

Research Insights

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Rhizosphere Microbiome Remodeling Enhances Salt-Alkali Tolerance in Proso Millet (*Panicum miliaceum* L.)

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Abstract Saline-alkaline stress is gradually becoming a major factor limiting agricultural productivity because it simultaneously causes osmotic stress, ion toxicity, nutrient precipitation, and high-pH damage within the same soil environment. Under this background, proso millet (*Panicum miliaceum* L.) has gained renewed attention. This study integrates current evidence on how proso millet achieves tolerance under saline-alkaline conditions through coordinated strategies at the morphological, physiological, biochemical, and molecular levels, and further discusses how rhizosphere microbiome reshaping strengthens these response mechanisms. The saline-alkaline tolerance of proso millet depends on the integrated coordination of root structural plasticity, osmotic adjustment, Na⁺/K⁺ homeostasis, antioxidant defense, and cell wall remodeling mechanisms.

The study also analyzes grain metabolic reprogramming in proso millet under saline-alkaline stress, including changes in the composition of amino acids, phenolic acids, flavonoids, organic acids, and antioxidant compounds, and discusses their potential significance for nutritional quality and functional food development. Finally, the study evaluates the application potential of proso millet in saline-alkaline land utilization, ecological restoration, low-input agriculture, and diversified food and feed systems. Rhizosphere microbiome reshaping is not a secondary result of saline-alkaline tolerance in proso millet, but rather a key component of the tolerance formation process itself, and it represents an important future research direction for breeding, microbiome engineering, and the design of climate-adaptive cropping systems.

Keywords Proso millet (*Panicum miliaceum* L.); Saline-alkali stress; Rhizosphere microbiome; Ion homeostasis; Antioxidant defense; Functional metabolites; Climate-resilient agriculture

1 Introduction

Soil salinization and alkalization have become major limiting factors in global agricultural production, especially in arid, semi-arid, and irrigated agricultural regions. The global area of saline soils has reached about 17 million km² and continues to expand under the influence of climate change, improper irrigation practices, and poor drainage conditions (Hassani et al., 2021). The main problem of saline-alkaline soils is the combined stress of salt and high pH. Salt stress reduces soil water potential and causes ion toxicity, while alkaline conditions decrease nutrient availability, disturb membrane transport, and inhibit root function. These effects finally lead to lower seed germination, unstable crop yield, and reduced land-use efficiency (Li and Yang, 2023). Saline-alkaline agriculture is not only an issue of soil management, but also an important topic related to crop structure adjustment and agricultural resilience.

Under this background, minor cereals with strong stress resistance have received increasing attention again. Compared with major staple crops that highly depend on resource input, minor cereals usually show better drought resistance, tolerance to poor soil conditions, and stronger adaptability to environmental stress. They can also maintain relatively stable yields on marginal land (Mudnakudu-Nagaraju et al., 2025). Proso millet is a typical example. It has a short growth period and low water requirement, and it also contains high nutritional value, including rich bioactive compounds, a low glycemic index, and gluten-free characteristics. Therefore, it is considered a potential crop for adapting to climate change and promoting agricultural diversification.

Proso millet originated in the dry farming regions of northern China, and its long domestication history has given it strong environmental adaptability. It is a self-pollinated C4 crop that can mature within 60~90 d and maintain relatively stable productivity under drought and saline-alkaline conditions (Baltensperger, 2002). Significant differences exist among genotypes in salt-alkaline tolerance, nutritional quality, and environmental adaptability.

The rhizosphere is not simply the soil surrounding roots, but an important interface where plants interact with microorganisms. Plant-associated microorganisms can improve plant salt tolerance through different mechanisms, including promoting nutrient uptake, regulating Na^+/K^+ balance, enhancing antioxidant capacity, and improving the soil environment (Zhao et al., 2020). Recent studies on proso millet have started to combine plant physiology, transcriptomics, and rhizosphere microbial community analysis, showing that the microbiome has become an essential component for understanding its saline-alkaline tolerance mechanisms (Yuan et al., 2023).

This study explains the characteristics of saline-alkaline stress and its effects on plant growth performance, summarizes the ecophysiological adaptation mechanisms that help proso millet survive and recover under saline-alkaline conditions, discusses how the rhizosphere microbiome is reshaped during stress and how microbial recruitment enhances plant tolerance, evaluates the effects of saline-alkaline stress on millet metabolism and nutritional quality, and analyzes the potential role of this crop in soil improvement, marginal land agriculture, feed security, and climate-resilient food systems. The aim is to provide theoretical references for the agricultural development of saline-alkaline land and the utilization of stress-resistant crops.

2 Saline-Alkali Stress and Ecophysiological Adaptation

2.1 Physicochemical characteristics of saline-alkali soils

Saline-alkali soil is not defined by a single threshold. Instead, it is characterized by a series of interconnected physicochemical imbalances. The continuous accumulation of soluble salts lowers soil osmotic potential, while sodium ions usually dominate both soil exchange sites and soil solution composition. In alkaline saline soils, bicarbonates and carbonates increase soil pH, sometimes above 8.5, which further promotes nutrient precipitation and weakens transport processes on the root surface. Therefore, crops growing in this type of soil are not simply facing “reduced water uptake,” but are exposed to a rhizosphere environment whose chemical properties have already been altered (Mukhopadhyay et al., 2021).

From the plant perspective, high concentrations of Na^+ are especially damaging because they compete with K^+ at ion transport and enzyme activation sites. Excess external sodium also disrupts cell membrane stability and induces secondary injuries, including oxidative stress. In alkaline soils, high pH further intensifies these problems by reducing the solubility of micronutrients and interfering with proton-driven transport systems. As a result, plants experience a combined stress environment in which water absorption, ion selectivity, and nutrient assimilation are all restricted at the same time.

2.2 Physiological damage caused by saline-alkali stress

Seed germination is one of the earliest life processes affected by saline-alkali stress. Germinating seeds must quickly mobilize stored reserves and establish root-soil contact, but high salinity reduces seed imbibition efficiency and alters the activity of enzymes required for reserve degradation. Elevated pH also suppresses root emergence and affects the maintenance of membrane integrity. In broomcorn millet, evaluations of different genotypes under alkaline stress showed clear differences in seed germination and seedling growth. This not only demonstrates the high sensitivity of the germination stage to saline-alkali conditions, but also indicates the existence of exploitable genetic variation (Ma et al., 2021).

Photosynthesis is then inhibited through several interconnected mechanisms. Salt stress reduces stomatal conductance, suppresses chlorophyll metabolism, damages chloroplast ultrastructure, and limits carbon assimilation. Since ion toxicity and osmotic stress often occur simultaneously, canopy symptoms usually show both dehydration and metabolic inhibition. Alkaline conditions further aggravate the problem by disrupting nutrient supply to the photosynthetic system. In proso millet and related systems, salt-tolerant genotypes are

generally better able to maintain leaf structure and photosynthetic activity than sensitive genotypes. This suggests that maintaining photosynthetic continuity is itself an important tolerance trait rather than only a secondary result of stress resistance.

Oxidative damage is another typical feature of saline-alkali stress. Reactive oxygen species (ROS) normally function as important signaling molecules, but under severe stress they accumulate excessively, causing lipid peroxidation, membrane leakage, protein damage, and cellular dysfunction. Many recent reviews on plant systems have identified ROS regulation as a central component of stress-resistance biology rather than just a secondary symptom. Salt-tolerant millet materials also show lower oxidative damage and stronger inducible antioxidant capacity, further indicating that controlled ROS scavenging plays an important role in plant tolerance under real stress conditions (Mittler et al., 2022).

Roots suffer from both direct and indirect damage. High salinity inhibits root elongation, while high pH suppresses root tip growth, root hair development, and nutrient uptake. Because roots are also responsible for maintaining ion selectivity and supporting beneficial microorganisms, root injury can trigger cascading effects on whole-plant adaptation. In millet, tolerant and sensitive genotypes differ significantly in root structure, surface integrity, and transport-related transcriptional responses, suggesting that root resilience forms the basis of shoot resilience (Yuan et al., 2022).

2.3 Agricultural challenges under saline-alkali conditions

At the field scale, saline-alkali stress not only reduces land quality but also limits the flexibility of agricultural management. It lowers seedling emergence, restricts cultivar selection, and decreases fertilizer use efficiency because plants cannot effectively absorb and assimilate nutrients applied to the soil. In areas with unstable rainfall, poor drainage, or secondary salinization, saline-alkali conditions also increase yield fluctuations between years. Therefore, saline-alkali agriculture is not only a productivity issue, but also a challenge for agricultural sustainability (Negacz et al., 2022).

The ecological costs are also serious. Salinization alters microbial diversity, biogeochemical cycling, and soil structural stability, while alkaline conditions further restrict nutrient cycling processes. In other words, degraded saline-alkali land is not simply soil with “too much salt,” but a land environment whose biological functions have been partially reshaped and are no longer suitable for conventional agricultural production. This is also why crop selection must be considered together with rhizosphere management.

3 Ecophysiological Adaptation Mechanisms of Broomcorn Millet under Saline-Alkali Stress

3.1 Morphological adaptation mechanism

The morphological adaptation of broomcorn millet under saline-alkali stress is not simply “slow growth,” but a structural adjustment aimed at survival and reproductive completion. As a typical drought-tolerant and barren-soil-tolerant minor cereal crop, broomcorn millet has characteristics such as a short growth period, strong root adaptability, and relatively moderate aboveground biomass investment. These features allow it to improve reproductive stability under stress by reducing the cost of vegetative growth in saline-alkali environments.

Root structure is the most crop-specific morphological basis for saline-alkali adaptation in broomcorn millet. An alkali stress evaluation of 296 millet germplasm resources showed that Ma et al. (2021) used mixed alkali concentrations of 80 mmol/L and 40 mmol/L to evaluate alkali tolerance at the germination and seedling stages, respectively. At the seedling stage, plant height, green leaf area, biomass, and root structure were further measured. Green leaf area can serve as a direct indicator of alkali tolerance during the seedling stage, while changes in root structure reflect the ability of the plant to maintain absorption functions under the combined effects of high pH and ion stress. Finally, 12 alkali-tolerant resources and 41 sensitive resources were identified.

The morphological adaptation mechanism of broomcorn millet can be summarized as the coordination of “low-consumption canopy-functional root system-rapid recovery.” Moderate control of leaf area expansion can reduce transpiration and ion transport burden, while maintaining the root absorption interface helps acquire water,

K⁺, and essential mineral nutrients. Compared with major cereal crops such as maize and wheat, the value of broomcorn millet in saline-alkali land is not in forming a large vegetative body, but in achieving stable production on marginal soils through a short growth cycle and strong root plasticity.

3.2 Osmotic adjustment mechanism

Saline-alkali stress first causes a decrease in external water potential, leading to inhibited water uptake, reduced cell turgor pressure, and restricted leaf expansion in broomcorn millet seedlings. To maintain cellular water status, broomcorn millet accumulates compatible solutes such as proline, soluble sugars, and soluble proteins. The role of these substances is not simply to “increase content,” but to improve osmotic adjustment capacity without significantly interfering with enzyme activity, while also stabilizing membrane structure and protein conformation.

An early study on mixed salt tolerance in 16 broomcorn millet genotypes found that under salt concentrations of 160 and 200 mmol/L, the proline content in shoots of materials such as Zhongwei Dahuangmi and Ningmi No.4 increased significantly, while the relative Na⁺/K⁺ ratio remained low. This indicates that osmotic adjustment and ion homeostasis together determine salt tolerance performance (Liu et al., 2012).

Octoploid broomcorn millet showed stronger antioxidant capacity under salt stress, with lower MDA content in leaves and significantly increased soluble sugar and proline content (Li et al., 2025). MDA is an important indicator of membrane lipid peroxidation damage. Its reduction suggests that the accumulation of osmotic adjustment substances is not an isolated response, but part of an integrated salt tolerance system involving membrane protection and antioxidant defense.

The core significance of the osmotic adjustment mechanism in broomcorn millet lies in maintaining cellular water status and metabolic continuity through the accumulation of small organic molecules, thereby avoiding excessive dependence on inorganic ions such as Na⁺ and Cl⁻ for osmotic compensation and reducing the risk of ion toxicity. This is also an important reason why some tolerant materials can still recover growth after rehydration or stress relief, even though growth inhibition occurs during saline-alkali stress.

3.3 Ion homeostasis and transport regulation mechanism

For broomcorn millet, the major damage caused by saline-alkali stress is not only “water deficiency,” but also excessive Na⁺ accumulation and difficulty in maintaining K⁺ levels. After entering cells, Na⁺ interferes with K⁺-dependent enzyme activity, disrupts membrane potential, and affects protein synthesis. Therefore, the key to salt tolerance in broomcorn millet is to limit Na⁺ uptake, promote Na⁺ efflux or vacuolar sequestration, and maintain a high K⁺/Na⁺ ratio. Studies on the molecular mechanisms of plant salt stress generally suggest that ion exclusion, compartmentalization, long-distance transport, and signal transduction together form the core regulatory network of crop salt tolerance (Ma et al., 2022).

A comparative study between broomcorn millet lines ST47 and SS212 provided direct evidence for this mechanism. Yuan et al. (2021) found that under 1% NaCl stress, the salt-tolerant variety ST47 maintained a better Na⁺/K⁺ balance and reduced toxicity by limiting Na⁺ uptake, promoting vacuolar Na⁺ sequestration, and enhancing Na⁺ efflux capacity. KEGG pathway analysis showed that pathways related to Na⁺ regulation, ion transport, and cell wall biosynthesis were significantly regulated in ST47. This indicates that salt tolerance in broomcorn millet is not simply a change in ion content, but a dynamic regulatory process involving transport proteins, signaling pathways, and tissue structure.

The adaptation of broomcorn millet to saline-alkali stress cannot simply be understood as “salt tolerance + alkali tolerance.” Neutral salt stress mainly highlights Na⁺ toxicity and K⁺ retention, while alkali stress additionally involves the effects of high pH on root absorption, cell wall stability, and proton pump activity. As a stress-tolerant minor crop, broomcorn millet has important research value because it can reveal the special strategies used by cereal crops to maintain ion homeostasis under complex saline-alkali conditions.

3.4 Antioxidant defense system

Saline-alkali stress disturbs chloroplasts, mitochondria, and plasma membrane systems in broomcorn millet, leading to increased accumulation of reactive oxygen species (ROS). ROS are not completely harmful because they also participate in stress signal transduction. However, if they are not removed in time, they can cause membrane lipid peroxidation, protein oxidation, and cellular structural damage. Broomcorn millet maintains a dynamic balance between ROS production and scavenging by increasing the activities of antioxidant enzymes such as SOD, POD, CAT, and APX, together with non-enzymatic antioxidant components including proline, soluble sugars, flavonoids, and phenolic compounds.

Research on alkali stress showed that alkali-tolerant broomcorn millet materials possess stronger antioxidant defense capacity. Under alkali stress, the activities of antioxidant enzymes and the contents of osmotic adjustment substances in millet leaves increased simultaneously. Tolerant materials showed lower MDA content and lower electrolyte leakage rates, indicating less oxidative damage to membrane systems (Ma et al., 2021). Antioxidant defense is not simply a passive repair process after saline-alkali stress, but an active adaptation mechanism that helps broomcorn millet maintain leaf function, stomatal structure, and the integrity of photosynthetic tissues.

Studies on exogenous 24-epibrassinolide showed that hormone regulation can alleviate alkali stress injury in broomcorn millet by improving photosynthesis and antioxidant capacity (Ma et al., 2023a) (Figure 1). Exogenous treatment can regulate photosynthesis-related genes, antioxidant-related pathways, and the accumulation of effective metabolites. This suggests that the antioxidant defense system of broomcorn millet is influenced not only by stress intensity, but also by plant hormone signaling regulation.

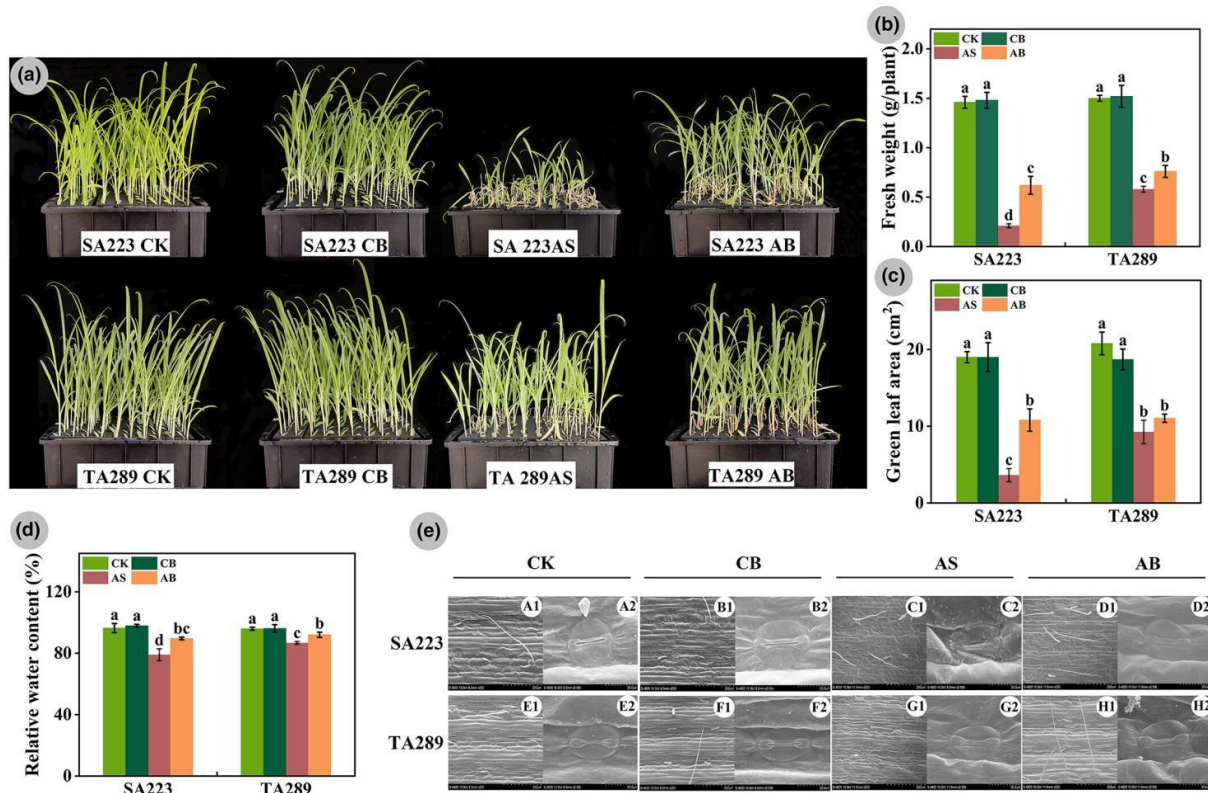


Figure 1 The growth status and leaf characteristics of SA223 and TA289 under different treatments. (a) The phenotypic differences of broomcorn millet plants grown in hydroponic culture for 7 days under different conditions. (b) The fresh weight per plant. (c) Green leaf area per plant. (d) Relative water content. (e) Scanning electron microscope of leaf surface. CK, CE, AS, and AE denote control (nutrient solution only), nutrient solution + 0.5 mg/L 24-Epicastasterone, 40 mM mixed alkali (molar ratio $\text{NaHCO}_3:\text{Na}_2\text{CO}_3 = 9:1$), and 40 mM mixed alkali + 0.5 mg/L 24-Epicastasterone. Data are mean $\pm$ standard error ($n = 5$). Different alphabetical letters show significant variations among the treatments ($p < 0.05$, least significant difference test). The error bars indicate the standard errors of the means (Adopted from Ma et al., 2023a)

4 Reshaping of the Rhizosphere Microbiome under Saline-Alkali Stress

4.1 Composition and ecological functions of the rhizosphere microbiome

The rhizosphere microbiome of broomcorn millet is not just a group of “associated organisms” around the root surface. It is an important ecological unit involved in adaptation to saline-alkali soils. Bacteria, fungi, archaea, and micro-eukaryotes in the rhizosphere jointly participate in organic matter decomposition, nitrogen/phosphorus/sulfur cycling, mineral activation, pathogen suppression, and root signal transmission. These functions become especially important in saline-alkali soils because high salinity, high pH, and ion imbalance reduce the availability of nutrients such as phosphorus, iron, and zinc, while also inhibiting the activity of common microorganisms. Under such conditions, microbial communities that can maintain nutrient transformation and stabilize rhizosphere metabolism largely determine whether broomcorn millet can continuously absorb nutrients and maintain growth on marginal land.

The rhizosphere microbiome is directly linked with salt-stress adaptation. Yuan et al. (2023) used the salt-tolerant variety ST47 and the salt-sensitive variety SS212 under a three-month salt-stress pot experiment. They simultaneously analyzed plant phenotype, physiological traits, microstructure, Na⁺ homeostasis-related genes, and rhizosphere bacterial and fungal communities. The salt-tolerant millet not only showed better Na⁺ balance and more stable tissue structure, but also reshaped the rhizosphere microbial community toward a direction beneficial for salt-stress buffering and soil nutrient cycling.

4.2 Changes in microbial communities under saline-alkali stress

The influence of saline-alkali stress on the rhizosphere microbial community of broomcorn millet is not simply a matter of “suppressing all microorganisms.” Instead, it shows clear selectivity. High-salt conditions eliminate some sensitive microbial groups while enriching functional microorganisms that can tolerate high osmotic pressure, high Na⁺ concentration, and high pH conditions.

More specifically, under high salinity, bacterial groups such as Nocardioideae, Saccharimonadales, and Nitrospiraceae become enriched in the millet rhizosphere. These groups are commonly associated with organic matter decomposition, nutrient transformation, and stress-resistant ecological niches. At the same time, fungi such as *Opereulomyces*, *Alternaria*, and *Cryptococcus* are also enriched in the rhizosphere and may participate in organic matter degradation and nutrient absorption. Under high-salt treatment, the rhizosphere recruits these specific bacteria and fungi, which promotes soil nutrient cycling and is associated with improved nutrient uptake capacity in broomcorn millet (Chen et al., 2025).

The adaptation of broomcorn millet to saline-alkali soils does not rely only on the roots “tolerating” unfavorable conditions. Instead, the plant reorganizes the microbial community through rhizosphere selection mechanisms into a structure more favorable for nutrient supply and stress buffering. In other words, the changes in the rhizosphere microbiome under saline-alkali stress have clear ecological functions: on one hand, they reduce nutrient limitations caused by salinity; on the other hand, they improve the resilience of the rhizosphere system under unstable environmental conditions.

4.3 Beneficial rhizosphere microorganisms in broomcorn millet

4.3.1 Plant Growth-Promoting Rhizobacteria (PGPR)

Plant growth-promoting rhizobacteria are one of the most valuable microbial resources for improving saline-alkali adaptation in broomcorn millet. PGPR can promote plant growth through nitrogen fixation, phosphate solubilization, IAA production, extracellular polysaccharide secretion, siderophore synthesis, and regulation of ACC deaminase activity. Under saline-alkali stress, these functions are converted into more direct stress-resistance effects. Extracellular polysaccharides can form protective biofilms on the root surface and reduce direct Na⁺ damage. ACC deaminase can lower stress-induced ethylene levels and alleviate root growth inhibition. Phosphate solubilization and siderophore production help improve the low availability of phosphorus and iron under high-pH conditions.

Salt stress can induce plants to recruit specific root-associated bacterial communities, but long-term salt tolerance is usually provided not by a single strain, but by bacterial consortia with complementary functions (Li et al., 2021). For broomcorn millet, this means future studies should not only search for a single “universal salt-tolerant bacterium.” Instead, synthetic microbial communities should be constructed around highly enriched rhizosphere bacteria of millet. For example, strains with different abilities such as phosphate solubilization, IAA production, antioxidant induction, and extracellular polysaccharide formation can be combined to form compound microbial agents suitable for millet production in saline-alkali soils.

4.3.2 Arbuscular Mycorrhizal Fungi (AMF)

Arbuscular mycorrhizal fungi have special importance in crop adaptation to saline-alkali soils. AMF can expand the root absorption area through fungal hyphae, improve phosphorus uptake efficiency, enhance water utilization, and influence Na^+/K^+ balance and antioxidant enzyme activity. This mechanism is especially important for broomcorn millet because saline-alkali soils are often characterized by low phosphorus availability, poor soil structure, and restricted root absorption. These limitations are difficult to overcome through root function alone.

Liu et al. (2024) analyzed the rhizosphere microbial community structure and metabolic characteristics under broomcorn millet/mung bean intercropping and further examined the relationship between microbial communities and nutrient limitation. Intercropping altered the rhizosphere microbial structures of both crops and affected nutrient utilization status. This indicates that the rhizosphere of broomcorn millet is not fixed, but can be reshaped by planting systems and rhizosphere interactions. Under saline-alkali conditions, coordinated regulation of the rhizosphere using AMF together with nitrogen-fixing microorganisms and phosphate-solubilizing bacteria may become an effective way to improve nutrient uptake and yield stability in broomcorn millet.

In saline-alkali cultivation systems, AMF should not simply be regarded as external additives. Instead, they should be incorporated into a broader “rhizosphere ecological management” framework. Future studies could focus on AMF colonization rates, hyphal density, changes in soil available phosphorus, Na^+/K^+ ratios, and yield performance among different millet varieties in order to identify which genotypes are more suitable for stable symbiosis with AMF.

4.3.3 Endophytic and salt-tolerant microorganisms

Endophytic and salt-tolerant microorganisms are another important potential resource for saline-alkali adaptation in broomcorn millet. Compared with ordinary rhizosphere microorganisms, endophytes can enter internal plant tissues such as roots, stems, and leaves, forming relatively stable colonization relationships within the host. Therefore, they are more likely to provide long-term effects under continuous salt stress. Salt-tolerant endophytes can help plants resist saline-alkali damage by regulating plant hormones, improving antioxidant capacity, promoting osmotic adjustment substance accumulation, enhancing membrane stability, and stimulating root growth.

Salt-tolerant bacteria isolated from saline environments have shown the ability to produce plant growth-promoting substances. Radhakrishnan and Krishnasamy (2024) screened four salt-tolerant bacterial strains and suggested that these microorganisms could be used to promote plant growth and improve soil conditions. Since broomcorn millet is often cultivated on dry, barren, and saline marginal lands, its rhizosphere and endophytic environments are likely to contain microbial resources already adapted to combined stresses.

The saline-alkali tolerance of broomcorn millet should therefore be evaluated not only from the perspective of “plant material,” but also from the perspective of “associated microbial material.” Salt-tolerant millet varieties may possess not only stronger ion homeostasis and antioxidant capacity, but also a greater ability to recruit or maintain salt-tolerant endophytes and rhizosphere microorganisms. In the future, functional strains could be isolated from the rhizosphere and tissues of salt-tolerant materials such as ST47 and tested for their growth-promoting effects on sensitive varieties. This would support the establishment of a “salt-tolerant variety + functional microbial agent” production model for saline-alkali soils.

4.4 Root exudates and microbial recruitment

Root exudates are the key medium through which broomcorn millet regulates the rhizosphere microbiome. Sugars, amino acids, organic acids, phenolic acids, flavonoids, lipids, and purine compounds not only provide carbon and nitrogen sources for microorganisms, but also play roles in chemotaxis, signal recognition, and selective screening. Under saline-alkali stress, the composition of root exudates usually changes, thereby influencing which microorganisms can migrate to the rhizosphere, colonize roots, and form stable communities. Root exudates can drive microbial recruitment and community assembly and promote plant health and stress resistance by influencing microbial chemotaxis, community diversity, and functional complementarity (Yang et al., 2025).

The reshaping of the rhizosphere microbiome in broomcorn millet is probably not a passive outcome, but an actively driven process induced by stress-related metabolic changes in roots. Under saline-alkali stress, millet roots may release organic acids to regulate rhizosphere microdomain pH, provide sugars and amino acids as substrates for salt-tolerant growth-promoting bacteria, and use phenolic or flavonoid compounds as selective signaling molecules. The final microbial recruitment pattern is determined not by a single exudate, but by the overall “metabolite combination” formed by roots under saline-alkali conditions. Future research on broomcorn millet should combine rhizosphere metabolomics with 16S/ITS sequencing to clarify which exudates are associated with enriched groups such as Nocardioideae, Nitriliruptoraceae, and Cryptococcus.

4.5 Plant-microbe synergistic mechanisms under saline-alkali stress

The plant-microbe synergistic mechanisms of broomcorn millet under saline-alkali stress are mainly reflected in four aspects. First, microorganisms alleviate nutrient limitations in saline-alkali soils by improving nutrient availability, such as promoting organic matter decomposition, phosphorus activation, and nitrogen cycling. Second, microorganisms reduce direct Na⁺ damage to roots through extracellular polysaccharides, biofilms, and ion adsorption. Third, PGPR and endophytes can regulate root elongation, lateral root formation, and stomatal behavior through IAA, ACC deaminase, and ABA-related pathways. Fourth, microorganisms can induce antioxidant enzyme systems and osmotic adjustment processes in the host, helping plants maintain higher cellular stability under ROS accumulation and membrane lipid peroxidation stress.

Salt-tolerant broomcorn millet under salt stress does not rely only on its own gene expression regulation. It also shows simultaneous reshaping of rhizosphere bacterial and fungal communities. Under saline-alkali conditions, nutrient accumulation in broomcorn millet is closely related to changes in rhizosphere microorganisms. Specific bacteria and fungi enriched under high-salt treatment are associated with soil nutrient cycling, nutrient absorption, and organic matter decomposition.

Cultivation of broomcorn millet on saline-alkali land should therefore not rely only on evaluating varietal salt tolerance, but should also pay attention to the recovery of soil microbial functions. In the future, salt-tolerant variety screening, rhizosphere functional microorganism isolation, AMF inoculation, organic fertilizer improvement, and intercropping systems can be integrated into a comprehensive rhizosphere regulation strategy. Only in this way can the stress-resistance potential of broomcorn millet be effectively translated into stable yields on saline-alkali soils.

5 Metabolic Reprogramming Induced by Saline-Alkali Stress and Agricultural Applications

5.1 Protein accumulation and nitrogen metabolism

The study of protein accumulation in broomcorn millet grains under saline-alkali stress should not simply follow the generalized conclusion that “stress increases protein content.” Instead, it should be understood within the combined framework of nitrogen redistribution, amino acid synthesis, and restricted grain filling. Saline-alkali conditions simultaneously affect root nitrogen uptake, nitrogen assimilation, amino acid transport, and grain protein deposition. Different proportions of neutral salts and alkaline salts produce different effects on millet germination and seedling growth, and they can distinguish the relative contributions of osmotic stress, ion toxicity, and high-pH damage. This indicates that the metabolic changes of broomcorn millet under saline-alkali stress are not caused by a single salt effect, but by the combined influence of multiple stresses altering growth and material allocation.

From the perspective of nitrogen metabolism, the accumulation of proline, soluble proteins, and related amino acids in millet under stress is not simply an increase in “protective substances.” It also reflects the shift of nitrogen allocation from structural growth to osmotic adjustment and stress defense. Ravichandran et al. (2025), through comparative transcriptomic and metabolic pathway analyses of foxtail millet and broomcorn millet under salt stress, showed that both millet crops activate complex metabolic interactions, enzyme activity changes, and transcription factor regulation under stress conditions. Amino acid metabolism, antioxidant defense, and energy metabolism jointly participate in stress responses. Therefore, nitrogen metabolic reprogramming in broomcorn millet should be regarded as a “growth-defense trade-off”: part of the nitrogen is used to synthesize proline, soluble proteins, and stress-related enzymes, rather than being fully deposited into grain storage proteins.

As a result, grain protein changes in saline-alkali environments may occur in two directions. First, yield reduction may lead to a relative concentration of protein in the grains. Second, severe stress may suppress grain filling and nitrogen transport, thereby limiting protein deposition. In agricultural applications, evaluation under saline-alkali conditions should not focus only on yield. Grain crude protein, free amino acids, proline, glutamine synthetase activity, and nitrogen harvest index should also be measured simultaneously. Only by combining “yield stability” with “nitrogen metabolic quality” can truly suitable broomcorn millet materials for saline-alkali land utilization be identified.

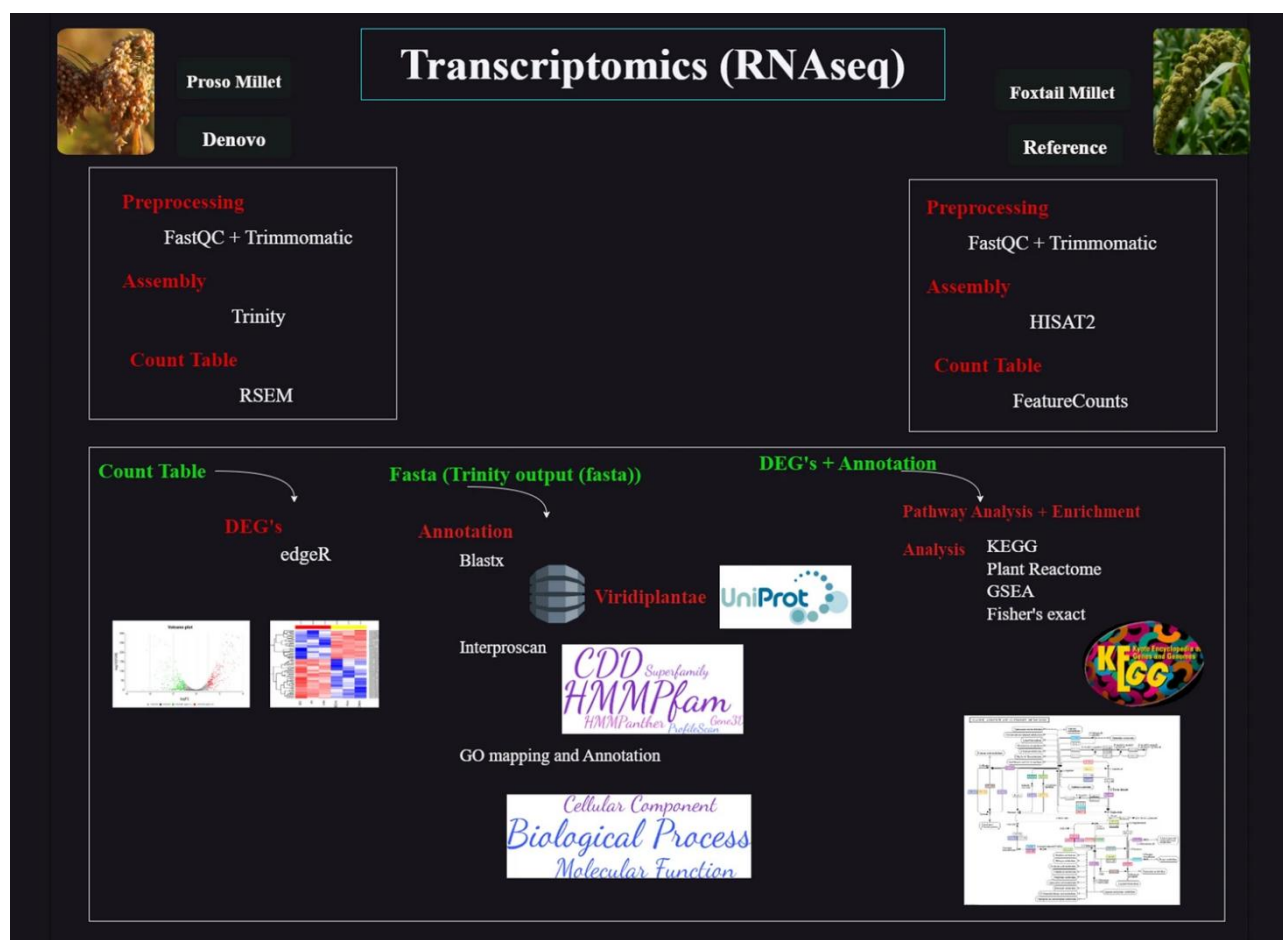


Figure 2 A detailed workflow of data collection, processing, analysis, and visualization used in this study for identifying and evaluating important transcription factors and pathways in foxtail and proso millets under salt stress (Adopted from Ravichandran et al., 2025)

5.2 Accumulation of bioactive compounds

Alkaline stress not only changes yield-related traits, but also affects the metabolite composition in broomcorn millet grains. Using two millet varieties, S223 and T289, Ma et al. (2023b) analyzed the effects of alkaline stress on non-volatile and volatile metabolites in mature grains. A total of 933 non-volatile metabolites and 313 volatile

metabolites were identified. Alkaline stress caused differential accumulation of 114 and 89 non-volatile metabolites in the alkali-sensitive and alkali-tolerant varieties, respectively, while 16 and 20 volatile metabolites also showed significant changes.

More importantly, alkaline stress altered pathways related to phenylpropanoid biosynthesis, flavonoids, flavone and flavonol biosynthesis, valine/leucine/isoleucine biosynthesis, arginine and proline metabolism, tryptophan metabolism, and ascorbate metabolism. This means that metabolic reprogramming in millet grains involves both primary and secondary metabolism. Branched-chain amino acids, arginine, and proline reflect changes in nitrogen metabolism and osmotic regulation, while phenylpropanoid and flavonoid pathways are closely associated with antioxidant activity and the accumulation of functional compounds.

From an agricultural perspective, these findings have dual significance. On one hand, alkaline stress may reduce yield or alter grain filling processes. On the other hand, moderate stress may increase the content of certain phenolic acids, flavonoids, amino acid derivatives, and organic acids, making broomcorn millet a promising raw material for functional foods produced on saline-alkali land. Therefore, broomcorn millet production in saline-alkali areas should not only pursue “stress resistance and yield maintenance,” but also explore the combined goal of “stable yield plus improved functional quality.” For example, in mildly to moderately saline-alkali soils, varieties that can maintain yield while accumulating higher levels of phenolic acids and flavonoids could provide valuable raw materials for functional millet rice, millet flour, and fermented foods.

5.3 Antioxidant and functional metabolites

The accumulation of antioxidant metabolites in broomcorn millet is an important link connecting stress resistance with its development as a functional food ingredient. Under stress conditions, metabolites such as phenolic acids, flavonoids, amino acids and their derivatives, and organic acids increase in millet grains, and the metabolic changes are more obvious in alkali-sensitive materials. This suggests that alkaline stress induces a more active antioxidant metabolic network in millet grains, although the response intensity and direction differ among varieties.

Xiang et al. (2023) investigated changes in phenolic composition and antioxidant activity during the germination of three millet varieties. The study found that total phenolic content and total flavonoid content increased significantly as germination progressed. After six days of germination, free total phenolic content increased by 6.30–8.66 times, while bound total phenolic content increased by 77.65%–116.18%. At the same time, compounds such as feruloyl quinic acid and N, N'-bis-(p-coumaroyl)-putrescine were reported for the first time during millet germination.

The functional metabolites of broomcorn millet show strong plasticity. Saline-alkali stress in the field can reshape grain metabolism, while postharvest processes such as germination and fermentation can further release or generate antioxidant active compounds. In agricultural applications, a complete chain of “saline-alkali cultivation-variety selection-germination processing-functional food development” can be established. For example, germination treatment of millet harvested from saline-alkali soils may further increase phenolic acid and flavonoid contents, supporting the development of antioxidant cereal powders, germinated millet beverages, and low-GI composite foods.

5.4 Nutritional and health value of broomcorn millet

The nutritional value of broomcorn millet should not only be understood from the traditional perspective of “coarse grains.” It should also be analyzed within the dual framework of climate-resilient food crops and functional food ingredients. Broomcorn millet is rich in protein and dietary fiber, and some nutritional indicators are superior to those of common cereals. Its gluten-free characteristics and relatively low glycemic index make it suitable for people with gluten intolerance, type 2 diabetes, and cardiovascular metabolic risks (Pavithra and Rawat, 2024).

Broomcorn millet is not only a traditional grain for cooking, but also has potential applications in the modern food industry. Research on millet nutritional biscuits evaluated biscuit quality from the perspectives of protein networks, tribology, and in vitro digestion. Biscuits made from different millet raw materials showed differences in protein network connectivity and porosity. In some samples, the protein network area reached 45.12%, while the lowest porosity was 10.33%, indicating that varietal differences directly affect the structure and digestive properties of baked products (Hu et al., 2025).

Research on cakes fortified with fermented millet bran dietary fiber also demonstrates practical value. After adding fermented millet dietary fiber, the total phenolic content of the product reached 0.46 mg GAE/g, the DPPH radical scavenging rate reached 66.84%, and the ABTS⁺ scavenging rate reached 87.01%, while predicted glucose release was reduced (Xiao et al., 2023). Millet and its by-products can therefore serve not only as basic raw materials for gluten-free foods, but also as ingredients with enhanced antioxidant and low-glycemic potential through fermentation and dietary fiber enrichment.

Metabolic reprogramming induced by saline-alkali stress has clear agricultural application directions. First, saline-alkali tolerant millet can be used to develop specialty grain crops for saline-alkali land. Second, high phenolic acid, high flavonoid, and high protein resources can be screened to establish functional quality breeding indicators. Third, processing technologies such as germination, fermentation, baking, and extrusion can be combined to improve the added value of millet products. In this way, broomcorn millet is no longer just a “survival crop” grown on saline-alkali land, but can become a characteristic crop connecting saline-alkali land management, nutritional health, and the functional food industry.

6 Agricultural and Ecological Applications of Proso Millet

6.1 Improvement of saline-alkali soils

The value of proso millet in saline-alkali soils is not only reflected in its own tolerance to saline environments, but also in its ability to improve the soil ecological environment. Salt-tolerant cultivation helps promote root-mediated soil stabilization, organic matter input, and rhizosphere microecological activation. In broomcorn millet, salt stress induces the enrichment of specific beneficial microorganisms and changes the structure of microbial communities related to nutrient cycling, indicating that this crop can promote the biological functions of saline-alkali soils toward a more productive state (Yuan et al., 2023).

This does not mean that proso millet alone can “restore” all saline-alkali soils. Instead, it shows that the crop is suitable as a biological synergistic factor within integrated land improvement strategies. These strategies usually also include drainage systems, water management, organic amendments, and microbial inoculants. Compared with highly salt-sensitive crops, proso millet can maintain root activity for a longer time, thereby creating favorable conditions for rhizosphere-driven soil improvement.

6.2 Sustainable crop production on marginal lands

The key to agricultural production on marginal lands is not achieving the highest yield in a single season, but maintaining stable returns under conditions of low water, low fertilizer input, climate fluctuations, and poor soil quality. Proso millet fits well within this production logic. It can generally grow under marginal soil and low-input conditions, with a growth period of about 65-75 days or 70-90 days. It requires relatively low amounts of water and fertilizer and shows strong adaptability to drought, poor soils, and climate variability (Nandini et al., 2025).

A long-term crop rotation experiment conducted in northeastern Colorado, USA, from 1995 to 2016 analyzed the relationship between water use and yield in proso millet. Nielsen and Vigil (2017) used multi-year dryland farming data to establish a water-limited yield model and identified environmental factors causing deviations between actual millet yield and theoretical water-based yield. Proso millet should not be regarded as a “low-yield substitute crop,” but rather as a short-season crop suitable for dryland rotation systems, improving water use efficiency and reducing production risks.

A more practical example comes from Karnataka, India. In 2025, it was reported that nearly 3 000 farmers in the drought-prone regions of Dharwad and Haveri introduced millet crops into degraded lands after long-term drought with support from the CROPS4HD project. The cultivation area expanded from about 50 acres to more than 2 000 acres across 23 villages, and a farmer producer company with around 5 000 members was established. The project promoted several millet crops, including proso millet, and reduced farmers' risks through seed supply, technical training, and market access support.

Agriculture on marginal lands is not only about crop stress resistance, but also about seed supply, technical services, farmer organizations, and market outlets. If proso millet is to be widely promoted in saline, drought-prone, and low-fertility areas, it should be integrated with crop rotation systems, cooperative organizations, contract purchasing, and functional food development, rather than being planted only as a scattered minor grain crop.

6.3 Proso millet as a functional feed resource

Proso millet also has strong agricultural potential as a feed resource. Unlike crops used only for grain production, proso millet can be used as silage or harvested forage and is suitable for dry regions, short growing seasons, and low-input crop-livestock farming systems. Research on forage production, feeding value, and silage suitability compared proso millet with whole-crop maize and Sudan grass hybrids (Wei et al., 2022). Although the fresh forage yield of proso millet was lower than that of maize and Sudan grass hybrids, its relative feed value was higher than that of Sudan grass hybrids. In addition, proso millet has a short growth cycle and rapid growth rate, making it an alternative forage resource in low-input regions.

The study also dynamically monitored the silage fermentation process by measuring fermentation quality on days 1, 2, 3, 5, 10, 15, 20, 30, and 45 after ensiling. During the fermentation process, lactic acid and acetic acid contents increased, while pH rapidly declined in the early stage and then became stable. However, the dry matter loss of proso millet was relatively high, indicating that harvesting time, moisture content, and silage additives still need optimization when using proso millet as a silage crop.

Therefore, the feed application of proso millet should not only emphasize that it “can be used as feed,” but should further distinguish four utilization pathways: grain feed, fresh forage, hay, and silage. In saline and drought-prone areas, proso millet can be rotated or intercropped with legume forages or feed legumes to improve protein supply and soil nitrogen cycling. In integrated crop-livestock farming systems, millet grain, straw, and processing by-products can be utilized together to form a “grain-feed-livestock-fertilizer” recycling model. This dual-purpose utilization capacity can provide farmers with greater flexibility when facing grain price fluctuations, feed costs, and climate risks.

6.4 Contribution to food security and sustainable development

The contribution of proso millet to food security is mainly reflected in three aspects. First, it expands the boundaries of food production on marginal lands. Second, it increases cereal diversity and dietary diversity. Third, it provides a crop foundation for low-input, low-water-consumption, and climate-adaptive agriculture. Millet crops possess strong climate resilience, high nutritional value, and significant rural economic potential, and they are expected to play a greater role in global food security and sustainable food systems in the future (Sharma et al., 2025).

After the “International Year of Millets” in 2023, millet crops were further incorporated into discussions on nutritional security, climate adaptation, and sustainable agriculture. Millets can help reduce dependence on high-input agricultural systems and are closely related to the United Nations Sustainable Development Goals, including zero hunger, climate action, and poverty reduction. In addition, the industrialization of millet cultivation and processing may create income opportunities for rural communities (Mohan et al., 2025).

For proso millet, this value is especially important. It is neither simply a famine-relief crop nor just a traditional minor grain for local diets. Instead, it is a multifunctional crop that can connect saline-alkali land utilization,

dryland farming, functional foods, feed resources, and farmer income growth. In the future, if coordinated development can be achieved among breeding salt-tolerant varieties, saline-land cultivation systems, forage utilization, functional food development, and regional brand building, proso millet may become not only an alternative crop for marginal lands, but also a strategic minor cereal for improving agricultural system resilience under climate change.

7 Current Challenges, Future Perspectives, and Conclusions

7.1 Limitations in understanding rhizosphere microbial networks

In recent years, research on salt-alkali stress in proso millet (*Panicum miliaceum* L.) has gradually expanded from simple physiological measurements to studies of the rhizosphere microbiome. However, this field is still transitioning from descriptive studies to mechanism-based research. Salt-tolerant millet materials can alter rhizosphere bacterial and fungal communities under salt stress and enrich microbial groups related to nutrient cycling, salt buffering, and organic matter transformation. Nevertheless, there is still limited understanding of how these microorganisms form stable networks, how they influence the host through metabolic interactions, and whether different microbial functions can replace one another.

One major difficulty in rhizosphere microbial network research is that community behavior is not equal to the behavior of a single strain. Salt stress can induce plants to recruit specific rhizosphere bacteria, but long-term salt tolerance is usually supported by bacterial communities with complementary functions rather than by one “universal strain” (Li et al., 2021). Even if some bacterial genera are enriched in the rhizosphere of salt-tolerant millet, it cannot be directly concluded that inoculation with a single strain will stably improve salt tolerance. The actual effect may come from a functional rhizosphere network jointly formed by bacteria, fungi, and their metabolites.

In addition, field saline-alkali environments are highly complex. Salinity level, Na^+/Cl^- ratio, carbonate and bicarbonate content, soil pH, texture, organic matter level, irrigation system, and previous crops can all influence rhizosphere microbial assembly. Therefore, microbial communities that perform well in one saline soil may fail to colonize effectively in another soil type, or may not show growth-promoting effects at all. For millet, future research should not only answer “which microorganisms are enriched,” but also clarify “under which soil conditions,” “recruited by which millet genotype,” “through which metabolic pathways,” and “whether the effect can remain stable across continuous growing seasons in the field.” These are the key issues that must be solved before rhizosphere microbiome research can move from basic science to agricultural application.

7.2 Multi-omics approaches in rhizosphere research

An important future direction for millet salt-alkali adaptation research is the establishment of an integrated multi-omics framework linking “host genotype–root exudates–rhizosphere microorganisms–ion homeostasis–yield and quality.” Previous studies usually measured physiological traits, transcriptomes, metabolites, or microbial communities separately. Although such studies can reveal changes at a specific level, they often fail to explain the causal relationships among different biological layers. For example, a salt-tolerant material showing a high K^+/Na^+ ratio may be related to transporter gene expression, regulation of microbial communities by root exudates, or interactions among root architecture and soil nutrient status. Without integrated analysis, it is difficult to identify the real limiting factor.

The improvement of millet genomic resources has provided the basis for this type of research. Zou et al. (2019) completed a high-quality chromosome-level genome assembly of millet, identifying 55,930 protein-coding genes and 339 miRNAs. They suggested that this genomic resource could support studies on stress resistance, C4 photosynthesis, and breeding improvement. This means that traits such as salt tolerance, alkali tolerance, root development, and rhizosphere recruitment ability can now be connected with genomic variation, promoting millet breeding from traditional experience-based selection to genome-assisted and microbiome-assisted breeding.

Methodologically, an ideal experimental design should simultaneously conduct phenotypic analysis, ionomics, root exudate metabolomics, rhizosphere metagenomics, metatranscriptomics, and host transcriptomics using the

same salt-tolerant and salt-sensitive millet materials. Research on wild soybean under salt stress has already provided a useful example. Researchers found that salt stress induced roots to secrete xanthine, which then recruited beneficial *Pseudomonas* species and improved host salt tolerance. Such studies indicate that only by placing “root exudates-microorganisms-host tolerance” within the same experimental system can the active recruitment mechanism of plants truly be explained. For millet, future work should further identify which organic acids, phenolic acids, amino acids, or sugars are associated with the enrichment of salt-tolerant rhizosphere microbial communities, and verify whether these metabolites can consistently induce beneficial microbial colonization.

7.3 Microbiome-assisted breeding strategies

Microbiome-assisted breeding should not be considered an additional technique outside traditional salt-tolerance breeding. Instead, it should become an important part of improving millet adaptation to saline-alkali soils. The basic concept is that host genotype not only determines root structure, ion transport, and antioxidant capacity, but also affects root exudate composition and rhizosphere microbial assembly. Therefore, two millet materials with similar phenotypes may show completely different field stability under continuous saline-alkali cultivation because of differences in their ability to recruit beneficial microorganisms.

In recent years, plant microbiome breeding studies have proposed that plant genetic backgrounds should be matched with compatible microbial inoculants, rather than treating microbial products as universal inputs independent of crop genotype. Future breeding should simultaneously consider plant genetics, microbial functions, and environmental adaptability, and enhance stress resistance through matching host genotypes with microbial inoculants (Shi et al., 2026). This idea is especially suitable for millet because it is often cultivated on marginal lands affected by drought, nutrient deficiency, and salinity, where environmental heterogeneity is high and simple selection for high-yield materials cannot guarantee stable field performance.

Breeding indicators with greater practical value for millet should expand from yield alone to comprehensive adaptability traits, including stable K^+/Na^+ selectivity, root recovery ability, biomass regeneration after salt stress, root exudate plasticity, enrichment capacity of beneficial rhizosphere microbes, and stability of microbial community networks. The rhizosphere microbiome is regulated by both environment and host genotype. Using the plant's natural ability to recruit beneficial microorganisms is becoming an important direction for precision microbial engineering and stress-resistant agriculture in the future (Shen et al., 2024). Therefore, salt-alkali breeding in millet should not only select materials that are “salt tolerant themselves,” but also materials that can “stably establish beneficial rhizosphere systems.”

7.4 Synthetic microbial communities and biofertilizers

In future millet production on saline-alkali land, microbial intervention technologies will likely shift from single-strain inoculation to synthetic microbial communities (SynComs). Although single strains are easier to screen and produce, they often face weak colonization ability, competition from native microorganisms, and unstable performance in the field. In contrast, synthetic communities can be designed according to functional complementarity, allowing different members to perform functions such as phosphate solubilization, nitrogen fixation, IAA production, extracellular polysaccharide secretion, antioxidant induction, and ion homeostasis regulation. In this way, they can provide more stable growth-promoting and stress-resistant effects.

SynComs are not only modular tools for studying plant-microbe interactions, but can also be used to promote plant growth and improve stress adaptation. Their construction strategies include bottom-up screening of functional strains and top-down simplification and reconstruction of native microbial communities (Xu et al., 2025). This provides a clear path for millet cultivation on saline-alkali land: first isolate locally adapted strains from the rhizosphere of millet grown long-term in saline soils, then construct functional microbial consortia based on complementary traits, and finally test their compatibility with different millet genotypes.

However, commercialization of synthetic microbial communities still faces major challenges. Plant microbiome research requires more unified standards for community construction, causal verification, data reporting, and field

evaluation. Otherwise, results from different studies are difficult to compare, and application outcomes are difficult to reproduce consistently (Northen et al., 2024). For millet, future biofertilizer development should avoid the concept of “universal microbial products.” Instead, it should emphasize regionalized and genotype-specific formulations. In other words, localized microbial consortia should be developed according to different saline-alkali soil types, soil textures, and millet cultivars, and their effects on yield, quality, and soil improvement should be validated through long-term and multi-location field trials.

7.5 Future role of millet in climate-resilient agriculture

The value of millet in climate-resilient agriculture comes from its multiple adaptive traits. It has a short growth cycle, high water-use efficiency, and strong adaptability to marginal lands. At the same time, it also has nutritional value, gluten-free characteristics, and potential for functional food development. Unlike major crops that depend on high inputs for high yields, millet is more suitable for low-input, low-water-consumption, risk-resistant, and diversified agricultural systems. Its role is not to replace rice, wheat, or maize, but to provide more flexible options for future food systems.

From the perspective of global agricultural trends, climate change, soil degradation, and water shortages are driving agricultural systems away from a single high-yield target toward a balance among stable production, nutritional security, and ecological sustainability. As an ancient and stress-tolerant minor cereal crop, millet deserves renewed attention in this context. Its short growth period makes it suitable for filling crop rotation gaps; its drought and poor-soil tolerance make it suitable for marginal lands; its nutritional quality supports functional food development; and the plasticity of its rhizosphere microbiome gives it potential as an important crop platform for biologically regulated agriculture.

In conclusion, the salt-alkali adaptation mechanism of millet should no longer be understood as simple physiological tolerance. Instead, it should be viewed as the combined result of plant genotype, root structure, ion homeostasis, metabolic regulation, and rhizosphere microbiome interactions. Future research should advance in three directions. First, multi-omics technologies should be used to reveal the causal mechanisms of salt-alkali tolerance in millet. Second, microbiome recruitment ability should be incorporated into breeding evaluation systems. Third, localized synthetic microbial communities and ecological cultivation technologies suitable for millet production on saline-alkali soils should be developed. Only in this way can millet evolve from a traditional minor grain crop into a strategic crop resource serving saline-alkali land utilization, food security, healthy food production, and climate-resilient agriculture.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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