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GENETIC IMPROVEMENT IN SMALL MILLETS: A REVIEW

MELHORAMENTO GENÉTICO EM MILHETOS PEQUENOS: UMA REVISÃO

MEJORAMIENTO GENÉTICO EN MIJO(S) PEQUEÑO(S): UNA REVISIÓN

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ABSTRACT

Small millets have emerged as strategic crops for agricultural systems in semi-arid and low-productivity regions due to their high adaptive efficiency, short growth cycle, and significant nutritional value. The broad genetic diversity present among different millet groups offers important opportunities for the development of more stable, productive, and stress-tolerant cultivars. However, the predominance of self-pollination and reduced floral structure hinder natural crossing, making the use of specific emasculation and hybridization techniques essential to enhance genetic recombination. In recent years, significant advances in genomics—such as the use of SNP markers, marker-assisted selection, and genome-wide analysis approaches—have accelerated the identification of alleles associated with stress tolerance, yield potential, and nutritional quality. International programs coordinated in India, Africa, and by institutions such as ICRISAT have expanded the available genetic base, while also promoting resilient cultivars adapted to different production systems. At the same time, the growing socioeconomic appreciation of these cereals reinforces their emerging role in food security. This review integrates biological, genetic, and applied aspects, presenting the main advances and perspectives for strengthening small millet breeding.

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Keywords: Resilient Cultivars. Self-pollination. Reproductive Phenology. Agricultural Sustainability.

RESUMO

Os milhetos pequenos têm se destacado como culturas estratégicas para sistemas agrícolas de regiões semiáridas e de baixa produtividade, devido à elevada eficiência adaptativa, ao rápido ciclo e ao valor nutricional expressivo. A ampla diversidade genética presente nos diferentes grupos de milhetes oferece oportunidades relevantes para o desenvolvimento de cultivares mais estáveis, produtivas e tolerantes a estresses ambientais. Entretanto, a predominância da autogamia e a estrutura floral reduzida dificultam o cruzamento natural, tornando indispensável o uso de técnicas específicas de emasculação e hibridização para ampliar a recombinação genética. Nos últimos anos, avanços significativos em genômica, como o uso de marcadores SNP, seleção assistida e abordagens de análise genômica ampla, têm acelerado a identificação de alelos relacionados à tolerância ao estresse, capacidade produtiva e qualidade nutricional. Programas internacionais coordenados na Índia, África e por instituições como o ICRISAT têm expandido a base genética disponível, além de promover cultivares resilientes e adequadas a diferentes sistemas produtivos. Paralelamente, a crescente valorização socioeconômica desses cereais reforça seu papel emergente na segurança alimentar. Esta revisão integra aspectos biológicos, genéticos e aplicados, apresentando os principais avanços e perspectivas para o fortalecimento do melhoramento dos milhetos pequenos.

Palavras-chave: Cultivares Resilientes. Autogamia. Fenologia Reprodutiva. Sustentabilidade Agrícola.

RESUMEN

Los millets pequeños se han destacado como cultivos estratégicos para los sistemas agrícolas de regiones semiáridas y de baja productividad, debido a su elevada eficiencia adaptativa, su ciclo corto y su notable valor nutricional. La amplia diversidad genética presente en los diferentes grupos de millets ofrece oportunidades relevantes para el desarrollo de cultivares más estables, productivos y tolerantes a estreses ambientales. Sin embargo, la predominancia de la autogamia y la reducida estructura floral dificultan el cruzamiento natural, haciendo indispensable el uso de técnicas específicas de emasculación e hibridación para ampliar la recombinación genética. En los últimos años, avances significativos en genómica —como el uso de marcadores SNP, la selección asistida por marcadores y los enfoques de análisis genómico a gran escala— han acelerado la identificación de alelos relacionados con la tolerancia al estrés, la capacidad productiva y la calidad nutricional. Programas internacionales coordinados en India, África y por instituciones como el ICRISAT han ampliado la base genética disponible, además de promover cultivares resilientes y adecuados a diferentes sistemas productivos. Paralelamente, la creciente valorización socioeconómica de estos cereales refuerza su papel emergente en la seguridad alimentaria. Esta revisión integra aspectos biológicos, genéticos y aplicados, presentando los principales avances y perspectivas para el fortalecimiento del mejoramiento de los millets pequeños.

Palabras clave: Cultivares Resilientes. Autogamia. Fenología Reproductiva. Sostenibilidad Agrícola.

1 INTRODUCTION

Small millets are a food crop domesticated about 5000 years ago in India (PATIL et al., 2024), which spread throughout the ancient civilization, being widely cultivated in the semi-arid tropical regions of Africa and Asia (RAMASHIA et al., 2025; UPADHYAY et al., 2025). It is an erect, self-pollinated and tetraploid annual plant (2n = 4x = 36), they are a type of cereal with tiny seeds belonging to the Poaceae family and the Panicoideae subfamily (LAKHANI et al., 2024; MISHRA et al., 2024).

Among pearl millets, small pearl millets form a distinct group, which includes finger pearl millet (*Eleusine coracana*), small pearl millet (*Panicum sumatrense), Italian pearl millet (Setaria italica*), common pearl millet (*Panicum miliaceum*), kodo pearl millet (*Paspalum scrobiculatum*), Japanese pearl millet (*Echinochloa frumentacea*), and brown pearl millet (*Brachiaria ramosa* (L.)) (TONAPI et al., 2022). The most cultivated millets are *Setaria italica* (foxtail millet), *Panicum miliaceum* (proso millet), *Panicum sumatrense* (little millet), *Eleusine coracana* (finger millet), *Paspalum scrobiculatum* (kodo millet) and several species of *Echinochloa*, which, despite being historically undervalued, have emerged again as strategic crops for agriculture in marginal environments (VETRIVENTHAN et al., 2020; KUMAR et al., 2024).

The high nutritional content combined with tolerance to limiting climatic conditions makes small pearls a relevant crop to ensure food and nutritional security, especially in contexts of abiotic stress (WELDEMICHAEL et al., 2024). Millet is an important source of dietary fiber, resistant starch, polyunsaturated fatty acids, and minerals such as Mg, P, Mn, Fe, and K (LAKHANI et al., 2024; RAMASHIA et al., 2025), which are crucial for human health and growth, and which are deficient in most cereals (BABU et al., 2013). In addition to being rich in nutrients and with a wide variety of phytochemicals, they are resistant to climate change and can grow even in extreme temperatures and in low-quality soils, without the need for external inputs (UPADHYAY et al., 2025). These cereals have gained prominence due to their hidden nutritional potential and better climate adaptability, being able to meet both nutritional demands and sustainability (UPADHYAY et al., 2025; SINGH et al., 2020).

Millet is a short-cycle plant, with high resistance to heat and has excellent recovery in periods of drought (CHERUKU et al., 2025; SATHYAMURTHY et al., 2024). Small millets have C4 metabolism and have better water use efficiency (USA), where photosynthesis in C4 crops is more efficient than in C3 plants, even under high light intensity and high temperatures (MUTHAMILARASAN et al., 2014). This crop has high efficiency and morphophysiological adaptations, such as a dense root system and antioxidant mechanisms, which ensure greater resilience to drought, heat, and low fertility soils, central attributes for agrifood systems under pressure from climate change (MURUGANANTHAM et al., 2024; KUMAR et al., 2024). Studies also show a wide intraspecific variability in pearl millets such as *Panicum sumatrense* and *Eleusine coracana*, which reinforces its potential as a source of adaptive variability for breeding programs (ARUNACHALAM et al., 2005; DABA & KENENI, 2010).

There is increasing advances in modern genomic approaches with small millets, which have allowed us to understand aspects of these crops that were previously little explored. Although they remain among the least investigated cereals from a molecular point of view, especially when compared to rice and wheat, new studies show progress in identifying genes associated with stress tolerance, water use efficiency, and nutritional quality (MISHRA et al., 2024). The use of molecular markers, diversity analyses, and comparative genomics tools has revealed significant genetic variability in species such as *Panicum sumatrense*, *Setaria italica* and *Eleusine coracana*, reinforcing their potential for breeding programs (LAKHANI et al., 2024). Despite this, there are still important gaps in the understanding of the genetic and physiological mechanisms that determine the wide adaptation of small pearl millets. The limitation of genomic panels, the scarcity of comparative studies, and the low investment in breeding programs for lesser-known species restrict the full use of their agricultural potential (MISHRA et al., 2024; LAKHANI et al., 2024).

Given this scenario, an updated review that summarizes the advances obtained between 2020 and 2025 in the areas of genetics, genomics, physiology, and improvement of small pearls is essential. Gathering this information is essential to guide new research and support initiatives aimed at food security, climate adaptation, and the sustainable use of these crops in vulnerable production systems. Thus, this work aims to critically analyze the recent literature on small millets, highlighting their potential, challenges and perspectives for future breeding programs.

2 METHODOLOGY

For the elaboration of this study, a literature review was carried out, which consisted of a careful and systematized analysis of relevant publications on the subject. This review allowed the identification, organization and discussion of the available knowledge, based on theoretical references from journals, books and magazines.

Searches were conducted in the following databases: SciELO, Web of Science, Scopus, Science Direct and Google Scholar. To locate studies related to small millets and genetic improvement, search terms such as "small millets", "genetic improvement", "germplasm diversity", "SNP markers in millets", "flower biology in millets" and "breeding strategies for minor cereals" were used. In addition, connectives through Boolean operators ("AND", "OR") were used to broaden or refine the search.

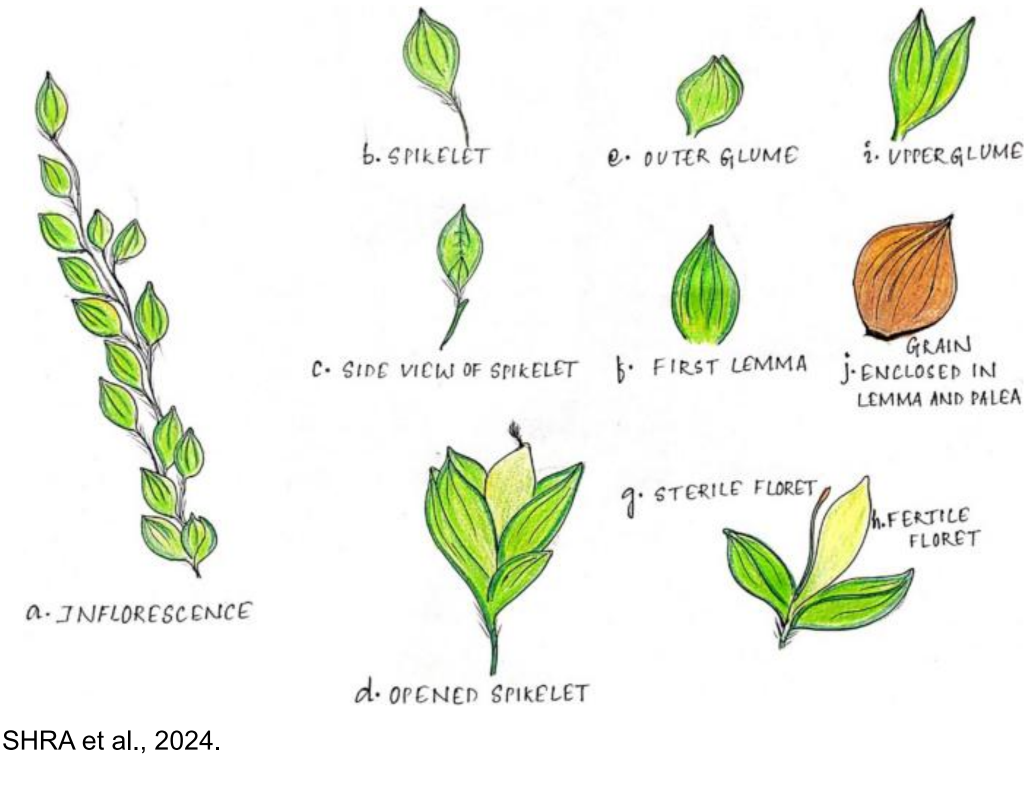
After this search, these articles were read and then this review material was made.

3 FLORAL BIOLOGY OF SMALL MILLETS

The floral biology of small millets is marked by the predominance of autogamy, often associated with cleistogamy, which directly influences gene flow, available variability, and breeding strategies. Small pearl millet has a strong prevalence of self-pollination, with natural crossing rates generally lower than 1%, occurring mainly by wind action (SHAMKUWAR et al., 2024). Flowering is mostly casmogamous, with pollination occurring before the flowers open, and the spikelets are composed of very small flowers: the lower one sterile and the upper one fertile or bisexual, which do not have prolongation of the rachilla, limiting the exposure of the reproductive organs (Figure 1) (PATIL et al., 2024).

Figure 1

Floral architecture of small millet



Source: MISHRA et al., 2024.

In addition to these characteristics, fertile flowers have three stamens with versatile anthers and two feathery stigmas that emerge quickly during anthesis, usually in the early morning. The extrusion of the anthers usually lasts a few minutes, and the rapid closure of the glumes prevents the entry of external pollen, reinforcing autogamy and hindering allogamy. The order of opening of flowers within the panicle varies between species, and may follow acropetal or basipetal patterns, which directly interferes with floral synchronism between plants and, consequently, with hybridization efficiency (Figure 2) (CHERUKU et al., 2024).

Figure 2

Floral biology of kodo millet: a) Dorsal side of the spikelet; b) Ventral side of the spikelet; c) Internal view of the spikelet; d) Arrangement of anthers and carpel on the lodicles; SSP - Subsessile Pedicel; G1 - Gluma 1; G2 - Gluma 2; L - Motto; P – Palea

Source: CHERUKU et al., 2025.

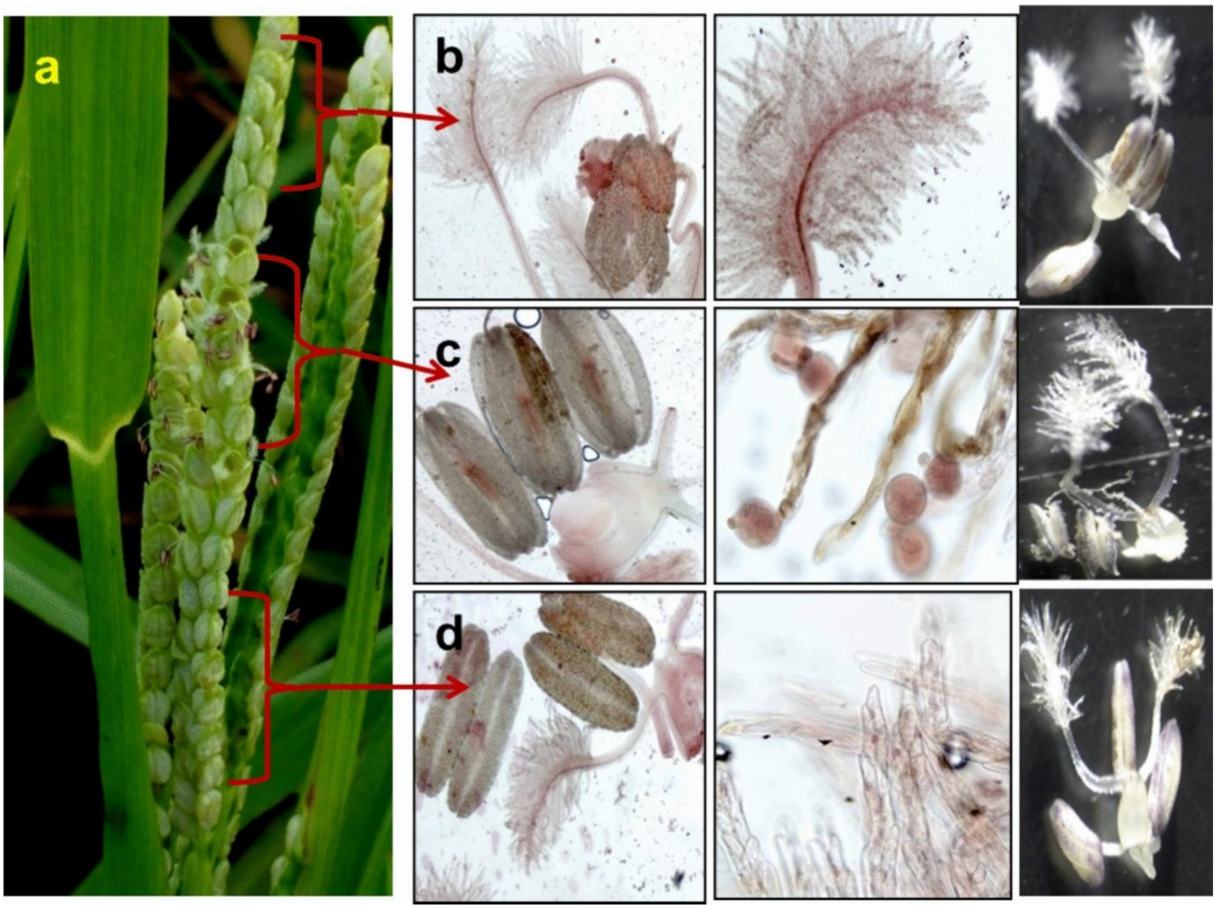
In the cultivation of small millets, different methods of emasculation and crossbreeding have been applied, although many cause damage to the stigma due to the delicate floral structure, reducing the efficiency of crosses and the production of viable F1 hybrids. To generate superior F1s, transgressive segregating lines or introduce alleles of interest in elite genotypes, breeding by recombination is essential; however, its success depends on efficient emasculation and crossbreeding techniques, especially in kodo millet (*Paspalum scrobiculatum* L.), which has high autogamy, highly cleistogamic spikelets, and almost zero natural crossing rates (SHAMKUWAR et al., 2024; CHERUKU et al., 2024; PATIL et al., 2024).

The flowers of small millets are very small and protected by rigid glumes, which limits floral opening and favors autogamy. Each spikelet has two flowers: the sterile lower one and the fertile upper one, composed of a monocarpella ovary, two feathery stigmas and three stamens with versatile anthers. The small size of the flowers and the rapid closure of the glumes after anthesis reinforce the predominant cleistogamy in these species (PATIL et al., 2024; SHAMKUWAR et al., 2024).

Anthesis occurs mainly in the early hours of the morning and lasts a few minutes, with rapid extrusion of the anthers and brief receptivity of the stigmas. The opening of the flowers follows acropetal or basipetal patterns depending on the species. This very short duration of anthesis and the rapid closure of the glumes reduce the allogamy and sustain the autogamous behavior of small millets (Figure 3) (CHERUKU et al., 2024). The reproduction of small millets is based on self-pollination, supported by partial cleistogamy, synchrony between anthers and stigmas, and protection of glumes. Cross-pollination, mediated by wind, is rare due to the short time of floral opening. Despite limiting gene flow, this system confers reproductive stability and ensures fertilization in dry environments with high climatic variability (SHAMKUWAR et al., 2024; KUMAR et al., 2024).

Figure 3

Floral opening pattern in the kodo pearl millet raceme: a) Anther dehiscence and pollen distribution in the stigma in b) Top, c) Middle, d) Base of the raceme



Source: CHERUKU et al., 2025.

In summary, the floral biology of small millets is characterized by very small flowers, strong autogamy and cleistogamy, ensures high reproductive efficiency in stressful environments, but limits natural breeding and hybrid breeding (GUPTA et al., 2011). This reduced structure makes conventional hybridization techniques difficult, reinforcing the need to understand anthesis dynamics and floral architecture to improve emasculation and crossbreeding methods (GANAPATHY et al., 2017). Therefore, deepening the study of the morphology and reproductive mechanisms of these millets is essential to enable more effective breeding programs (DWIVEDI et al., 2012).

4 BREEDING PROGRAMS FOR SMALL MILLETS

Breeding programs for small pearl millets have grown in recent decades, driven by the global need for crops that are more resilient to drought, heat, low soil fertility and nutritionally rich. Small millets are predominantly autogamous species, with very small and cleistogamic flowers, with a low rate of natural crossing, which limits spontaneous recombination and makes breeding more dependent on controlled strategies (PATIL et al., 2024; SHAMKUWAR et al., 2024). Given this scenario, the proper management of genetic resources is essential to maintain the diversity of these crops, ensuring their potential for use and improvement over time (ELANGOVAN et al., 2024).

Institutions dedicated to germplasm conservation, such as the Indian Millet Research Institute (ICAR-IIMR) are part of the network of National Active Germplasm Sites (NAGS), playing a central role in expanding the available genetic base with functions of collection, conservation, characterization, documentation and availability of millet genetic resources to authorized users in the country (ELANGOVAN et al., 2024; UPADHYAYA et al., 2025). In India, the All India Coordinated Research Project on Small Millets (AICRP-SM) plays a central role in the development of more productive, early, and drought-tolerant varieties, including biofortified strains with higher iron and zinc contents (MANE et al., 2024; SUTHAR et al., 2023).

On a global scale, FAO has reinforced, as of 2023, policies and initiatives aimed at germplasm conservation, database modernization, digital phenotyping, and encouraging the adoption of resilient cultivars, including millets in the "Millets for Nutrition and Climate Resilience" agenda (FAO, 2023). In Africa, national programs and efforts conducted by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) have prioritized lines adapted to degraded soils, high temperatures, and water deficit, integrating SNP markers, assisted selection, and functional genomics to accelerate the release of superior varieties (HABIYAREMYE et al., 2017).

Traditional breeding strategies include mass selection, selection of pure strains, and crosses between phenotypically superior accessions, practices compatible with the reproductive biology of these cereals (GANAPATHY et al., 2021; TONAPI et al., 2022). However, the difficulty of manipulating small flowers and synchronizing anthesis has led to the development of improved emasculation and hybridization techniques, such as the use of chemical agents, thermal emasculation, and methods based on plastic wrappings, which increase the efficiency in obtaining F1 hybrids (CHERUKU et al., 2025).

In recent years, molecular and genomic tools have become part of breeding programs, expanding the ability to identify genes and QTLs associated with drought tolerance, water use efficiency, productivity, and nutritional quality (MISHRA et al., 2024; HABIYAREMYE et al., 2017). Technologies such as high-density genotyping (GBS), comparative genome analyses, and diversity panels have strengthened marker-assisted selection, allowing for reduced breeding cycles and increased accuracy in the choice of superior genotypes (VETRIVENTHAN et al., 2020; WEN et al., 2024).

In addition to laboratory advances, participatory strategies have been adopted in agricultural communities, especially in regions of Africa and Asia, allowing the development of cultivars adapted to local conditions and with greater social and nutritional acceptance (GUPTA et al., 2011; RAMASHIA et al., 2025). The use of molecular markers, such as RAPD, ISSR, SSR, and SNP, has been one of the most efficient strategies to characterize diversity and support assisted selection, although their application is still incipient in many research programs (SUTHAR et al., 2025). Recent work also highlights the potential of genomics, transcriptomics, and gene editing to accelerate the development of more productive cultivars, adapted to abiotic stresses, and with higher nutritional value (MANE et al., 2024). This integration between modern science and traditional knowledge has amplified the impact of breeding programs and favored the adoption of new varieties.

Thus, breeding programs for small pearl millets have evolved from systems based exclusively on phenotypic selection to integrated approaches, which combine extended genetic variability, efficient hybridization, and high-resolution genomic tools (TONAPI et al., 2021; MISHRA et al., 2024; LAKHANI et al., 2024).

5 RECENT ADVANCES IN GENETIC IMPROVEMENT OF SMALL PEARL MILLETS

Small millets have been the subject of studies in recent years due to the increase in genetic studies and the strengthening of research programs in Asia and Africa. Germplasm analysis with modern tools, such as SNP markers and sequencing, showed that these species have wide genetic variability, an essential point for developing more productive and climate-adapted cultivars (HABIYAREMYE et al., 2017; MENSAH et al., 2024).

Among the most important advances is the use of marker-assisted selection, which makes it possible to locate regions of the genome associated with drought tolerance, yield, and nutritional quality. In species such as *Eleusine coracana* and *Setaria italica*, recent studies have identified genes linked to photosynthesis, stress resistance, and water use efficiency, helping to accelerate the selection process in breeding programs (ZHANG et al., 2024; LI et al., 2024).

Another relevant progress is the growth of digital phenotyping, which uses drones and sensors to measure plant characteristics quickly and accurately. This type of information facilitates the identification of superior genotypes and improves the integration between field data and genetic data (SUTHAR et al., 2023; MANE et al., 2024). In classical breeding, crossbreeding techniques are also being improved. New methods of emasculation have reduced stigma damage and increased the production of F1 hybrids, which is essential in predominantly autogamous species, such as kodo pearl millet (PATIL et al., 2024; SHAMKUWAR et al., 2024). Programs in India and East Africa have been able to develop genotypes richer in iron, zinc, and antioxidant compounds, with the support of genetic and gene expression analyses (FAO, 2023).

Thus, gene editing tools, such as CRISPR, are beginning to be tested to improve drought tolerance, grain size, and resistant starch content. Although they are still in their early stages, the results indicate that this technology can become a fast track to overcome the limitations of cleistogamy and expand genetic gains (ZHANG et al., 2024).

6 AGRONOMIC AND SOCIOECONOMIC APPLICATIONS OF SMALL MILLETS

Small millets have high agronomic relevance due to their ability to produce even under limiting environmental conditions, such as in arid and semi-arid regions of Africa and Asia where they tolerate drought, heat, and poor soils, outperforming cereals such as rice and wheat (VETRIVENTHAN et al., 2020; KUMAR et al., 2024). This resilience is associated with characteristics such as short cycle, high C4 photosynthetic efficiency, and the ability to explore deep soil layers, allowing better productive stability in water-stressed environments (WELDEMICHAEL et al., 2024; SINGH et al., 2020). In addition, these crops integrate well into agroecological systems, rotations, and intercropping, contributing to fertility recovery, increased organic matter, and reduced pests and diseases (DWIVEDI et al., 2021; UPADHYAY et al., 2025).

In the nutritional field, small millets are recognized as "nutri-cereals" because they have high levels of fiber, essential minerals (Fe, Zn, Mg, Ca) and bioactive compounds, making them strategic in the fight against malnutrition and anemia in vulnerable populations (RAMASHIA et al., 2025; LAKHANI et al., 2024). Global initiatives have promoted its inclusion in school feeding policies, biofortification programs, and more sustainable food systems, with emphasis on efforts by FAO, CGIAR, and ICAR-IIMR (FAO, 2024). Recent studies also reinforce the potential of pearl millets in the formulation of healthy industrialized products, expanding their acceptance in the urban market (MISHRA et al., 2024).

When analyzing the socioeconomic aspects, small millets play a crucial role in family farming and traditional communities in the semi-arid tropics, due to the low cost of production, reduced dependence on external inputs, and multiple uses, such as human consumption, feed, forage production, and artisanal food processing (HABIYAREMYE et al., 2017; RAMASHIA et al., 2025). Thus, the agronomic and socioeconomic applications of small millets reinforce their strategic role in global food security, in tackling climate change, and in promoting sustainable agricultural systems with low environmental impact.

7 GAPS, CHALLENGES AND FUTURE PERSPECTIVES IN THE IMPROVEMENT OF SMALL MILLETS

Despite recent scientific advances, the improvement of small pearl millets still faces important obstacles that limit the speed of genetic gains. There is a gap related to the reduced number of complete genomic studies for species such as *Panicum sumatrense*, *Paspalum scrobiculatum* and *Echinochloa frumentacea*. Therefore, the absence of robust sequencing and large panels of SNPs restricts the identification of genes associated with drought tolerance, stable yield, water use efficiency, and nutritional quality (LI et al., 2024; ZHANG et al., 2024).

Another challenge stems from cleistogamy, is the drastic reduction in natural crossing. This characteristic makes the hybridization process more complex, requiring precise emasculation techniques, often with low efficiency or risk of stigma damage. In species such as kodo millet, the production of viable F1 hybrids is still limited, which makes it difficult to recombine and generate lines with superior combinations of traits (PATIL et al., 2024; SHAMKUWAR et al., 2024; CHERUKU et al., 2024)

In addition, phenotypic evaluations are still insufficient in real agricultural environments. Most of the analyses are conducted under controlled experimental conditions, which do not adequately represent the climate variability faced by farmers in semi-arid regions. More recent studies highlight the importance of phenotyping, but the application of this technology in pearl millets is still restricted (SUTHAR et al., 2023; MENSAH et al., 2024). Integrating advanced phenotyping with genomic data is critical to unraveling the genetic basis of complex traits such as drought tolerance and water use efficiency (HABIYAREMYE et al., 2017).

In the field of nutrition, biofortification has been a global priority, with efforts aimed at increasing the levels of iron, zinc, phenolic compounds and dietary fibers. Even so, many small millets remain poorly characterized in terms of the nutritional content and stability of these components under stress conditions, which limits the development of biofortified cultivars adapted to different environments (FAO, 2023; WELDEMICHAEL et al., 2024; RAMASHIA et al., 2025).

For the future, the prospects are promising. Gene editing technologies, particularly CRISPR-Cas, are beginning to be explored to modulate genes related to plant structure, resistance to water stress, grain size, and improvement of nutritional quality. Although still at an early stage, studies already indicate that these tools can significantly accelerate genetic gains in small millets (ZHANG et al., 2024; LI et al., 2024). At the same time, initiatives coordinated by institutions such as ICAR, ICRISAT, AFRICARICE, and FAO are expanding germplasm banks, evaluating core collections, and promoting participatory programs that bring researchers and farmers closer together, especially in East Africa and India (FAO, 2023; MANE et al., 2024). Thus, the future of small pearl millet breeding depends on the integration of modern genomics, scale-up and characterization of genetic variability, advances in hybridization techniques, and the strengthening of international research networks.

8 FINAL CONSIDERATIONS

Small millets are consolidated as strategic crops for semiarid regions due to their high tolerance to abiotic stresses, nutritional value and wide adaptability. Recent literature highlights important advances in genomics, genetic diversity, and breeding methodologies, which have expanded the possibilities of selection and development of superior cultivars (ZHANG et al., 2024; LI et al., 2024). However, limitations such as cleistogamy, the still restricted genomic base, and the scarcity of multilocational phenotyping continue to limit the pace of genetic gains (PATIL et al., 2024; SHAMKUWAR et al., 2024).

Future prospects include greater integration between molecular tools, digital phenotyping, and international collaborative programs, especially initiatives led by FAO, ICAR, and ICRISAT, which have advanced in germplasm characterization and biofortification (ICRISAT, 2024; FAO, 2023). Emerging technologies, such as gene editing, should also accelerate breeding and contribute to more productive, nutritious, and resilient cultivars in the face of climate change (ZHANG et al., 2024).

Thus, strengthening genetic strategies, using advanced resources, and continuing global cooperation will be key to consolidating small pearl millets as essential crops for food security and sustainable agricultural systems.

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