

REVIEW ARTICLE

Small millets: A multifunctional crop for achieving sustainable food security under climate change

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Abstract

Millets, a varied collection of small-seeded crops from the Poaceae family, are re-emerging as a viable alternative for sustainable food and nutritional security in the context of climate change. Historically a staple in India, millet consumption declined during the Green Revolution due to emphasis on rice and wheat. However, their nutritional enrichment and climate resilience are rekindling interest. Over ten millet species, including sorghum, pearl, and finger millet, are cultivated globally and thrive in marginal lands with minimal water and low nutrients. Their C₄ photosynthetic pathway enhances wateruse efficiency, making them suitable for hot, dry climates. Despite their benefits, millets face challenges, such as consumer preferences for rice and wheat and vulnerabilities to extreme weather events. Nevertheless, they offer significant nutritional advantages, including high levels of dietary fiber, essential amino acids, vitamins, and minerals. India is a leading millet producer, cultivating various types and experiencing a recent production surge. Investigations into the resilience of millets underscore their capacity to endure environmental stresses. Strategies for improving millet crops include conventional breeding, mutation breeding, and advanced techniques like CRISPR-Cas9. Bio-fortification efforts aim to address micronutrient deficiencies, with promising results in finger millet varieties. Advancements in genetic engineering and genome editing tools are revolutionizing millet improvement. The pangenome concept, which explores genetic diversity within species, offers a framework for developing enhanced cultivars. Integrating wild millet varieties into breeding programs can further unlock their potential. Comprehensive policy initiatives supporting millet cultivation, research, and public awareness are crucial for promoting these nutrient-rich grains, enhancing food security, and fostering sustainable agriculture.

Keywords

millets; climate resilience; nutritional benefits; C₄ photosynthesis; biofortification; advanced breeding techniques

Introduction

Millets have re-emerged as a potential crop for sustainable food and nutritional security in the face of climate change. Once a staple food in India, their consumption declined due to the Green Revolution's focus on high-yielding cereals like rice and wheat (1). However, a renewed interest stems from their exceptional nutritional profile and remarkable resilience to harsh environmental conditions.

Over ten millet species are cultivated globally, including *Sorghum bicolor* (sorghum), *Pennisetum glaucum* (pearl millet), *Eleusine coracana* (finger millet), *Panicum sumatrense* (little millet), *Setaria italica* (foxtail millet), *Panicum miliaceum* (proso millet), *Echinochloa esculenta* (barnyard millet), *Paspalum scrobiculatum* (kodo millet), *Urochloa ramosa* (browntop millet), *Fagopyrum esculentum* (buckwheat millet), and *Amaranthus caudatus* (amaranth millet). These grains are categorized into naked (finger millet, pearl millet, sorghum) and husked (kodo millet, foxtail millet, little millet) varieties based on the presence or absence of a rigid outer hull (2).

Small millets demonstrate exceptional adaptability. Unlike major cereals with high fertilizer requirements, they thrive in marginal lands with low nutrient availability and minimal water resources. Their short life cycles, inherent pest and disease resistance, and extended shelf life contribute to their suitability for rain-fed regions of Africa and Asia, where millets were first domesticated millennia ago (3). Dwivedi et al. (4) highlight their remarkable tolerance to environmental stresses, including drought, heat, and low soil fertility. This resilience allows them to flourish in challenging environments where other crops struggle.

Millets possess a unique advantage in the form of the C4 photosynthetic pathway. Unlike the C3 pathway used by major cereals like rice and wheat, C4 photosynthesis employs a more efficient mechanism for carbon dioxide fixation. This allows millets to concentrate $CO₂$ around the enzyme responsible for its assimilation, boosting their photosynthetic efficiency, particularly in hot and dry environments (5). While the C4 pathway requires slightly more energy, the benefits outweigh the drawbacks. This enhanced efficiency translates into improved water-use efficiency, allowing millets to thrive in conditions where C3 plants struggle (6).

Beyond their hardiness, millets offer a plethora of nutritional benefits. They are rich in dietary fiber, essential amino acids, vitamins, and storage proteins (7). Despite these advantages, consumer preference for rice, wheat, and maize has limited millet consumption and research efforts due to factors like taste, texture and higher yields (8,9,10).

Asia and Africa remain the primary centers for millet production and consumption. India is the world's largest producer, accounting for roughly 80% of Asia's and 20% of global millet production. Notably, India cultivates all millet varieties and ranks the fifth-largest exporter (11, 12). Rajasthan, Maharashtra, Karnataka, Gujarat, and Madhya Pradesh lead millet production in India. Sorghum and pearl millet dominate Indian production, constituting nearly 90% of the national output (13, 84, 85). The remaining 10% comprises finger millet, proso millet, foxtail millet, and other small millet (Table 1, Figure 1). Encouragingly, India witnessed a 27% increase in millet production during 2021-22, reaching 15.92 million metric tons (14). This upsurge signifies a growing recognition of millet's potential in a climate-changing world.

Table 1: Area and production of millet worldwide (FAO, 2021)**.**

Figure 1. Status of millet production in India (84, 85)

Climate change poses a substantial risk to global food security since the heightened frequency and severity of extreme weather events such as droughts, floods and heat waves adversely affect agricultural production. Millets, however resilient, are not exempt from these problems. Prolonged droughts can induce water stress across various growth stages, affecting germination, flowering, and crucial grain development. Finger millet, in particular, exhibits sensitivity to changing rainfall patterns. Inconsistent or unpredictable rainfall can lead to uneven germination, hindered crop establishment and ultimately, reduced yields. Conversely, excessive rainfall events can create water-logging conditions, promoting the development of root rot diseases.

While climate change threatens crop productivity, millet can also play a vital role in mitigating nutritional deficiencies associated with changing weather patterns. Finger millet, for example, is a valuable source of iron and zinc, essential micronutrients often deficient in diets, particularly in developing countries. This inherent nutritional richness makes finger millet a promising candidate for biofortification programs, aiming to develop crops with enhanced micronutrient content (15). Recent research has identified fifteen potential candidate genes in finger millet that potentially regulate iron and zinc homeostasis. These genes, with high sequence similarity to their counterparts in major cereals like rice, wheat, maize, barley and foxtail millet, offer exciting avenues for biofortifying other cereal crops (16).

This review delves deeper into the scientific basis for millet resilience, exploring their physiological adaptations. It also emphasizes the scientific evidence of climate change's impact on millet production, introduces the concept of bio-fortification and highlights finger millet's potential in addressing micronutrient deficiencies.

Millets: Champions of Climate Resilience and Sustainable Agriculture

Millets emerge as powerful contenders in the fight against climate change due to their exceptional resilience to various environmental stresses. Stress, as defined by Dey & Raichaudhuri (17), refers to adverse environmental conditions that disrupt an organism's normal physiological processes. These stresses are abiotic (nonliving) or biotic (living). Abiotic stresses, including temperature extremes, drought, flooding, salinity and air pollution, are the leading culprits behind significant crop losses globally (18). Climate change poses an alarming threat, with these stressors becoming increasingly prevalent and severe (19).

Millets: Masters of Water Conservation

One of the most attractive qualities of millets is their exceptional drought tolerance. Unlike major cereals like rice and maize, which require significantly higher water inputs (20), millets thrive with considerably less water during their growth period (21). Typically, millet cultivation requires only 350-500 mm of water, contrasting rice's minimum requirement of 1100-1250 mm and maize's 800-1000 mm. This inherent water efficiency makes millets a beacon of hope in regions facing water scarcity. The over -dependence on rice cultivation, a system heavily reliant on irrigation, has significantly exacerbated water scarcity issues in various parts of India (22). By requiring significantly less irrigation, millets offer a sustainable alternative, reducing the strain on precious water resources (23).

Short Maturation Periods and Enhanced Efficiency

Millets possess a significant adaptation characterized by an exceptionally brief maturation time spanning 84 to 98 days. Barnyard millet enhances this efficiency by ripening in only 45 to 50 days, almost half the duration required for rice, which takes 120 to 140 days. This rapid growth cycle

Table 2: Various genes identified in millet conferring tolerance to abiotic stress.

allows millets to swiftly complete their life cycle, minimizing their vulnerability to prolonged drought.

Furthermore, millets possess the C_4 photosynthetic pathway, a powerful mechanism that enhances their ability to utilize water and nutrients efficiently (24). This pathway promotes water conservation and allows for adaptive biomass allocation, improved growth and superior tolerance to high temperatures.

Adaptability to Marginal Lands and Reduced Greenhouse Gas Emissions

Millets demonstrate extraordinary adaptability, thriving in marginal lands unsuitable for major cereals due to low nutrient content (25). Unlike major cereals requiring significant fertilizer inputs, millets exhibit remarkable nutrient-use efficiency, excelling in environments where other crops struggle. This characteristic expands the potential land area suitable for cultivation.

Moreover, compared to major cereals like wheat, rice, and maize, which rely heavily on synthetic fertilizers, millets require minimal to no fertilization (26, 27). This significantly reduces greenhouse gas emissions associated with fertilizer production and use, particularly nitrous oxide, a potent greenhouse gas released during nitrogen fertilization (28).

The combined attributes of drought tolerance, namely water efficiency, short maturation periods, reduced hydraulic conductivity per unit leaf area, and minimal fertilizer requirements, establish millets as successful model crops for climate-resilient agriculture. Millets possess several genes conferring tolerance to various abiotic stresses (Table 2). Their ability to thrive in marginal lands and their low greenhouse gas footprint further contribute to their environmental sustainability. The following section will delve deeper into the exceptional nutritional profile of millets and their potential to address dietary needs in a changing climate.

Global Status of Millet Germplasm Resources

The conservation of germplasm resources is paramount for safeguarding genetic diversity within a species. This diversity serves as a vital foundation for developing improved crop varieties with desirable traits, such as enhanced yield, disease resistance and improved nutritional content (29). Fortunately, a significant collection of small millet germplasm exists worldwide, with an estimated 133,849 accessions currently safeguarded in gene banks (30).

The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) plays a critical role in this conservation effort, meticulously preserving over 10,193 small millet germplasm accessions from 50 countries (31). Notably, Asia holds the majority of these conserved accessions (around 64.4%), followed by Africa (13.8%) and Europe (13.5%) (32). This geographic distribution reflects the historical centers of millet domestication and cultivation.

Specific millet varieties exhibit distinct conservation patterns. Foxtail millet germplasm, for instance, is primarily preserved in China, India, France, and Japan (33). Finger millet collections are mainly concentrated in India and various African nations like Kenya, Ethiopia, Uganda and Zambia. Proso millet, with roughly 29,000 accessions constituting the largest share of conserved germplasm, is predominantly preserved in Russia, China, Ukraine, and India (34). ICRISAT itself safeguards 849 proso millet accessions (35). Kodo millet and barnyard millet boast over 8,000 germplasm accessions, primarily conserved in India and the USA for kodo millet (36) and Japan and India for barnyard millet (37). Little millet germplasm, with around 3,000 accessions, is predominantly found in India (38).

India shows its strong dedication to the conservation of millet germplasm. As of 2022, the ICAR-Indian Institute of Millet Research (IIMR) has meticulously preserved 48,462 millet accessions within their Millet Gene Bank (MGB). Furthermore, recent reports indicate the characterization of 5472 sorghum and small millet germplasm accessions (39).

Strategies for Millet Improvement: Conventional and Advanced Techniques

Small millets, characterized by self-pollination, offer a unique opportunity for crop improvement through various breeding methods. Pedigree selection, a cornerstone of conventional breeding, has significantly influenced millet variety development. This approach involves selecting desirable traits from indigenous landraces and refinement through controlled hybridizations and subsequent selection cycles. It has resulted in the release of 248 small millet varieties across six species (Kodo millet, barnyard millet, finger millet, foxtail millet, proso millet, and little millet) in India. Additionally, the USA has released 19 proso millet varieties using similar methods. However, hybridization for harnessing heterosis (hybrid vigor) presents challenges due to small millets' floral morphology and anthesis behavior. The development of male sterile lines offers a potential solution to exploit heterosis. Currently, finger millet has a single documented male sterile line, INFM 95001, utilizing a Genetic Male Sterility (GMS) system derived from mutagenesis (31).

Mutation breeding emerges as another valuable tool in overcoming these limitations. This technique has led to the development of 13 small millet cultivars in India, with a focus on finger millet (8 cultivars), kodo millet (3 cultivars), and little millet (2 cultivars). Notably, a study by Rodiansah et al. (47) demonstrated the successful induction of polyploidy in foxtail millet, resulting in plants with altered morphology (more diminutive stature and seed production) but possessing larger leaves, panicles, and bolder seeds. This approach holds promise for exploring novel traits.

Double haploid (DH) technology offers a powerful tool for accelerating breeding by significantly reducing generation times (48). In foxtail millet, CRISPR-Cas9 technology has been successfully employed to manipulate the SiMTL gene, creating a haploid inducer line (49). This advancement paves the way for developing DH lines in foxtail millet, potentially expediting breeding cycles (84, 85).

The Rise of Advanced Breeding Techniques

Recent breakthroughs in genome editing tools like zincfinger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and the CRISPR/Cas system have revolutionized crop improvement (50). The potential of CRISPR is exemplified by the development of "Xiaomi," a foxtail millet mutant with a shortened life cycle and reduced stature, enabling researchers to achieve five to six generations annually in controlled environments. This distinctive attribute makes Xiaomi a C4 model plant, an excellent research instrument, like *Arabidopsis* as a C3 representative. Moreover, CRISPR offers the exciting prospect of precisely targeting specific Quantitative Trait Loci (QTLs) associated with desirable agronomic traits, enabling the development of improved millet varieties (51).

Genetic Engineering for Enhanced Traits

The first attempts at genetic modification in finger millet involved the introduction of the prawn pin gene, conferring resistance against the fungal pathogen *Pyricularia grisea* (52). Similar approaches have been employed to express rice chitinase (chi11) for resistance against leaf blast disease (53). Furthermore, transgenic finger millet lines expressing serine-rich protein (PcSrp) and mannitol-1-phosphate dehydrogenase (mtlD) have demonstrated enhanced salt and drought tolerance (54). Notably, Ramegowda et al. (2013) (55) successfully developed transgenic finger millet plants (f35S and fBx17) expressing OsZIP1, leading to a significant increase in zinc and manganese accumulation. Recently, Agrobacteriummediated transformation has been established in kodo millet (56). These successful applications in finger millet and kodo millet provide a foundation for extending genetic modification approaches to other small millets, accelerating their improvement (31).

Biofortification: Addressing Micronutrient Deficiencies

Efforts are underway to establish biofortified small millet cultivars by traditional breeding and recombinant DNA technology to combat micronutrient deficiencies in developing countries. Finger millet varieties like VR-929 (Vegavathi), CFMV-1 (Indravati), CFMV-2, and little millet CLMV-1 (57) are examples of successful biofortification initiatives. These efforts hold immense potential for improving nutritional and food security in vulnerable populations.

Pan Genomics and Unleashing Millet Potential

The pangenome concept serves as a robust framework for understanding the complete genetic makeup of a species. It covers both the core genome, shared by all individuals, and the accessory genome, exhibiting variation among individuals (58). This approach provides comprehensive information on genomic diversity, including conserved elements essential for species survival and variable elements contributing to phenotypic variation. While the super-pangenome concept delves into genetic diversity across an entire genus, its application to small millets remains unexplored. Integrating wild millet varieties into breeding programs is significant for unlocking these crops' resilient potential. Their genetic diversity can be valuable for breeders seeking to develop improved cultivars with enhanced traits (59).

Using the pangenome approach, breeders can identify and incorporate advantageous genes from landraces and wild relatives into cultivated varieties, thus developing superior cultivars with enhanced traits such as higher yields, improved nutritional content, and better stress tolerance (59). This approach has been successfully applied in other crops and could significantly accelerate genetic improvements in small millets. Breeders can develop improved cultivars with improved traits by harnessing the genetic diversity within the species and wild varieties. Furthermore, policy initiatives promoting millet cultivation, research and public awareness play a crucial role in the broader adoption and consumption of these nutrient-rich grains. This multifaceted approach holds immense promise for enhancing food and nutritional security and promoting sustainable agricultural practices.

Challenges and Limitations of Millets

Although millets are abundant in nutritional value and climate tolerance, various hurdles impede their broad adoption and use. A key limitation is the existence of antinutrients, including tannins, polyphenols, phytic acid, and enzyme inhibitors (specifically trypsin and amylase inhibitors), which markedly diminish the bioavailability of essential minerals (73). These antinutritional factors can limit nutrient absorption, potentially negating the inherent nutritional advantages of millets (74). Phytates, for instance, bind to minerals and inhibit their absorption, while tannins can reduce protein digestibility. These compounds pose challenges, especially in populations that rely heavily on millet as a staple food and are at risk of mineral deficiencies. Addressing these challenges involves exploring processing techniques such as germination, fermentation and malting,

which have been shown to significantly reduce antinutrient levels in millets. For example, fermentation can lower phytate content by up to 40%, improving mineral bioavailability. Further breeding efforts to minimize these antinutrients in millets, thereby enhancing their nutritional value, may help promote their utilization as a reliable source of dietary minerals (75). Future research may include identifying genetic variants with naturally low antinutrient levels, developing biofortified varieties that maintain high nutrient content while minimizing antinutrients, and exploring enzymatic treatments that break down antinutrients during processing.

Another critical challenge lies in the insufficient conservation efforts for certain millet varieties. While finger millet, foxtail millet and proso millet germplasm are relatively well-represented in global gene banks, other small millets face a significant conservation gap. This leads to the potential loss of valuable landraces as farmers shift towards cash crops and improved varieties of widely cultivated cereals (72).

Millet production is also significantly hampered by various biotic stresses, which pose a substantial threat to small-scale farmers' livelihoods and necessitate the development of resistant cultivars to enhance the overall efficiency and sustainability of millet farming systems (76). Blast disease, for instance, can cause yield losses of up to 88% in finger millet. Similarly, blast, rust and smut pose significant threats to foxtail millet, while proso millet suffers from sheath blight, bacterial spot and head smut. Other small millets, including barnyard millet, kodo millet and little millet, are susceptible to grain and head smut, leaf spot diseases and shoot fly infestations (77). Stem borers further attacks, particularly for finger millet and barnyard millet cultivation.

Lodging presents another challenge in millet cultivation. Stem weakness, improper crop management practices, and unfavorable environmental conditions can contribute significantly to lodging. This can lead to severe yield and quality losses, emphasizing the need for developing cultivars with enhanced lodging resistance, enabling them to withstand challenging environmental conditions (78).

Grain shattering, where mature seeds detach prematurely from the panicle, is another critical factor contributing to yield losses in millets. This phenomenon reduces harvest efficiency and seed quality. Breeding programs focused on developing shattering-resistant or shattering-tolerant small millets are crucial to minimize yield losses and ensure the sustainability of millet-based farming systems.

Thus, overcoming these challenges through targeted research efforts on antinutrient reduction, germplasm conservation, disease and pest resistance breeding, lodging resistance improvement and the development of shattering -tolerant varieties is essential to unlock the full potential of millets and promoting their widespread adoption for more sustainable and food-secure future.

Opportunities

Nutritional Powerhouses for Combating Malnutrition

Small millets are a treasure trove of essential nutrients, boasting high levels of iron, calcium, zinc, and dietary fiber. Finger millet, for example, contains around 364 mg of calcium per 100 g, significantly higher than other cereals like rice and wheat. This makes it an excellent option for addressing calcium deficiency, particularly in children and women prone to osteoporosis. Similarly, small millets like kodo and barnyard millet provide 3.5-4 mg of iron per 100 g, helping alleviate anemia in regions with iron-deficient diets. The high dietary fiber content, especially in foxtail millet (8.0 g/100 g), supports digestive health and helps regulate blood sugar levels, making millet a beneficial addition for diabetic individuals (79). This unique nutritional profile positions them as a powerful tool for combating deficiencies in regions facing micronutrient malnutrition (Table 3). Their inclusion in dietary regimes can significantly improve overall nutrition and well-being, particularly in vulnerable populations.

Promoting Biodiversity and Sustainable Agriculture

Cultivating small millets offers a valuable strategy for conserving biodiversity. Compared to major cereal crops, they have a demonstrably lower environmental impact. Conservation of genetic diversity also ensures the preservation of essential traits such as nutrient use efficiency, early maturation and stress tolerance, which are vital for food security in regions facing climatic uncertainties (80). Integrating them into agroecological farming systems promotes sustainable agricultural practices by fostering crop diversity within ecosystems. This diversification enriches the agricultural landscape and enhances the resilience of agricultural systems in the face of environmental challenges.

Enhancing Crop Rotations and Diversification

The incorporation of small millets into crop rotation strategies presents a multifaceted benefit. These rotations disrupt the life cycles of pests and diseases associated with major cereal crops, thereby improving pest and disease management. Millets' genetic diversity and pest resistance help reduce disease pressure, as they are generally less affected by common pests and diseases of major cereals like rice and wheat. Small millets enhance soil fertility by improving organic matter content and promoting microbial

activity. Their extensive root systems help break down compacted soil, facilitate better water infiltration, and increase soil aeration. Their minimal requirement for external inputs, such as fertilizers, makes them suitable for low-input farming systems, promoting sustainable and resilient agricultural practices (81). This approach fosters a more sustainable and resilient agricultural landscape.

Catering to Health and Wellness Trends

The growing consumer awareness of the nutritional value of millet has opened up a vast market potential for milletbased products. These include innovative food items such as gluten-free snacks, healthy beverages, and nutritious flours. Millets are particularly well-suited for individuals managing diabetes due to their low to moderate glycemic index and high dietary fiber content (82). These factors contribute to better blood sugar control and promote overall health, aligning perfectly with the growing focus on preventive healthcare and functional foods.

Fueling Research and Development

Millets present a fertile ground for ongoing research and development endeavors. Exploring avenues for crop improvement, including breeding for enhanced yield, increased disease resistance and superior nutritional quality, holds immense promise. Additionally, advancements in processing technologies and the development of optimized agronomic practices can further streamline small millet cultivation, making it a more attractive proposition for farmers (83).

Strengthening Food Security in Marginalized Regions

Small millets demonstrate remarkable adaptability, thriving in challenging environments where mainstream crops struggle. Their suitability for cultivation in marginalized and remote areas makes them a crucial contributor to food security and livelihood improvement for populations in such regions (1). By promoting the cultivation and consumption of small millets, we can empower vulnerable communities and build more resilient food systems.

Consequently, little millets present significant opportunities to tackle critical problems in global food security, nutrition and agricultural sustainability. By harnessing their potential through targeted research, development and market expansion efforts, we can unlock a brighter future for food systems and human health.

Table 3: Nutrient composition comparison of small millet and fine cereals per (100 g)

Conclusion

Despite sometimes being referred to as "orphan crops" due to their lower yields than major cereals, small millets hold immense potential for sustainable agriculture and enhanced food security. They offer a critical lifeline for subsistence farmers, providing sustenance with minimal resource requirements. Their integration into diversified cropping systems alongside other crops can significantly enhance soil health and reduce reliance on chemical inputs. This diversification fosters a more resilient and sustainable agricultural landscape.

Establishing robust millet-based value chains presents a compelling strategy for creating sustainable market opportunities. Investments in millet processing and marketing infrastructure can empower farmers by improving market access and stimulating economic growth in rural areas. As we strive towards a more sustainable agricultural future, embracing millets offers a powerful solution for fostering resilience, preserving biodiversity, and safeguarding cultural heritage.

Millets are renowned for their remarkable adaptability and resilience, thriving in diverse and often challenging environmental conditions, including droughtprone regions and low-nutrient soils. Their frugal water requirements make them well-suited for cultivation in arid and semi-arid areas. Additionally, millets boast a superior nutritional profile and are rich in dietary fiber, essential amino acids, vitamins, and storage proteins. Notably, their utilization of the C4 photosynthetic pathway enhances their overall photosynthetic efficiency. These characteristics render millet a significant asset for creating biofortified foods amid the problems posed by climate change. Moreover, their suitability for low-input agriculture makes them an excellent solution for implementing climate-smart management techniques.

In conclusion, adopting small millets in agricultural practices presents many benefits for farmers, consumers, and the environment. Their role in promoting sustainable agriculture, enhancing food security, and fostering climate resilience necessitates further research, development, and market expansion efforts. By harnessing the full potential of these versatile grains, we can cultivate a brighter future for food systems and global well-being.

Authors' contributions

SK, HS: Original drafting of the manuscript

AK, HSJ, SM, PS, AMC: Review and editing

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