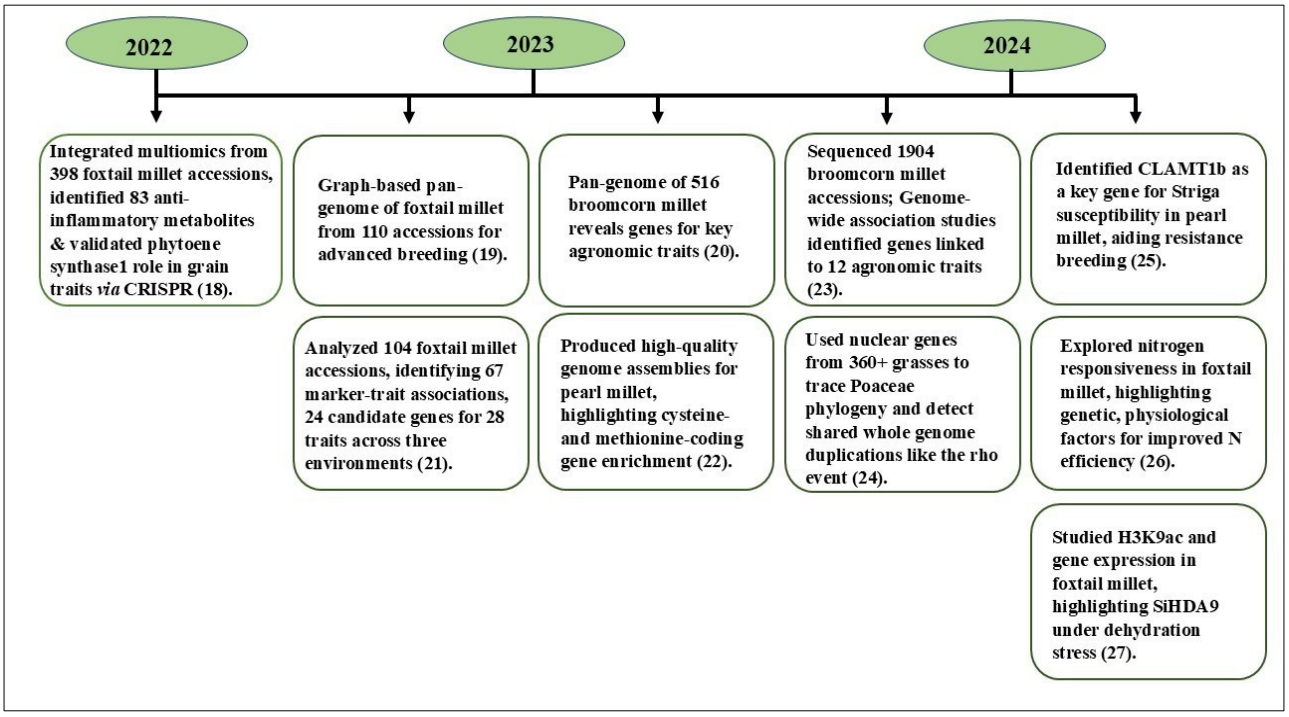


Fig. 1. Major research advancements in millet research for adaptation to climate change. Numbers in parentheses indicate the corresponding references.

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Significance of drought stress on plants

Drought causes seeds not to germinate at all and when a drought hits during the vegetative stage, it has a substantial impact on plant height. Reduced cell expansion, increased leaf loss and compromised mitosis during dry conditions are the main causes of the decrease in plant height. In response to drought, plant leaves take on greater leaf tissue density, greater leaf thickness and smaller leaf areas. When plants experience water deficiency, leaf rolling occurs which results in the loss of potential pressure from the upper epidermis of the leaf (31). Shoot biomass generally decreases more than root biomass under drought conditions, resulting in an increased root-shoot ratio (32). Drought stress significantly influences the anatomical structure, internal hormone levels, osmotic balance and antioxidant activity (33).

Resistance mechanisms of plant to drought stress

When exposed to drought stress, plants perform three main survival strategies viz. stress avoidance, escape and tolerance (34). In order to escape the effects of drought stress on productivity, the plants perform the following mechanisms, such as rapid development and condensation of the life cycle, self-reproduction, earlier than the commencement of the dry period and early flowering (35, 36). Under the avoidance strategy, by reducing the stomatal transpiration loss and increasing the water uptake from well-established root structures, plant water potential is maintained at a maximum. To escape drought, plants rapidly close their stomata, roll their leaves and increase leaf surface wax deposition to reduce water loss through transpiration. The existence of hairy structures and cuticles on leaves may help to uphold high water potential in plant tissues and the surplus development of these structures may lessen plant productivity (30). The antioxidant defence system, consisting of antioxidant enzymes, is a key mechanism that helps plants eliminate excess reactive oxygen species (ROS) and protect against oxidative stress (22).

Mechanism of drought tolerance

The mechanism behind drought tolerance involves a number of genes and metabolic processes to diminish the damage which includes key processes such as, maintaining cell membrane integrity and reducing toxic substance accumulation. Phytohormones such as abscisic acid (ABA) and ethylene serve key roles in drought stress signalling and tolerance. The cell membrane integrity and cell homeostasis are maintained by increasing cell osmoregulatory molecules to maintain the cell turgor pressure thereby allowing physiological processes to occur (37). The 2-hydroxybenzoic acid (salicylic acid) and jasmonic acid improve plant resilience to moisture stress, salinity and heat stress (38). In millets, when cell dehydration occurs, cell respiration is disrupted and photosynthesis is reduced, which leads to reactive oxygen species generation resulting in oxidative stress. Plants activate enzymes such as catalase (CAT), superoxide dismutase and peroxidase which are ROS-scavenging enzymes and non-enzymatic compounds such as ascorbic acid, flavonoids, carotenoids, glutathione, proline, etc., which helps in reducing ROS activity (37).

Plants respond to water stress by producing signal molecules like inositol-1, cyclic adenosine 5'-diphosphate ribose, ABA and calcium ions. These signalling molecules then cause structural and functional changes in plants through signal transduction. Functional gene products, including proline, glycine betaine, non-structural carbohydrates, stress-associated hydrophilic proteins and water channel proteins (aquaporins) also get involved in plant metabolic processes. Regulatory gene products or transcription factors, like calcium-responsive phosphotransferases, mitogen-activated polypeptide-phosphorylating enzymes, ethylene-responsive factors and myeloblastosis can be responsible for modifications in physiology and morphology of plants by regulating signal transduction pathways to adjust the activation of downstream genes (31). The drought tolerance mechanism can be explained in another way as the mechanism by which osmotic adjustment maintains turgor pressure, whereas protoplasmic resistance causes cells to become more elastic and shrink (39).

Millets exhibit C4 photosynthetic pathways, which improve carbon fixation efficiency and reduce water loss. In barnyard and finger millets, certain antioxidant enzymes, including CAT, phenolic compounds and flavonoid content, serve as adaptive mechanisms to combat water stress (40). Catalase detoxifies hydrogen peroxide (H_2O_2) by catalysing its conversion to water and molecular oxygen ($2H_2O_2 \rightarrow 2H_2O + O_2$), whereas phenolic and flavonoid compounds contribute to ROS scavenging, thereby constraining the drought-induced damage to cellular components (41). The increased activities of these enzymes result in the removal of superoxide radicals (O_2^-) and their product, H_2O_2, thereby reducing ROS accumulation. In pearl millet, during drought stress, the flowering stage exhibits an increased expression of genes involved in secondary metabolite pathways, including those for bioactive amines, terpenoids, lignin, wax, mevalonic acid (MVA) and aromatic amino acid biosynthesis pathways compared with the vegetative state (42). The preliminary genome assembly of pearl millet, Tift23D2B1-P1-P5, led to the identification of 27893 protein-encoding genes, accounting for 72.30 % of the genome. Notably, there was an increase in gene families related to terpenoid biosynthesis, which may contribute to pearl millet's superior tolerance to heat and drought compared with other cereals. This pearl millet genome is hosted in the National Centre for Biotechnology Information (NCBI) and European Nucleotide Archive repositories. Overexpression of the *SbMYC2* gene enhances drought tolerance in sorghum and enhanced expression of *SbNAC9* gene in sorghum seedlings enhances the drought tolerance (43, 44). Table 1 summarises the genes involved in abiotic stress responses.

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Table 1. Characterised genetic element in response to the abiotic stress - drought

Sl. No.	Crop	Gene	Reference
1	Sorghum	*SbMYC2*	(43)
		SbNAC9	(44)
2	Pearl millet	*PgRWP-RK*	(45)
		PgDREB2A	(46)
		PgPIP2;6	(47)
3	Finger millet	*EcDREB2A*	(48)
		EcCaM	(49)
4	Foxtail millet	*SiGRF1*	(50)
		SisHSP21.9	(51)
		SiNRX1	(52)

Drought tolerance strategies and adaptive responses in millets

The effect of mannitol-induced osmotic stress on six Kenyan preferred finger millet cultivars during germination explained the fact that mannitol was used as an osmotic agent for the selection of many plant species for drought characterisation (53). The variety GBK043137 showed higher germination at 0 mM and 200 mM mannitol, while GBK043124 registered a germination percentage of 16.25 at 400 mM, whereas other varieties except GBK043128 (1.25 %) exhibited no germination at this level. This explains the mechanism by which the presence of mannitol would have resulted in decline in the internal osmotic potential of the seeds, thus permitting water uptake and leading to germination and also increased the proline concentration in stressed plants. Mannitol is commonly used as an osmotic agent to simulate drought stress during seed germination studies (53). The effects of drought on four millets under early, terminal and long-term water deficits were recorded that the maximum yield loss was observed in little millet (62.6–80.5 %) and the minimum yield loss in foxtail millet (30.1–64.0 %) across all the drought treatments and root depth was maximum in foxtail millet, indicating that deeper root development may play a role in sustaining the water uptake under water-deficit conditions (54).

The harvest index (HI) of proso millet (*Panicum miliaceum* L.) was reduced when drought stress occurred at ear emergence, compared with adequately watered conditions. This reduction was associated with increased floret mortality and decreased seed weight, resulting from impaired assimilate translocation within the ear to developing florets (55). Pearl millet is highly susceptible to drought due to excessive ROS production, which disrupts its antioxidant defence metabolism when subjected to drought stress 21 days after sowing (DAS) (56). Drought stress for 14–21 days reduced relative water content (RWC) and increased proline content in brown and black pearl millet at 45 days, aiding osmotic adjustment and drought survival. The enhanced level of proline helps in adaptation by increasing the osmotic strength of cell sap, thereby helping plants to survive drought stress (57). Relative electrical conductivity (REC) and malondialdehyde (MDA) content were measured from the pearl millet root samples and after 3 hr, there was a substantial difference in REC, possibly due to antioxidant enzyme activity converting ROS. The production of several proteins, such as antioxidases, in pearl millet, which convert ROS into less harmful compounds, may be the cause of the decrease in MDA level after one hour of drought stress (58). Drought increased root length in foxtail millet (*Setaria italica* (L.) P.Beauv.) when the crop was exposed to 13 days of drought, which may be due to stress hormones and increased partitioning of carbohydrates to roots (59).

Elongation of very long-chain-fatty acids (e.g., C24) is an important step in the biosynthesis of cuticular wax and suberin, which is aided by the enzyme 3-ketoacyl-CoA synthase (KCS) (60). The primary transpiration barriers in leaves are called cuticle waxes and several crops have demonstrated a correlation between their wax concentration and their capability to withstand drought (61). Certain root cell walls, especially those in the endodermis, are given hydrophobic characteristics by suberin, a polymer composed of aliphatic and aromatic compounds that acts as a barrier against water diffusion (62). Changes in wax and suberin biosynthesis, might contribute to variations in biomass under drought stress, attributable to the KCS-encoding gene. It is possible that the KCS-encoding gene is responsible for the biomass production during early drought stress and is connected to pearl millet's drought tolerance mechanisms (Fig. 2) (63).

Application of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase-producing plant beneficial microbes (PGPR), *Bacillus amyloliquefaciens* MMR04 enhanced the growth of pearl millet under 5 days of drought stress, increasing plant height and leaf area, which may be due to the breakdown of ACC into α-ketobutyrate and ammonia rather than its conversion to ethylene. The ACC deaminase-positive rhizobacteria can reduce the ethylene concentration and help the plants to withstand drought (64).

A few stress-responsive genes, such as farnesyl pyrophosphate synthase, protein phosphatase 2A, metallothionein and farnesylated protein ATFP6, that are said to play critical roles in giving finger millet with the hardiness needed to withstand drought (65). The stimulation of several drought stress signalling cascade genes, such as serine/threonine residue targeting phosphatase 2A, farnesyl pyrophosphate synthase (FPS), calcium signalling-associated kinase (CIPK31), alpha subunit of the signal recognition particle (SRPRα), etc., has been reported in finger millet (66). Furthermore, it was noted that drought responsiveness was observed in basal regulatory genes, such as TATA-binding protein-associated factors. During drought, the genes related to housekeeping or basic regulatory

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functions are triggered. Some genotypes have a drought resistance trait known as "stay-green," which is responsible for maintaining photosynthesis for longer by delaying leaf senescence through an elaborate signalling cascade. The semi-dwarf pearl millet inbred lines developed in the US exhibit these "stay-green" characteristics. This enables plants to linger with photosynthesis regardless of soil moisture availability and maintain a good grain production in under water-stress conditions (5). The increased ratio is mostly the result of a decline in shoot growth rather than a substantial increase in root growth under stress. Considering both indoor and outdoor research, laboratory studies often involve simplified structures and environments when compared with field studies. Laboratory studies exhibit reduced stress application such as rapid water withholding, that fails to reflect the soil drying and various interacting stressors, whereas this contrasts with field or real-world environments (67).

Salinity stress

Salinity of the soil is a key driver of the diminishing fertility of soils and leads to desertification. The area covered by salinised soils are growing and irrigated soils are particularly affected by this issue. About 10 million hectares of global farmland are degraded by salt build-up each year another one billion hectares of land are at risk due to the climate crisis which is intensified by climate change, groundwater overexploitation, particularly in coastal regions, intensive irrigation, deprived drainage and the use of low-quality irrigation water (68). According to FAO (2024), 10 countries (Afghanistan, Australia, Argentina, China, Kazakhstan, the Russian Federation, the United States, Iran, Sudan and Uzbekistan) account for 70 per cent of the world's saline-affected soils. According to the USDA salinity laboratory, saline soil is defined as soil having an electrical conductivity of the saturated soil extract (ECe) of 4 dSm^{-1} (deciSiemens per metre), which is approximately equal to 40 mM NaCl. This value is obtained from the water-saturated soil paste and this threshold represents the salinity level at which the salt-sensitive crop species start to exhibit reduced growth and yield (69). In plants, the initiation and progression of saline stress affect essential processes, including photosynthesis, protein biosynthesis and lipid metabolism. Prolonged exposure to salt causes plants to endure ionic stress, which can cause adult leaves to senesce prematurely, decreasing the amount of photosynthetic surface area and reducing leaf and shoot dry weight and shoot length (70). Saline stress is an important abiotic factor that severely hampers the vegetative and reproductive progression of plants, causing yield losses of 15–90 % in key crops under moderate to high soil salinity conditions (71).

Causes of saline stress

Salinity can be classified as primary or secondary depending on its causes. The main causes of soil salinity include rock erosion, upward movement of water from shallow brackish aquifers, coastal seawater intrusion, saline sand blown by sea breeze and inadequate drainage (72, 73). Irrigation with saline groundwater, industrial effluents, excessive fertiliser use, deforestation and vegetation removal floods with saline waters, high water tables and the introduction of irrigation without an appropriate drainage system or leaching are the secondary reasons (72). The proportional contribution of primary and secondary salinisation remains difficult to quantify because their importance varies with climatic, hydrological, edaphic and land-management factors that accelerate salinisation. Evapotranspiration and lack of rainfall are the major causes of saline soil formation in arid soils. In dry climates with heavy-textured soils, overuse of irrigation results in salt build-up because insufficient rainfall fails to wash the salts away (73, 74).

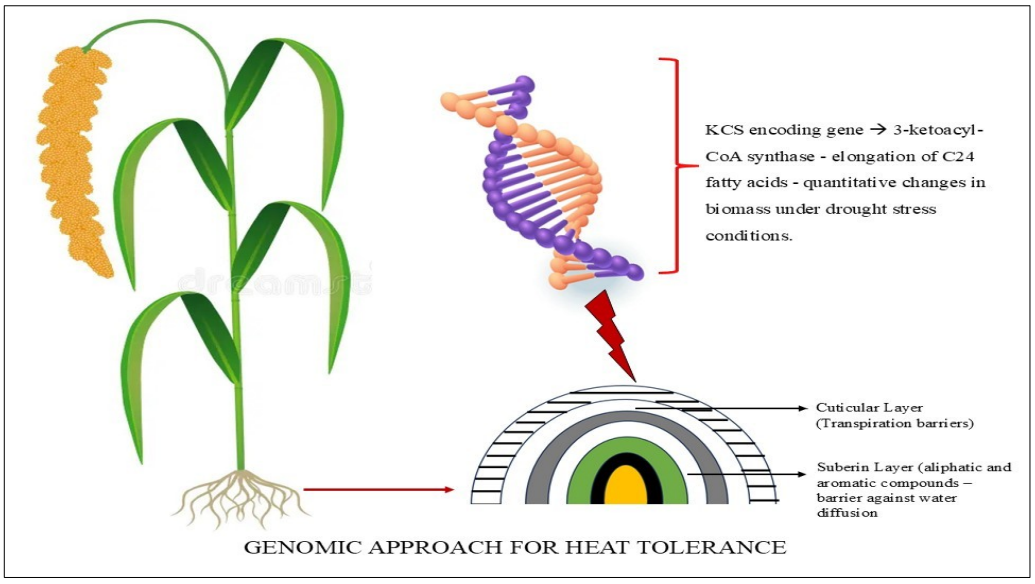


Fig. 2. 3-ketoacyl-CoA synthase (KCS) encoding gene responsible for drought tolerance.

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Effect of saline stress on plants

Salinity adversely affects plant growth through three main mechanisms viz., osmotic stress, specific ion toxicity and nutrient imbalance. Salinity stress brings numerous plant responses, including morphological, functional, chemical and genetic alterations to plant systems. The root structure is the first to sense salinity, which leads to osmotic imbalance and toxic ion accumulation due to cytosolic nutrient imbalances (75). Three factors oppose water uptake by plants: gravitational, matric and osmotic potential of the soil, which is influenced by soil salt concentration. These factors altogether denote the total water potential in the root zone. Water flows from zones of high potential (moist, low-salinity soil) to areas of lower potential (drier, more saline soil) if two zones are hydraulically connected. This gradient drives the water flow through the plant from soil to the atmosphere.

Salinity stress tolerance mechanism

Plants tolerate saline stress through multiple physiological, biochemical, molecular and microbe-mediated pathways, including regulating ion balance and pH, stimulating osmotic adjustment compounds, stimulating antioxidant enzyme activity, modulating hormone production, inducing gene expression and signal transduction, enhancing photochemical systems and involving microbial regulatory mechanisms (76).

Salinity stress perception and signal transduction

Signals produced by hormones, ROS, ions, or the osmotic difference regulate the plant's ability to detect and respond to saline stress. These signals engage corresponding receptors to start the biological processes that allow a plant to cope with stress. Ionic signalling, osmolyte regulation and gene regulation are the three different signal transduction pathways that are linked to abiotic stress. Calcium plays a central role in ionic signalling by activating pathways that regulate enzyme activity, ion channels and gene expression. By enhancing signal transduction, exogenously administered calcium controls K^+/Na^+ selectivity and provides salt adaptation (77). The calcium dependent protein kinases (CDPKs) control the downstream factors in these pathways. Transcriptional regulation plays a vital role, with various transcription factors controlling stress-responsive genes involved in stomatal movement, ROS scavenging, osmolyte synthesis and ion transport when in saline stress.

A shotgun proteomic approach in foxtail millet exposed to drought stress led to the identification of 2281 proteins, with notable changes in leaves compared with roots and seeds (78). Around 21 jasmonate-interacting proteins that have roles in stress signalling, highlight drought tolerance traits in neglected crops over conventional crops that cannot be predicted from genome sequencing. Glycosyl inositol phosphoryl ceramide (GIPC) sphingolipids could act as sensors for saline stress in plants (79).

The osmotic effect

Large soil pores (macropores) contain water when the soil is irrigated or receives rainfall, which can be readily absorbed by plant roots. Gradually, when the soil becomes dry, the amount of water available becomes less near the roots and due to increased matric and osmotic pressures, the remaining moisture is adhered tightly by the soil. It is clear that the salt concentration increases when the moisture level decreases, which becomes worse under saline soil conditions. Due to the presence of higher salt concentration, the osmotic pressure increases, which makes the movement of water from soil into plant roots difficult. This reduced ability of the plant to absorb water under high salinity is known as the osmotic effect, that results in stress, ultimately limiting the vegetative development and productivity (80) (Fig. 3). Plant growth promoting rhizobacteria (PGPR) and endophytes can enhance plant tolerance to salinity by accumulating compatible solutes and improving plant physiological responses.

Salt overly sensitive (SOS): A mechanism of saline tolerance in millets

Increased intracellular Na^+ (an elevated Na^+/K^+ ratio), Ca^{2+} signalling and the calcium B-type-like calcium-binding protein SOS3 (salt-overly-sensitive) are all triggered by salinity stress (81). The SOS3 interacts with SOS2 after attaching itself to the plasma membrane, where SOS2 acts as a serine/threonine specific protein kinase, thus forming SOS2-SOS3 complex (82, 83). This complex phosphorylates and activates SOS1, a plasma membrane Na^+/H^+ antiporter. Activated SOS1 extrudes sodium from the cell in exchange for H^+ using the proton gradient established by plasma membrane H^+-ATPases, thereby maintaining cellular ion homeostasis under salinity stress (84, 85). The SOS1 regulates the amount of Na^+ in the transpiration stream and its movement from root to shoot by regulating sodium loading into the xylem (Fig. 4). Therefore, activation of the SOS pathway maintains ion homeostasis by sodium extrusion and regulating its transport, thereby enhancing plant tolerance to salinity. Resistance to saline stress is provided by the up-regulation of SOS pathway proteins.

Proteomic investigations under salinity have demonstrated increased expression of SOS proteins (86). In comparison with wild-type plants, finger millets exhibited overexpression of the *OsSOS1* gene from rice, enhanced salt tolerance, improved growth traits and reduced ROS levels. This gene is essential for salt extrusion from root epidermal cells (65, 86). The saline-stressed plant executes signalling that activates transcriptome, genome and proteome factors, leading to the production of tolerance-related factors (87). To endure saline soils, plants perform various mechanisms such as ion equilibrium and compartmentalisation, ion mobility and intake, biosynthesis of compatible solutes, up-regulation of antioxidative enzyme activity, formation of protective antioxidant compounds, biosynthesis of polyamines and emission of nitric oxide (NO). The main methods by which plants tolerate salt are hormone

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regulation, ion homeostasis and compartmentalisation. Potassium (K^+) primarily helps plants survive a diverse environmental stressor, such as cold, salinity and drought. Due to potassium's competitive abilities with sodium (Na^+) for binding and preserving plants' RWC, regulating ROS levels and enhancing photosynthesis enhancement, K^+ serves a beneficial role under saline conditions (65). Sodium enters the root by two major mechanisms, viz., non-selective cation channels and strong-binding K^+ transporters (88). Pseudomonas, bacillus and arbuscular mycorrhizal fungi maintain ion homeostasis and reduce the sodium uptake and enhance potassium retention. In addition, arbuscular mycorrhizal fungi (AMF) and rhizobacteria perform antioxidant defence mechanisms to enhance saline tolerance.

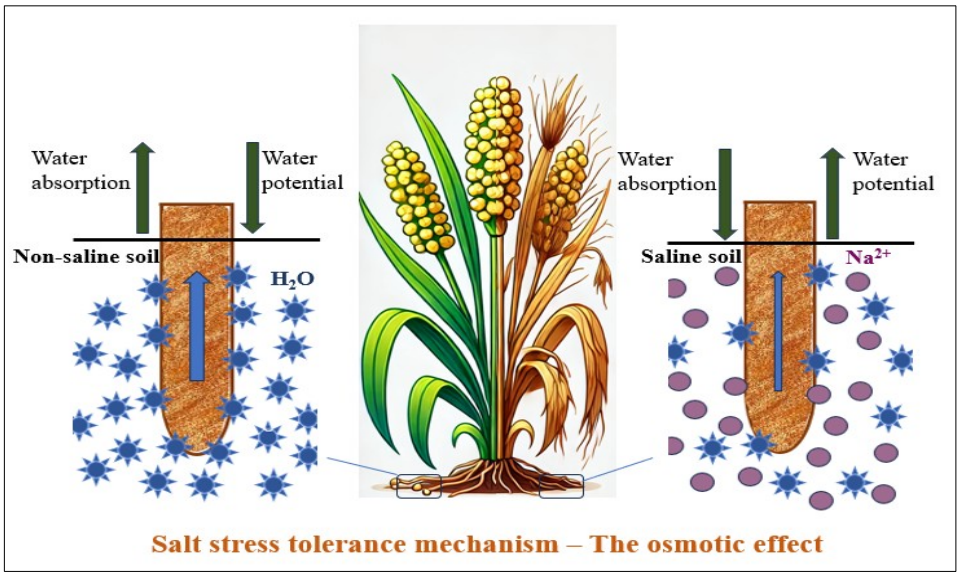


Fig. 3. The osmotic effect in saline and non-saline condition.

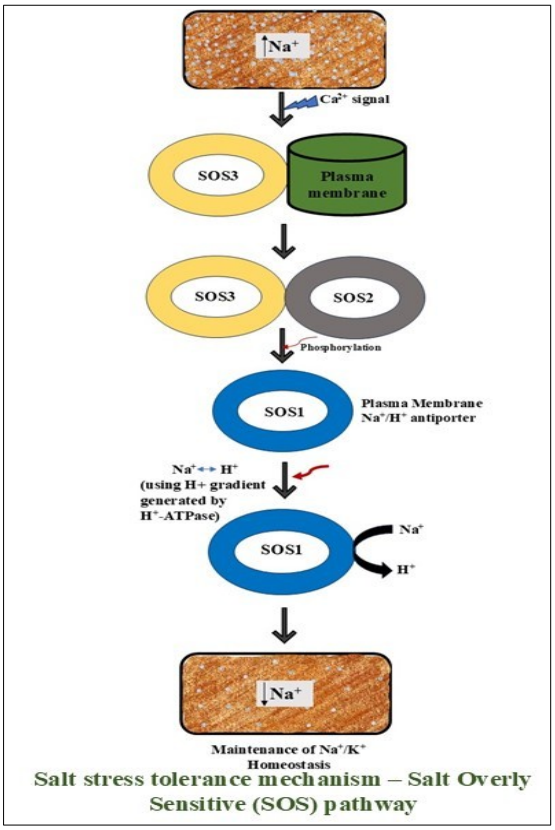


Fig. 4. Salt stress tolerance mechanism – salt overly sensitive (SOS) pathway.

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Plant growth-promoting bacteria mediated saline tolerance

The mechanisms that are performed by PGPR to relieve the plant from saline stress include osmolyte accumulation, phytohormone production, antioxidant activity, siderophores, exopolysaccharide (EPS) production and nutrient acquisition (89). Under salinity, PGPR enhances the accumulation of osmolytes, including proline, glycine betaine and soluble sugars, which lower cellular osmotic potential and facilitate osmotic adjustment, thereby promoting water retention and maintaining cellular turgor under salinity (90). The PGPR regulates aquaporins to improve water transport and root hydraulic conductivity under salinity, which helps in facilitating water movement across cell membranes and improves plant water relations under saline stress (91, 92). The PGPR also produces phytohormones such as ABA, which regulates aquaporin expression (plasma membrane intrinsic protein), thereby altering membrane water permeability and root hydraulic conductivity (93, 94). It also helps in producing siderophores, which chelate iron (Fe) and increase its availability for plant growth, thereby alleviating Fe deficiency under salinity stress (95). Exopolysaccharide production binds and sequesters sodium ions (Na^+) in the rhizosphere, thereby reducing sodium uptake and maintaining the ionic balance. It also improves soil aggregation and water retention, providing a favourable root-zone environment under saline conditions (96).

Rhizospheric fungi also enhance plant yield under stress conditions. During biofilm formation, PGPB produces EPS (97). The fundamental components of EPS are monosaccharides, neutral sugars, uronic acids, amino sugars, substituents of organic esters and pyruvate ketals. The EPS generated by PGPB binds to Na^+ ions during salinity stress conditions, lowering the amount of Na^+ in the root zone and maintaining ionic balance. These also aid in water retention, soil aggregation and metal ion chelation. The threshold salt tolerance of some agricultural crops is presented in Table 2. Salt-tolerant PGPB can lower shoot sodium levels, activate stress-related genes, enhance ROS scavenging, increase proline production and improve plant biomass. Similarly, water uptake and potassium levels in shoots can be increased by arbuscular mycorrhiza, making rhizospheric organisms an effective strategy to enhance crop performance under saline conditions.

Stress proteins

A protein known as "osmotic" was identified in *Nicotiana tabacum* and *Mesembryanthemum crystallinum* (crystalline ice plant) is reported to serve an important role in osmotic adjustment and cellular protection under saline stress (99, 100). A similar protein, termed "germin," was later identified in barley plants under salinity stress (101). Following this, a salinity stress-associated protein was discovered and named "mangrin" in a mangrove species (102). Late embryogenesis abundant (LEA) proteins, originally isolated from cotton, perform a dynamic role in stress resistance by protecting biomolecules under stress conditions (103, 104). Aquaporins, ubiquitous water channel proteins, play a distinct role in water transport across the cell membrane (105). The certain genes responsible for saline stress tolerance is represented in Table 3.

Table 2. Threshold salt tolerance of agricultural crops (86, 98)

Sl. No.	Crop	Salt threshold (ECe) (dsm^{-1})
1	Rye	11.4
2	Sorghum	6.8
3	Foxtail millet	6
4	Proso millet	5.5
5	Rice	3.0
6	Pearl millet	100 mM NaCl
7	Barnyard millet	200 mM
8	Finger millet	6

Table 3. Characterised genes in response to the abiotic stress - saline stress

Sl. No.	Crop	Gene	References
1	Sorghum	*SbMYBHv33*	(106)
		SbWRKY55	(107)
		miR-6225-5p	(108)
2	Foxtail millet	*SiMYB19*	(109)
		SiCYP19-a and b	(110)
		SiNRX1	(52)
3	Pearl millet	*PgWRKY74*	(111)
		PgDREB2A	(46)
4	Finger millet	*EcCaM*	(49)

Response of millet crops to salinity stress

Salinity tolerance in finger millet was enhanced by treating seeds with Pseudomonas strains SPF 33 (*P. aeruginosa*) and SPF 37 (*P. resinovorans*), which exhibited a notable improvement in plant growth characteristics and stress-related physiological responses. The total chlorophyll content (14 µg mL^{-1}) and RWC (84 %) were highest in the plants that were treated with SPF 37, followed by SPF 33 (112). Humic acid also helped in mitigating saline stress by decreasing oxidative stress and upregulating genes involved in the ROS scavenging pathway thereby boosting the activity of superoxide dismutase (SOD), antioxidant enzyme CAT, ascorbate peroxidase (APX) and the enzyme regenerating reduced glutathione (GR). Additionally, it was reported that the land configuration influenced finger millet performance under saline conditions; the ridges and furrows method led to taller plants and more tillers, which was due to better moisture retention and nutrient availability, thereby enhancing photosynthesis and biomass production (113).

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Drought significantly reduces the antioxidant enzymes such as peroxidase and catalase, whereas the salinity increases the levels of these enzymes, which compensates for the dearth of peroxidase (POD) activity and decreases the concentration of ROS (114). Additionally, it was discovered that silicon (1.8 mM) enhances salinity and drought resistance by boosting CAT and POD activity and increasing proline content for osmotic balance under salinity. The overproduction of ROS, including H_2O_2, peroxide anion, singlet oxygen and excessive malondialdehyde content due to lipid peroxidation, is caused by physiological dryness brought on by salinity and is mitigated by high POD activity and flavonoid metabolism, improving stress resistance (115).

An experiment to observe the effect of chloride salts and salt extracts on the growth and yield attributes of little millet (*P. miliaceum*) was conducted and it was noted that the chloride salt, especially sodium chloride-treated plants registered significantly lower plant height (66.27 cm), number of tillers (3.97) and grain yield (3.31 g per plant), when compared with control and other treatments. The maximum plant height (73.67 cm), number of tillers (5.13) and grain yield (3.72 g per plant) were registered by crops treated with magnesium chloride salts. Because of their harmful effects, salt efflorescence and chloride salts were extremely detrimental to little millet plants. Additionally, it was recommended that little millet be grown in soil with acceptable saline levels in order to guarantee healthy crop growth and high-quality grains. In addition to causing a particular ion imbalance and salinity stress, the addition of sodium chloride salts, decreased the quantity and quality of tiny millet, making it harmful to plant health and having a detrimental effect on soil quality (116).

Chlorophyll stability index (CSI) is one of the important indicators of plants' tolerance capacity to salinity stress and it was also discovered that the CSI value of proso millet (73 %) decreased with increasing levels of NaCl (200 mM) concentration. A high CSI (%) score indicates that plants endure saline stress to produce their maximal yield and that the stress has little effect on the chlorophyll content of the plants (117). The foliar spray of silver nanoparticles aids in enhancing the osmotic and ROS scavenging mechanisms in sodium chloride stressed pearl millet seedlings to reduce the oxidative stress damage, thus improving the growth of plants (118). Upregulation of silicon calcineurin B-like protein-interacting protein kinase (24SiCIPK24) and *S. italica* calcineurin B-like protein 5 (SiCBL5) upsurge the tolerance to saline stress in foxtail millet (119, 120). Other hormones also serve a role in foxtail millet's response to salinity stress. Overexpression of *brassinazole resistant 1* (*BZR1*), a key transcriptional modulator in the brassinosteroid (BR) signalling pathway, has been shown to negatively regulate osmotic stress in foxtail millet. This suggests that BR signalling may be involved in osmotic stress responses activated by saline stress. Supplying finger millet with silicon has been recorded to alleviate biotic and abiotic stress by stimulating the antioxidant defence mechanisms, while minimising membrane damage in finger millet genotypes (121). Silicon supplementation of 0 to 25 ppm to the finger millet landraces can help them tolerate the saline stress induced by 200 mM sodium chloride (122). In summary, the level of tolerance that millet crops exhibit is given in Table 4.

Table 4. Millet species and their stress tolerance levels

Sl. No.	Millet species	Drought tolerance	Salinity tolerance
1	*Pennisetum glaucum* (L.) R.Br.	High	Moderate
2	*Eleusine coracana* (L.) Gaertn.	Moderate	High
3	*Setaria italica* (L.) P.Beauv.	High	Moderate
4	*Panicum miliaceum* L.	Moderate	Low
5	Echinochloa spp.	High	High
6	*Paspalum scrobiculatum* L.	High	Moderate
7	*Panicum sumatrense* Roth	Moderate	Moderate

Future insights

Significant advances have been made in understanding the physiological, biochemical and molecular mechanisms of drought and salinity tolerance in dryland cereals. Most of the studies reviewed have been conducted under controlled environments and future research in this area should prioritise the experiments under realistic field conditions. Integrating phenotyping through transcriptomics, proteomics, metabolomics and functional genomics could facilitate the identification and validation of key genes and the regulatory mechanisms for stress tolerance. Greater emphasis should be placed on rhizosphere microbiome interactions and plant growth-promoting microorganisms, which are among the sustainable approaches at present. Integration of these multidisciplinary approaches into breeding programmes will accelerate the development of resilient dryland cereals, promoting sustained productivity under future climate change scenarios.

2. Conclusion

India is self-sufficient in cereal production, supported by assured procurement policies and sustained income from the rice-based cropping system. However, this has led to overexploitation of scarce water resources in several states. Millet cultivation practices are easy to perform and have many health benefits and are adaptable to any sort of environmental conditions. Millets tolerate abiotic stressors such as drought and salinity through physiological, biochemical and molecular mechanisms. Root-system modification, osmotic adjustment, stomatal regulation, antioxidant

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defence, stress-responsive signalling are some drought tolerance mechanisms through which plant water status and cellular protection are supported under drought stress (123). Salinity is associated primarily with stress perception and signalling, sodium/potassium ion (Na^+/K^+) homeostasis, reactive oxygen species (ROS) detoxification and regulation of stress-responsive genes (124). Plant growth promoting bacteria further enhance salinity tolerance by regulating osmolyte accumulation, phytohormone production, exopolysaccharide production and ionic balance. Future studies should integrate physiological phenotyping with proteomic, transcriptomic and functional gene validation approaches to identify mechanisms that maintain crop growth under drought and salinity. Maximum emphasis on genotype × environment interactions and reproductive-stage tolerance is required to identify traits that sustain grain yield under field conditions. Finger millet, proso millet, pearl millet and foxtail millet are the most abiotic stress-tolerant varieties. There are many policies that promote efficient water use and salinity management to complement millet cultivation, improving soil fertility and productivity. Making farmers aware of these precious gold crops and spreading their distinctive character of abiotic stress resistance in millet crops will fetch a great price in the future.

Authors' contributions

SS contributed to the preparation of the article outlines and created figures. UCT, SPP, RG, BR and PPG were involved in the collection and provision of relevant and authenticated review and research articles. RC assisted with collecting international articles. SP was responsible for cross-checking the references and managing the content. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

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