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NOVEL APPROACHES FOR ENHANCING SEED QUALITY AND SEED YIELD IN MILLETS

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ABSTRACT
Millets are climate resilient cereals that play a vital role in food and nutritional security in arid and semi-arid regions. However, their productivity and seed quality remain constrained by limited technological interventions. This review highlights recent advances in enhancing seed quality and yield through intergrated approaches. Optimal harvesting at physiological maturity (35-42 days after anthesis) ensures maximum seed vigor and viability. Seed priming techniques including hydropriming, osmopriming, biopriming and nano-priming, significantly improve germination, seedling vigor and stress tolerance. Micronutrient management particularly boron and zinc application, enhances reproductive development, seed filling and nutritional quality. Advances in molecular breeding such as marker-assisted selection, genomic selection and CRISPR/Cas9 genome editing, enable rapid development of improved millet varieties. Integrated nutrient management and plant growth promoting rhizobacteria further enhance productivity and sustainability. Collectively, these innovations provide a comprehensive strategy for improving millet seed systems under climate change conditions.

KEYWORDS: Seed quality; Seed priming; Nanopriming; Micronutrient management; Genomic selection; Abiotic stress tolerance; Climate-smart agriculture

1. INTRODUCTION

Millets represent a diverse group of small-seeded cereals including foxtail millet (*Setaria italica*), pearl millet (*Pennisetum glaucum*), proso millet (*Panicum miliaceum*), finger millet (*Eleusine coracana*), browntop millet (*Brachiaria ramosa* L.) and numerous other species that serve as crucial staple crops for over one billion people across Africa, Asia and other regions (Ceasar & Maharajan, 2022). Despite their critical importance to food security and livelihoods in arid and semi-arid regions, millets have received considerably less research attention compared to rice, wheat and maize, resulting in suboptimal productivity levels and limited adoption of modern production technologies (Harish *et al*., 2024). The agronomic significance of millets extends beyond direct human consumption to encompassing diverse end-uses including animal feed production, biofuel development and industrial applications, positioning these crops as strategically important for sustainable intensification of agricultural systems in climate-vulnerable regions (Kumar *et al*., 2022).

The intensifying impacts of climate change, characterized by increasingly frequent and severe droughts, elevated temperatures, erratic precipitation patterns and soil salinization, present unprecedented challenges to global crop production and food security (Abebaw, 2025). Abiotic stresses are currently responsible for significant losses in quantity and reduction in quality of global crop productions, with drought representing the most dramatic and widespread constraint affecting agricultural productivity across diverse environments (Oyebamiji *et al*., 2024). Within this context, millets demonstrate exceptional resilience to environmental extremes, with foxtail and pearl millet cultivars exhibiting remarkable tolerance to prolonged drought, heat stress and poor soil conditions through multiple physiological, biochemical and molecular adaptation mechanisms (Begna *et al*., 2021). This inherent stress resilience positions millets as strategically important crops for climate-smart agriculture and the development of climate-resilient food systems capable of sustaining agricultural productivity and human nutrition amid rapidly changing environmental conditions (P. *et al*., 2023).

High-quality seeds form the biological foundation of crop production systems, with seed vigor, germination potential, genetic purity and health status fundamentally determining field establishment, crop development and ultimate productivity (Reed *et al*., 2022). Seed quality encompasses multiple attributes including physiological maturity, viability and vigor, genetic identity, and freedom from seed-borne pathogens, collectively influencing the uniformity and reliability of crop establishment under diverse environmental conditions (Kannababu *et al*., 2024). The determination of optimal harvest timing based on physiological maturity represents a critical control point for seed production, as premature or delayed harvesting substantially compromises subsequent seed quality, vigor and longevity characteristics essential for commercial seed certification and farmer adoption (R. *et al*., 2021). In millets, where seed production often occurs in resource-limited contexts with limited access to certification infrastructure, the development of practical, evidence-based protocols for seed quality assessment and enhancement becomes particularly critical for scaling improved varieties to farming communities (Nadarajan *et al*., 2023).

Seed yield enhancement, simultaneously with quality improvement, represents a dual imperative for sustainable intensification of millet production systems (Mukherjee *et al*., 2025). Seed yield depends on complex interactions of genetic potential, environmental conditions, crop management practices and plant health status, with optimization requiring integrated approaches that address multiple limiting factors concurrently (Ramalingam *et al*., 2024). The development of high-yielding seed production technologies that simultaneously maintain superior quality parameters requires deep understanding of physiological processes governing seed development, the genetics underlying yield components and the environmental and management factors influencing their expression (Zhang *et al*., 2023). The critical challenge facing the global millet research community involves developing and deploying practical, accessible technologies that smallholder farmers and seed producers can implement to achieve simultaneous improvements in seed yield and quality without requiring substantial infrastructure investments or technical expertise beyond their current capacity (Keerthanan *et al*., 2025).

Contemporary approaches to millet seed quality and yield enhancement increasingly recognize that single-intervention technologies offer limited transformative potential in complex production systems characterized by multiple interacting constraints (Kumar *et al*., 2024). Instead, integrated solutions frameworks that combine advances across multiple disciplines—including seed science, plant breeding, genetics, biotechnology, agronomy, soil science and crop protection—offer realistic pathways for achieving substantial, sustainable improvements in millet productivity and quality (Louhar *et al*., 2021). Novel seed priming technologies utilizing nanoparticles, beneficial microorganisms and bioactive compounds provide cost-effective methods for improving germination, vigor and stress tolerance simultaneously, while microbial inoculants and optimized nutrient management enhance plant nutrition, stress resilience and resource use efficiency (Janah *et al*., 2025). Advances in genomic technologies including genome-wide association studies (GWAS), high-throughput phenotyping and genome editing via CRISPR/Cas9 enable rapid identification of genetic variation controlling yield and quality traits, facilitating accelerated development of improved varieties through precision breeding approaches (Chandra *et al*., 2024).

This comprehensive literature review synthesizes current knowledge and recent advances in novel approaches for enhancing seed quality and yield in millets, providing a contemporary reference for researchers, breeders, seed producers, agricultural extension professionals and policymakers engaged in millet improvement and production intensification (Suman & Chandra, 2024). The review encompasses six interconnected thematic areas: (1) physiological and quality assessment protocols defining seed maturity and quality parameters; (2) advanced seed priming technologies incorporating nanomaterials and bioactive compounds; (3) genetic diversity and germplasm resources available for targeted breeding; (4) breeding methods and trait introgression strategies enabling rapid variety development; (5) integrated nutrient management and seed production protocols optimizing yield and quality; and (6) abiotic stress tolerance mechanisms and climate-smart agricultural practices ensuring resilience under environmental variability (Choudhary *et al*., 2023). The synthesis demonstrates that combining multiple innovative approaches from precision phenotyping and genomic selection to nano-enabled technologies and integrated crop management creates synergistic effects that enable substantial improvements in millet productivity, quality and resilience (Shivhare & Lata, 2017). By consolidating current evidence while identifying research gaps and future priorities, this review aims to catalyse research investments and technology adoption pathways that accelerate millet productivity improvements and contribute meaningfully to enhanced food and nutritional security in millet-dependent regions worldwide (Gebreyohannes *et al*., 2024).

2. Seed Quality Assessment and Physiological Maturity in Millets

2.1 Determination of Physiological Maturity Stages

Identifying the optimal harvest stage is fundamental to achieving superior seed quality in millets. Research on foxtail millet cultivars has demonstrated that physiological maturity is reached between 35 and 42 days after anthesis (DAA), with seeds exhibiting maximum quality at 35 DAA during favorable growing seasons and 38 DAA during seasons with varying climatic parameters (Kannababu *et al*., 2025). At physiological maturity, distinctive visual indicators become apparent: panicles turn brown, seeds become hard and shiny, pale-yellow coloration develops and a dark-brown depression appears at the hilar end (Lainufar *et al*., 2021). These characteristics serve as practical field guides for determining optimal harvest timing, which is critical because delayed harvesting results in rapid quality deterioration, particularly in aged seeds, indicating loss of viability (N. *et al*., 2024).

The seed maturation process progresses gradually through distinct phases, with continuous moisture loss and concurrent gains in hardness, test weight, and seed yield during weekly harvests extending to 42 days after anthesis (Kannababu *et al*., 2023). Polynomial regression analysis provides predictive capability for maximum quality timing, offering breeders and farmers evidence-based strategies for harvest scheduling (Rao *et al*., 1993). This precise timing is essential for maintaining physiological quality traits, including germination percentage, vigor indices and storability potential (Pannase *et al*., 2024). Seed development in pearl millet follows a well-defined sequence of morphological and physiological stages that collectively determine final seed quality, yield potential and storability. The initial stage begins immediately after fertilization, where the developing caryopsis exhibits a club-shaped structure, representing early embryo and endosperm differentiation (Taylor & Vasil, 1995) in Fig. 1.

2.2 Seed Germination and Vigor Assessment

Germination parameters serve as primary indicators of seed quality and viability in millet production systms. In foxtail millet, maximum germination percentages (up to 100%) and seedling vigor indices are achieved through optimized micronutrient applications (Sirinandini *et al*., 2022). Vigor Index-I, calculated as the product of germination percentage and seedling length, represents an integrated measure of seed quality that reflects both the capability to produce normal seedlings and the vigor of seedling development. Vigor Index-II, based on dry weight of seedlings, provides additional insight into reserve mobilization capacity (Ananthi, 2025).

Field emergence is another critical quality parameter that differs from laboratory germination percentage under suboptimal field conditions. Studies show that dual-stage foliar sprays of boron and zinc during panicle initiation and 50% flowering stages achieved 95% field emergence in foxtail millet, outperforming soil application methods (Jung *et al*., 2019). This distinction between laboratory germination and field emergence emphasizes the importance of comprehensive quality testing protocols, as field conditions introduce additional stresses including soil pathogens, moisture variability and temperature fluctuations that laboratory tests cannot fully simulate (Keerthanan *et al*., 2025).

2.3 Seed Size and Weight Components

The thousand-seed weight (TSW) represents a crucial quality parameter influencing both yield potential and seedling vigor. Maximum TSW values of 356 mg in foxtail millet were recorded with dual-stage foliar applications of boron and zinc, directly correlating with superior seed quality traits (Zhang *et al*., 2022). Seed size categories, including individual seed weight and panicle dry weight, collectively determine the overall productivity of individual plants and contribute substantially to harvest index calculations (Aniskina *et al*., 2025).

Varietal maturity groups significantly influence seed size development. Early and mid-early ripening varieties of panicum millet demonstrated higher seed yield and consistent quality indicators compared to late-ripening varieties, with the highest quality indicators observed in very early to medium-ripening varieties (Dryga *et al*., 2023). The genetic control of seed size, combined with environmental influences during seed filling stages, results in substantial variation across germplasm collections, providing opportunities for selection of large-seeded varieties that often possess enhanced vigor characteristics (Boccaccini *et al*., 2024).

2.4 Seed Viability and Longevity

Long-term seed viability and storage potential are increasingly important considerations in millet seed production, particularly for conservation and export applications (Solberg *et al*., 2020). Seed viability is maintained through careful management of harvest timing, as premature or delayed harvesting significantly compromises storability (Rao *et al*., 1991). The decline in quality traits accelerates at later harvest stages, with more prominent deterioration observed in aged seeds, indicating that delayed harvests impose substantial fitness costs on resulting offspring.

Environmental conditions during seed maturation, including temperature fluctuations and moisture availability, directly influence the vigor and longevity of harvested seeds (Thenveettil *et al*., 2024). Seed moisture content at harvest, typically ranging from 12-14%, requires proper conditioning and storage protocols to maintain viability during extended periods (Choudhary *et al*., 2022). This aspect becomes particularly relevant for seed certification and commercial distribution systems where long-term storage is necessary.

3. Novel Seed Priming Technologies for Quality Enhancement

3.1 Nano-Based Seed Priming Approaches

Nanoparticle-based seed priming represents a cutting-edge technology for dramatically improving seed quality parameters and enhancing stress resilience in millets (Donia & Carbone, 2023). Zinc oxide nanoparticles (ZnO NPs) applied through seed priming at 25-50 ppm concentrations significantly enhanced shoot and seedling length, improved overall vigor and resulted in the highest germination percentages in rice and other cereals (Li *et al*., 2020). The superiority of nano-formulations over traditional ionic sources lies in their enhanced bioavailability, reduced particle size enabling deeper penetration into seed tissues and their ability to reach the embryo region, as confirmed by transmission electron microscopy studies (Adhikary *et al*., 2022).

Bacterial-assisted synthesis of iron and zinc nanoparticles combined with plant growth-promoting rhizobacteria (PGPR) demonstrated exceptional synergistic effects, improving wheat biomass up to 96% and grain weight up to 28% compared to recommended fertilizer doses (Kumar *et al*., 2025). The integration of seed priming with foliar applications of nanoparticles produced even more pronounced effects, with foliar spray combining PGPR and nanoparticles increasing biomass up to 59% and iron content by 27% (Jalal *et al*., 2023). This dual-application approach capitalizes on both early seedling vigor enhancement and sustained nutrient availability during critical growth stages.

3.2 Conventional Seed Priming Methods and Improvements

Hydropriming, the controlled imbibition of seeds with water, forms the foundation of seed priming technology and enhances millet seed germination by initiating pre-germinative metabolism without allowing radicle emergence (Corbineau *et al*., 2023). When applied to foxtail millet, hydropriming for 8 hours improved shoot emergence to 91.3% and reduced shoot fly incidence compared to unprimed controls (Cardarelli *et al*., 2022). This technique activates enzyme systems including amylase and protease, mobilizes food reserves and triggers antioxidant accumulation, preparing seeds for rapid germination upon optimal moisture and temperature conditions (Balaji *et al*., 2024).

Osmopriming, involving seed imbibition in osmotic solutions, provides superior germination and vigor enhancement compared to hydropriming alone (Srivastava *et al*., 2023). Application of calcium chloride (2%) as an osmotic priming agent achieved maximum seed germination of 95.75% and grain yield of 19.47 q/ha in foxtail millet (S. *et al*., 2025). The osmotic regulation during priming allows controlled water uptake rates that minimize leakage of cellular contents while maximizing metabolic activation (Hijab *et al*., 2024). Biopriming, involving seed treatment with beneficial microorganisms, further enhances these benefits by introducing stress-alleviating microbes that colonize seed surfaces and roots, extending protection beyond the immediate germination phase (Mahmood *et al*., 2016).

3.3 Micronutrient-Based Priming for Biofortification

Seed priming with micronutrient solutions represents a direct mechanism for biofortification, simultaneously enhancing germination vigor and increasing nutrient accumulation in developing grains (Haider *et al*., 2020). Zinc chemo-priming of mungbean with 0.01M zinc solution increased grain yield by 15% and grain zinc concentration by 14% compared to control, with varieties like BARI Mug-3, BARI Mug-5 and BARI Mug-6 showing superior zinc content(Awal *et al*., 2024). The optimal concentration identifies a balance between nutrient enhancement and potential osmotic stress, as higher concentrations (0.05M) demonstrated significantly reduced plant growth and yield despite increased grain zinc enrichment (Awal *et al*., 2024).

Zinc oxide nanoparticles applied through seed priming at various concentrations demonstrated dose-dependent responses, with 200 ppm showing maximum enhancement in lentil seed germination (12.6% increase), root length (65.9% increase) and shoot length (97.4% increase) (Afzal & Singh, 2021). Hydrolytic enzyme activities including amylase, protease, and phytase were substantially elevated in chitosan nanoparticle-primed seeds compared to untreated controls, indicating enhanced mobilization of seed reserves (Alhammad *et al*., 2023). These enzymatic improvements translate to superior field establishment and crop productivity, with field trials confirming that primed seeds produced significantly higher yields and harvest indices (Gamit *et al*., 2025).

3.4 Integrated Priming Strategies for Stress Resilience

Combining multiple priming agents addresses the complex challenge of developing seeds that can simultaneously maximize germination, enhance nutrient accumulation and tolerate environmental stresses (Setty *et al*., 2023). Seed priming combining zinc oxide nanoparticles, sodium selenite and sodium selenate for direct-seeded rice resulted in early emergence with improved vigor and enhanced nutrient uptake (nitrogen, phosphorus, potassium, boron, zinc and silicon) compared to hydro-priming controls (Guha *et al*., 2021). The combinations consistently increased chlorophyll, phenol and protein contents, improved leaf area index and crop growth rate and enhanced final grain yield (Xing *et al*., 2024).

Selenium nanoparticle priming demonstrated particular effectiveness for heat stress mitigation in tomato, with boron nanoparticles (both bare and polyvinylpyrrolidone-coated forms) increasing germination rate, potential and index under high-temperature conditions of 45°C. These integrated approaches recognize that modern agriculture faces multiple simultaneous stressors, requiring multifaceted solutions that enhance both baseline seed quality and stress-specific tolerance mechanisms (Ishtiaq *et al*., 2023). The cost-effectiveness of nanopriming, combined with its sustainability advantages over chemical alternatives, positions these technologies as practical solutions for scaling up millet production in resource-limited regions (Zhang *et al*., 2025).

4. Genetic Diversity and Germplasm Resources for Millet Improvement

4.1 Population Structure and Genetic Variation

The genetic basis of seed quality and yield in millets is extensively documented through genome-wide association studies (GWAS) and population structure analyses, revealing substantial variation available for targeted breeding (Vetriventhan *et al*., 2024). Proso millet germplasm diversity structured according to geographic centers of origin shows the race miliaceum exhibiting highest diversity with an average modified Roger's Distance of 0.268 among 160 diverse accessions, enabling identification of 40 marker-trait associations (MTAs) for agronomic traits and grain nutrients (Boukail *et al*., 2021). Among these 40 MTAs, 34 were associated with agronomic traits including plant height, grain weight, and seed quality parameters, while 6 were associated with grain nutrients, with 20 located within annotated genes offering direct targets for breeding (Khound *et al*., 2024).

Finger millet germplasm characterized across three diverse production environments identified 15 major quantitative trait nucleotides (QTNs) with more than 30% phenotypic variance explained (PVE) for agronomic traits, with pleiotropic major QTNs identified for days to maturity/flowering on chromosome 9B and iron/zinc content on chromosome 2B (Gebreyohannes *et al*., 2025). Two genotypes from the Tigray region and one from

Amhara region harbored favorable haplotypes for simultaneous improvement of maturation timing and micronutrient content, representing high-priority breeding targets (Brhane *et al*., 2024).

4.2 Mini-Core Collections and Trait-Specific Gene Pools

Mini-core germplasm collections, representing approximately 1% of total germplasm holdings with full representation of phenotypic and genetic diversity, provide efficient entry points for millet improvement programs (Upadhyaya *et al*., 2010). The finger millet mini-core collection of 310 accessions identified grain nutrient-dense accessions useful for biofortification breeding, with estimated percent daily values indicating that consumption of 100g of finger millet grains could potentially contribute to 49% calcium, 52% magnesium, 23% protein, 23% iron, and 26% zinc recommended dietary allowance (Backiyalakshmi *et al*., 2023). This assessment reveals substantial variation in nutritional profiles across available germplasm that can be exploited through targeted breeding.

Pearl millet core collection germplasm evaluation identified accessions rich in specific and multiple nutrients grouped into five clusters, with most nutrients positively and significantly associated among themselves and with days to 50% flowering and 1000-grain weight (Govindaraj *et al*., 2020). The availability of such core collections substantially reduces the screening burden for conventional breeding programs while maintaining comprehensive genetic representation. The formation of trait-specific gene pools further enhances breeding efficiency by grouping accessions based on desired characteristics, enabling rapid development of breeding lines combining multiple desirable traits in Fig. 2.

4.3 Agronomic Trait Variation and Breeding Targets

Phenotypic diversity for morpho-agronomic traits in proso millet germplasm core collection (77 genotypes from 24 countries) revealed significant variations across multiple traits, with nine traits explaining maximum phenotypic variance suitable for use as selection indices in breeding (Rajput *et al*., 2024). Several genotypes were identified as sources of desired traits such as early maturity, reduced lodging and low grain shattering, which collectively define breeding targets for developing improved cultivars. Principal component analysis identified key traits determining phenotypic variance, enabling targeted selection strategies that optimize multiple objectives simultaneously (Zhang *et al*., 2019).

Evaluation of proso millet germplasm in Kazakhstan identified high correlation between seed weight per panicle and number of seeds per panicle (r=0.73-0.92), while correlations between 1000-seed weight and number of seeds per panicle were negative (r=-0.48). These correlations provide insights into trade-offs in yield component development, with breeding strategies potentially targeting either numerous small seeds or fewer large seeds depending on end-use requirements (Dyussibayeva *et al*., 2024). The identification of low-lodging and high-yielding genotypes across diverse environments demonstrates the availability of germplasm well-adapted to varied production systems (Nagaraja *et al*., 2025).

4.4 Genomic Resources and Reference Sequences

High-quality reference genome assemblies of pearl millet, proso millet, and foxtail millet provide foundational resources for genomic-assisted breeding, enabling identification of sequence variations linked to agronomic traits (Ramu *et al*., 2023). The platinum-grade assembly of pearl millet Tift 23D2B1-P1-P5 achieved contig N50 of approximately 7,000-fold improvement (126 Mb) compared to previous versions, with better alignment in centromeric regions containing important genetic variation. Comparative genomic analysis identified differential gene expression enriched for serine O-acetyltransferase and glycerol-3-phosphate metabolic process genes, which play important roles in improving nutritional quality, seed protein content, and disease resistance (Salson *et al*., 2023).

The green millet (*Setaria viridis*) genome resource, representing the wild progenitor of domesticated foxtail millet, enabled discovery of agronomically valuable loci and identification of the Less Shattering1 (SvLes1) gene controlling seed shattering through a loss-of-function mutation involving transposable element insertion (Srivastava *et al*., 2020). This discovery directly improved utility for understanding domestication genes in closely related crop species. Whole genome sequencing technologies now enable resequencing of diverse germplasm panels and identification of novel allelic variation for targeting rapid trait introgression through marker-assisted selection and genomic prediction (Mamidi *et al*., 2020).

5. Breeding Methods and Trait Introgression Strategies

5.1 Conventional Breeding and Marker-Assisted Selection

Conventional breeding combined with molecular marker-assisted selection (MAS) represents the most widely adopted approach for millet improvement, offering rapid development of improved varieties with minimal regulatory barriers (Rouamba *et al*., 2023). The establishment of genomic regions controlling agronomic traits and Striga resistance in pearl millet identified 28 SNPs significantly associated with low Striga emergence on chromosomes 1-7, facilitating marker-assisted breeding and trait introgression (Srivastava *et al*., 2022). Four SNPs were associated with days-to-50%-flowering, five with panicle length, and seven with thousand-grain weight, providing putative markers for accelerated breeding of varieties with improved yield components and reduced parasitic weed burden (Shivhare & Lata, 2017).

Pearl millet genome sequences provide comprehensive frameworks for marker development and genomic selection, enabling whole-genome prediction of breeding values and identification of heterotic patterns (Singh &

Nara, 2022). The improved pearl millet genomes representing global heterotic pool pools identified multiple marker-trait associations for range of agronomic traits and grain yield through genome-wide association study, with improved marker resources providing comprehensive platform for future applications of marker-assisted selection and whole-genome prediction for haplotype-based complex traits (Varshney *et al*., 2017).

5.2 Genomic-Assisted Breeding and Rapid Trait Introgression

Genomic selection, utilizing genome-wide marker panels to predict breeding values of untested individuals, substantially accelerates breeding cycles by enabling selection among large segregating populations without phenotyping (Robertsen *et al*., 2019). Genome-wide assessment of proso millet population structure identified marker-trait associations and favourable alleles for agronomic and grain nutrient traits, providing the genomic foundation for implementing rapid genomic selection cycles (Vetriventhan *et al*., 2024). Association mapping models including single-locus, multi-locus and haplotype-based approaches identified quantitative trait loci (QTLs) significantly associated with measured traits, most of which represent novel associations not previously reported in genomic databases (Jiang *et al*., 2024).

Transcriptome analysis in foxtail millet under drought stress during germination identified differential gene expression related to phenylpropanoid biosynthesis pathway, revealing that foxtail millet regulates drought tolerance through modulation of endogenous allelochemicals (Chang *et al*., 2024). Four genes of phenylalanine ammonia-lyase, 4-coumarate-CoA ligase 3, cinnamoyl-CoA reductase 1 and cationic peroxidase SPC4 play important roles in foxtail millet drought response, providing specific targets for genomic selection and potentially for genome editing approaches (Yu *et al*., 2020).

5.3 Mutation Breeding and Novel Phenotypes

Induced mutations through gamma irradiation and chemical mutagenesis generate novel genetic variation for trait improvement beyond what exists in natural germplasm collections (Sao *et al*., 2022). A novel virescence mutant induced in finger millet with delayed flowering and reduced plant height but stable expression of other agronomic traits demonstrated potential for simplifying hybridization through seedling-stage marker identification (T. *et al*., 2021). The virescence phenotype provided visual marker for F1 identification with hybrid recovery ranging from 0.2% to 15.7% (average 5.1%), substantially improving efficiency of hybrid development compared to conventional cross methods (Thada *et al*., 2024).

Gamma ray-induced mutagenesis of three traditional rice landraces generated mutants with 4.94-21.40% reduction in days to 50% flowering and 11.28-37.65% reduction in plant height compared to parents (Rani *et al*., 2025). Notably, several mutants showed yield advantages, with Samundchini Mutant S-18-1 increasing yield by 22.45%, Vishnubhog Mutant V-74-6 by 36.87%, and Jhilli Mutant J-13-5 by 25.96% over their respective parents (Meenakshi *et al*., 2026). SSR marker-based genome similarity analysis confirmed 95.60-71.70% similarity with parents (for Vishnubhog), 95.62-89.10% (for Samundchini), and 95.62-80.40% (for Jhilli), demonstrating that mutagenesis generates stable heritable variation while maintaining essential genetic background (Sellapillai *et al*., 2022).

5.4 CRISPR/Cas9 Genome Editing for Trait Improvement

Genome editing technologies using CRISPR/Cas9 systems enable precise modification of specific genes controlling desired traits without altering the genetic background, offering advantages over conventional breeding in speed and precision (Sharma *et al*., 2022). While direct applications to millet genomes are emerging, the suitability of genome editing for improving abiotic stress tolerance, grain quality, and yield components has been demonstrated in model systems and major crops (Zafar *et al*., 2020). The technology enables base editing and prime editing approaches that introduce subtle sequence modifications with minimal off-target effects, as well as multiplexing strategies simultaneously targeting multiple genes to address polygenic trait complexities (Ceasar, 2021).

For millets, genome editing holds promise for developing climate-smart varieties through rapid introgression of stress tolerance genes, modification of seed quality traits, and enhancement of nutritional properties (Sapara *et al*., 2024). The identification of specific genes controlling yield components and quality traits in millet germplasm, combined with availability of reference genomes, provides foundation for implementing precision breeding approaches that accelerate variety development cycles while reducing breeding population sizes and resource requirements (Prasad *et al*., 2017). Agronomic techniques include nutrient priming, foliar and soil fertilization, and microbe-mediated biofortification to improve the availability and uptake of essential micronutrients such as iron (Fe), zinc (Zn), and magnesium (Mg). Conventional breeding approaches utilize genetic variability and selection methods to develop nutrient-dense crop varieties. Advanced biotechnological tools, including CRISPR/Cas9-mediated genome editing, RNA interference (RNAi), gene overexpression, and transgenic approaches, enable precise manipulation of genes associated with nutrient accumulation and metabolism in Fig. 3.

6. Integrated Nutrient Management and Seed Production

6.1 Micronutrient Application Strategies

Micronutrient availability profoundly influences seed quality, yield, and nutritional composition in millets, with boron and zinc particularly important for reproductive development (Kannababu *et al*., 2026). Dual-stage foliar sprays of boron (0.5%) and zinc (1%) applied at panicle initiation and 50% flowering stages in foxtail millet produced maximum plant height (118 cm), productive tillers (5), primary branches per panicle (119), panicle dry weight (10 g), seed yield per plot (1.40 kg), 100-seed weight (356 mg) and harvest index (48%) (Manjunath & Debbarma, 2023). The combined application achieved superior results compared to individual applications or soil application methods, indicating synergistic effects between boron and zinc in enhancing reproductive development (Shabir *et al*., 2023).

Foliar application of Zn at both physiological initiation and 50% flowering stages recorded the highest benefit-cost ratio (1.6), making this treatment economically optimal for resource-limited farming systems (Dass *et al*., 2022). The economic analysis including input costs, labor requirements, and market prices for grain and straw provides practical guidance for technology adoption across diverse farm sizes and production intensities. Soil micronutrient status before applying these treatments requires assessment through soil testing protocols, with adjustments made based on baseline nutrient availability to optimize input efficiency (Vineetha *et al*., 2024).

6.2 Organic and Integrated Nutrient Management

Organic fertilizers improve seed quality and abiotic stress tolerance through multiple mechanisms including soil organic matter accumulation, enhanced microbial activities, improved water-holding capacity and sustained nutrient availability (Tian *et al*., 2022). Application of organic materials improves soil structure, aggregate stability and nutrient use efficiency while supporting diverse soil microbial communities that enhance nutrient cycling and stress tolerance mechanisms (Feng *et al*., 2025). Combined application of organic nitrogen sources (farmyard manure) and inorganic nitrogen (urea) with seed inoculation of rhizobacteria in pearl millet resulted in significant improvements in grain yield, with combined applications producing 23.19-25.0% increase in grain yield compared to no inoculation (Jiang *et al*., 2025).

The integration of seed inoculation with plant growth-promoting bacteria alongside balanced nutrient applications provides cost-effective strategy for sustainable intensification in millet production (Dawood *et al*., 2023). Combined application of nitrogen, phosphorus, and potassium fertilizers significantly improved seed yield, seed quality and seed vigor of Elymus nutans in alpine regions, with balanced fertilization at 150 kg N ha^{-1}, 120 kg P2O5 ha^{-1}, 90 kg K2O ha^{-1} identified as optimal rates. Nitrogen fertilizer demonstrated greater effects on seed yield and quality compared to phosphorus and potassium, indicating that nitrogen remains the most critical nutrient for seed production systems (E. *et al*., 2024).

6.3 Plant Growth-Promoting Rhizobacteria and Biological Amendments

Plant growth-promoting rhizobacteria (PGPR) enhance seed quality through multiple mechanisms including enhanced nutrient solubilization, production of plant growth-promoting substances and induced systemic resistance to environmental stresses. PGPR strains including Stenotrophomonas maltophilia improved productivity and nitrogen use efficiency when combined with seed inoculation in pearl millet, with rhizobacteria-inoculated plants demonstrating significantly improved shoot and root dry weight under both adequate and drought-stressed conditions (Mitra *et al*., 2021). The inoculation of pearl millet seeds with endophytic bacteria Shewanella putrefaciens and Cronobacter dublinensis under drought stress conditions significantly improved root architecture, relative water content and proline accumulation, with inoculated plants showing higher content of abscisic acid and indole-3-acetic acid under all moisture regimes (Sun *et al*., 2024).

Biological seed treatments incorporating beneficial microorganisms provide dual benefits of seed quality enhancement and established pathogenic microorganism suppression. Seed treatment with aqueous extract of Viscum album increased germination and seedling vigor in pearl millet while inducing resistance to downy mildew disease, with enhanced peroxidase and phenylalanine ammonia-lyase enzyme activities in treated seedlings indicating induced defense system activation. The integration of PGPR inoculation with reduced chemical fertilizer applications (50% of recommended dose) maintained grain yield while reducing input costs and environmental impacts (Bhardwaj *et al*., 2025).

6.4 Agronomic Management Practices for Seed Production

Optimal agronomic management practices during seed production ensure achievement of maximum seed yield and quality targets (Hassan *et al*., 2020). Nitrogen application at 100-150 kg ha^{-1} with appropriate seeding rates (15 kg/ha) optimized pearl millet fodder and seed production in diverse production environments. While seeding date and growing season conditions influenced forage dry-matter yield and quality in annual crops, high-yielding varieties maintained consistent production across variable environmental conditions, indicating genotypic stability and environmental responsiveness of elite germplasm (Awala *et al*., 2023).

Potassium and manganese fertilization effects on pearl millet seed yield, quality and forage potential of residual stalks show that balanced micronutrient application improved seed yield, with TifGrain 102 averaging 5900 $kg \cdot ha^{-1}$ compared to 4680 kg ha^{-1} for browntop millet (Kering & Broderick, 2018). The residual stalk material demonstrated variable nutritional composition related to fertilizer treatments, with opportunities for dual-use production systems combining grain and quality forage. Selection of sowing date to optimize development relative to expected rainfall patterns, combined with cultivar selection for early maturity and water-use efficiency, provides risk mitigation strategies in water-scarce production environments (Sher *et al*., 2023).

7. Abiotic Stress Tolerance Mechanisms and Resilience Building

7.1 Drought Stress Tolerance and Water-Use Efficiency

Millets, particularly foxtail and pearl varieties, exhibit exceptional drought tolerance through mechanisms including enhanced antioxidative systems, osmotic adjustment via osmolyte accumulation and root system modification (Terfa *et al*., 2025). Foxtail millet's ability to maintain productivity under extreme temperatures and prolonged drought reflects adaptive mechanisms providing strategic advantages for climate-smart agriculture (De La Fuente *et al*., 2023). Glutaredoxin gene PgGRXC9, identified through combined linkage mapping and GWAS approaches in pearl millet, regulates primary root growth enhancement that correlates with increased early drought stress tolerance in field conditions (Yu *et al*., 2020). This gene's functional validation through heterologous expression in Arabidopsis confirmed its role in regulating cell elongation and conferring root system resilience to Sahelian environmental conditions.

Transcriptomic analysis of foxtail millet germination under polyethylene glycol-induced drought stress revealed differential gene expression patterns during distinct germination phases, with phenylpropanoids-related pathway genes playing prominent roles in drought response. Expression of four genes in phenylpropanoids pathway (phenylalanine ammonia-lyase, 4-coumarate-CoA ligase 3, cinnamoyl-CoA reductase 1, cationic peroxidase SPC4) showed substantial upregulation under drought, indicating coordinated regulation of secondary metabolite biosynthesis in drought tolerance. Biofortification breeding targets including iron and zinc content demonstrated positive correlation with drought tolerance traits, suggesting that simultaneously selecting for nutritional quality and stress tolerance may be feasible through compound trait assessment (Pan *et al*., 2020).

7.2 Nanoparticle-Mediated Stress Mitigation

Nanoparticles represent emerging tools for modulating crop yield and overcoming abiotic stress constraints through inducing physiological and biochemical readjustments and modulating gene expression involved in drought response (Rasheed *et al*., 2022). Zinc oxide nanoparticles applied through seed nano-priming at 25 ppm for direct-seeded rice mitigated drought-induced damages, with 53% reduction in malondialdehyde (MDA) content under drought stress conditions (Mazhar *et al*., 2022a). Nanopriming treatments imparted significant protective effects on biomass characteristics including plant height improvement and enhanced yield components including panicle length, number of tillers and grain weight enhancement (Mazhar *et al*., 2024). Elevated proline and amino acid levels, combined with increased activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) by 11%, 13%, and 38% respectively, demonstrate multiple protective mechanisms activated by nanoparticle pretreatment (Mazhar *et al*., 2022b).

Iron oxide nanoparticles applied through seed priming at 75 mg L^{-1} improved water relations and photosynthetic efficiency of drought-stressed maize plants through enhanced relative water content (13% increase), improved water potential (44% increase), photosynthetic water use efficiency (64% increase) and leaf intrinsic water use efficiency (17% increase) compared to control (Ishfaq *et al*., 2025). Enhanced antioxidant systems including increased total chlorophyll (37% increase), total flavonoids (22% increase) and ascorbic acid (36% increase) contributed to improved drought stress tolerance. Combining seed priming with foliar application of nanoparticles provided sustained stress mitigation extending from early establishment through grain maturation (Sadati *et al*., 2022).

7.3 Transcription Factors and Molecular Breeding Targets

Transcription factors, particularly from WRKY, DREB, MYB and NAC families, represent key regulatory switches controlling gene expression for diverse drought stress response mechanisms (Manna *et al*., 2020). In pearl millet, differential expression of genes encoding transcription factors responding to drought and abscisic acid signaling (SbAP2, SbSNAC1, PgDREB2A) and phytohormone biosynthesis (SbNCED, SbGA20oX, SbYUC) underscores the complexity of stress response pathways. Identification of these molecular targets enables implementation of targeted breeding strategies through CRISPR/Cas9 gene editing or marker-assisted selection of alleles conferring enhanced expression of stress-responsive genes (Manjunatha *et al*., 2022).

Novel ASR (Abscisic stress ripening) gene isolated from drought stress-responsive suppression subtractive hybridization library in pearl millet conferred multiple abiotic stress tolerance when expressed in transgenic Arabidopsis, with enhanced relative water content, chlorophyll, and proline levels but decreased malondialdehyde under drought stress. The PgASR3 gene overexpression in Arabidopsis at maturity stage improved drought stress tolerance, validating this target for potential genetic engineering approaches in pearl millet improvement programs (Meena *et al*., 2020).

7.4 Integrated Stress Management and Climate-Smart Agriculture

Heat stress on nutritional status reveals that millets maintain productivity under extreme temperatures through inherent resilience mechanisms distinct from staple crops including rice, wheat and maize (Ponmani *et al*., 2025). C4 photosynthetic pathway, unique morphological adaptations including deep root systems and biochemical mechanisms including osmoprotectant accumulation and stress-responsive gene regulation enhance millet thermotolerance (Saleem *et al*., 2021). Integration of advanced biotechnological tools including molecular breeding, transcriptomics and CRISPR/Cas9-based genome editing with traditional breeding methods offers potential strategies for further improving millet varieties for enhanced heat resilience and nutritional quality (Numan *et al*., 2021).

Agronomic management practices for abiotic stress include optimization of seeding timing to synchronize crop development with favorable periods, selection of varieties with appropriate maturity groups for specific environments, and implementation of water-saving technologies including micro-irrigation and mulching practices (Wilson & VanBuren, 2022). The adoption of drought-adapted pearl millet varieties with early maturity and superior water-use efficiency within existing cropping systems provides immediate risk mitigation strategies for farming communities. The combination of improved variety selection, optimized agronomic management and climate-smart agricultural technologies creates synergistic effects that maximize resilience while sustaining productivity and profitability (Aiswarya *et al*., 2025).

8. CONCLUSION

Novel approaches for enhancing seed quality and yield in millets integrate advances in seed science, agronomy, genetics and biotechnology to address the complex challenge of sustainable production intensification. The identification of optimal physiological maturity stages guides precise harvest timing that maximizes both yield and quality parameters. Advanced seed priming technologies, particularly nano-based approaches, offer cost-effective and sustainable strategies for improving germination, vigor, and environmental stress resilience simultaneously. Integration of biofortification through strategic micronutrient application, particularly boron and zinc, addresses both productivity and nutritional security objectives concurrently.

The substantial genetic diversity available within millet germplasm collections, combined with emerging genomic tools and reference sequences, enables accelerated breeding cycles through marker-assisted selection and genomic prediction. The identification of specific genes controlling yield components, quality traits and stress tolerance provides foundation for implementing precision breeding approaches that develop climate-smart varieties adapted to projected future production environments. Integration of conventional breeding with CRISPR/Cas9 genome editing enables rapid pyramiding of multiple desirable alleles, substantially reducing breeding timelines.

Sustainable intensification through integrated nutrient management combining organic amendments, balanced mineral fertilization and plant growth-promoting microbial inoculants provides holistic strategies that simultaneously enhance productivity, resource use efficiency and environmental sustainability. The recognition that multiple abiotic stresses operate simultaneously in farmers' fields necessitates development of varieties with multistress resilience, achieved through comprehensive trait assessment in multivariate environments.

9. Future Perspectives

Future research priorities include: (1) expanding reference genome assemblies and resequencing of diverse germplasm to enable comprehensive characterization of allelic variation; (2) scaling up nano-enabled technologies through appropriate delivery mechanisms accessible to smallholder farmers; (3) validating genome-edited millets for enhanced yield and quality under diverse field environments; (4) clarifying interactions between seed priming, genotype, and environmental factors affecting trait expression; (5) developing farmer-participatory breeding approaches that integrate scientific knowledge with local preferences and socio-economic constraints; and (6) establishing seed certification standards aligned with emerging quality metrics including nutritional content and stress resilience indicators.

The comprehensive integration of these novel approaches offers realistic pathways for achieving significant improvements in millet productivity and nutritional quality while enhancing resilience to climate-induced environmental variability, thereby contributing substantially to global food and nutritional security.

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Figures

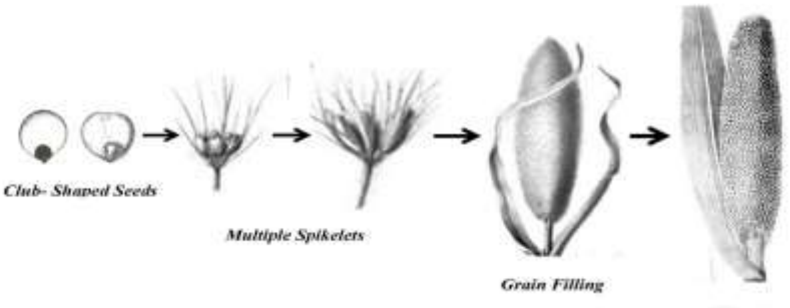

Figure 1. Developmental stages of seed formation in pearl millet (*Pennisetum glaucum*) from early seed morphology to physiological maturity.

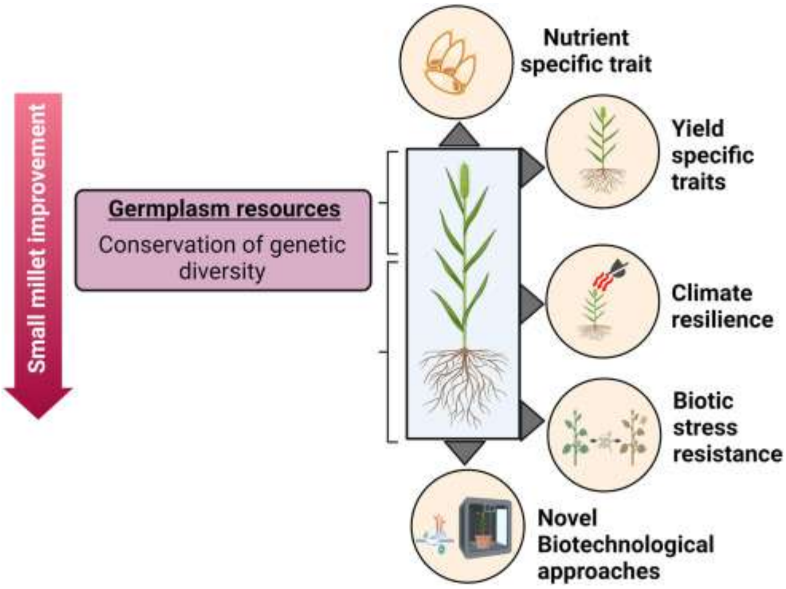

Figure 2. Integrated framework for small millet improvement through germplasm conservation, trait-based selection and biotechnological interventions.

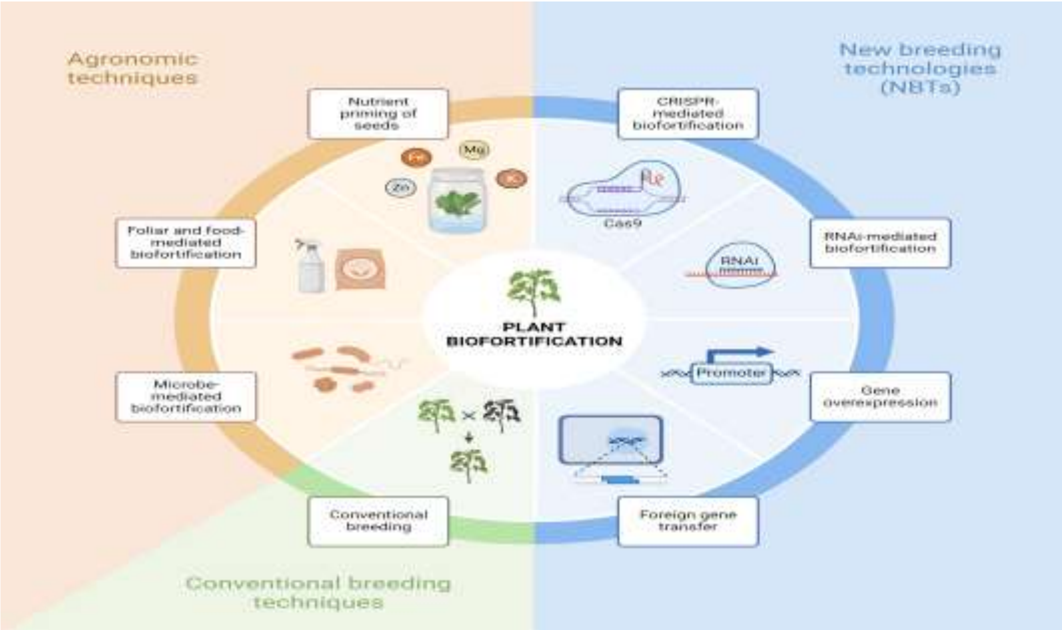

Figure 3. Integrated strategies for plant biofortification through agronomic, conventional breeding and modern biotechnological approaches.

Table

Summary Table: Key Innovations for Millet Seed Quality and Yield Enhancement

Innovation Category	Technology/Approach	Key Benefits	Millet Species	Citation
Physiological Maturity	Timing based on DAA	Maximized quality traits	Foxtail millet	(Meena *et al.*, 2021)
Seed Priming	Nano-priming (ZnO NPs)	+60% germination, +85% vigor	Multiple species	(Iqbal *et al.*, 2021)
Biofortification	Zn chemo-priming	+14% Zn, +15% yield	Mungbean/Millets	(Rehman *et al.*, 2021)
Micronutrients	B+Zn foliar spray	356 mg TSW, 100% germination	Foxtail millet	(Patel *et al.*, 2023)
PGPR Integration	Seed inoculation	+25% grain yield, improved NUE	Pearl millet	(Kour *et al.*, 2023)

Genomic Selection	GWAS-MAS	40 MTAs identified	Proso millet	(Jaiswal *et al*., 2023)
Stress Tolerance	Nano-priming + stress	+53% drought mitigation	Pearl/Foxtail	(Rizwan *et al*., 2022)
Harvest Timing	Visual maturity indicators	Optimal seed quality	Foxtail millet	(Karthikeyan *et al*., 2024)