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REVIEW ARTICLE

Millets and pseudocereals: A treasure for climate resilient agriculture ensuring food and nutrition security

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Abstract

Once, a staple food for civilizations and a popular feed for centuries, millets are a treasure trove of micronutrients and essential amino acids. Despite being side-lined during the Green Revolution, these small-seeded powerhouses are perfectly adapted to harsh dryland conditions such as low rainfall, drought, and high temperatures. The millets require minimal maintenance and thrive under stress, showcasing their rich genetic diversity and adaptability. However, boosting genetic gain and developing high-yielding varieties remains a challenge due to restricted research, limited genomic tools, poor market demand and accessibility to germplasm. As our climate and cropping systems are changing, millets offer a promising solution for diversification and adaptation. Beyond their impressive nutrition, they possess therapeutic benefits, making them valuable for medicinal purposes. However, the cultivation of millets, especially the minor millets, has declined due to their underutilization in daily diets. Genetic improvement and application of modern technologies are needed to increase production and integrate these millets as alternative food sources in Indian cuisine. Fortunately, growing awareness of their nutritional value, health benefits, and industrial uses is fuelling a revival. Recognizing their potential, national and international organizations are working to restore millet cultivation. The United Nations even declared 2023 as the "International Year of Millets" at Indian initiative. This review highlights the progress made in the genetic improvement of both major (sorghum, pearl millet, finger millet) and minor millets (foxtail, proso, kodo, barnyard, little and browntop millets). Additionally, pseudo-cereals like buckwheat and amaranth are included. The areas of future research have also been indicated for urgent attention and immediate action to make millets and pseudo-cereals a household food ensuring food and nutrition security and climate resilient agriculture in India.

Key words: Millets, alternative food, micronutrient, environmental stress, genetic improvement

Introduction

India's vast agricultural landscape faces a harsh reality: aridity, erratic rainfall, and scorching temperatures. Nearly half the farms rely solely on monsoons, leaving them vulnerable to climate change's whims. This is where science steps in. New strategies are crucial to help farmers cope with droughts, rising temperatures, and unpredictable weather patterns. Adapting farm policies to these evolving risks is essential, especially as extreme weather events intensify with each degree of global warming.

Rice, wheat, and maize, the current dominant crops, guzzle water, impacting water tables and electricity costs. Incentives to shift from these water-intensive crops to millets could be a game-changer. M.S. Swaminathan said-"Millets are not only nutritious but are also climate smart in the sense that they are more resilient to rainfall distribution". Long considered a non-staple, millets have gained global recognition as "nutri-cereals" due to their superior nutritional profile and climate resilience. In fact, the UNO declared 2023 the International Year of Millets, highlighting their potential.

The different types of millets are grown in about 131 countries and serve as traditional food for 590 million people

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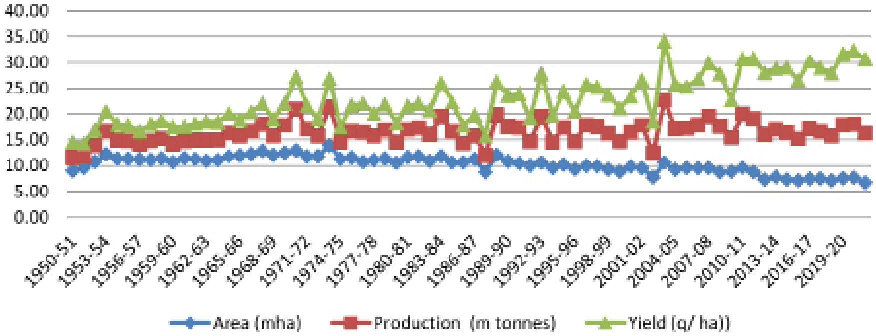


Fig. 1. Trends in area, production and productivity of pearl millet during 1950-51 to 2020-21

in Asia and Africa. India produces 170 lakh ton (80% of Asia's and 20% of global production. The global average yield is 1229Kg/ha as compared to India (1239 Kg/ha). However, incorporating millets into daily diets remains a challenge. While chefs and experts report growing acceptance, widespread integration requires overcoming hurdles like low productivity limiting availability, processing technologies, and ingrained food habits. Millets offer a niche market for now, but their potential impact on larger populations depends on demand, particularly among the middle and lower classes.

With their ancient cultivation history dating back to the Indus Valley civilization, Millets offer a unique opportunity (Singh 2023). Despite their nutritional superiority and drought tolerance, they were overshadowed by wheat and rice. Recognizing their potential, India is the world's largest producer, but the area under cultivation has declined. Reversing this trend requires a comprehensive approach. Greater research, advanced farming methods, quality seeds, mechanization, and training are crucial. Clinical trials to validate millets' medicinal properties could further elevate their status in human diets and animal feed. Their ability to thrive on poor soil with minimal chemical inputs makes them a sustainable alternative for food and nutrition security. Harnessing the potential of millets requires a multi-pronged approach. By addressing challenges, educating the public, and investing in infrastructure and research, India can transform these ancient grains into a powerful tool for climate-resilient agriculture and improved nutrition for millions. Therefore, the present review deals with the current status of grain and fodder production, productivity, and breeding, including heterosis breeding, mutation, molecular breeding and recent trends of developments in major millets (pearl millet, sorghum and finger millet), minor millets (finger millet, foxtail millet, proso millet, kodo millet, barnyard millet, little millet and browntop millet) and pseudocereals (amaranth and buckwheat).

Pearl millet

Pearl millet (*Pennisetum glaucum* (L.) R. Brown, [= *Pennisetum typhoides* (Burm.) Stapf et Hubb., and *Pennisetum americanum* (L.) Schumann ex Leeke] ($2n = 2x = 14$, genome AA) belongs to Poaceae (Graminae) family. Its relative species, Napier grass (*P. purpureum* Schum.) is tetraploid ($2n = 4x = 28$, genome AABB) valuable for its fodder grown throughout the world. Pearl millet, a valuable grain and forage crop serves as a staple food for millions in arid and semi-arid regions of Asia and Africa (Rai et al. 2012). It thrives under harsh conditions where other cereals struggle, making it crucial for food security. Key characteristics of pearl millet includes: a). Drought and heat tolerance- adapted to low rainfall and high temperatures, making it ideal for dry land agriculture; b). Nutritional profile- rich in protein, resistant and slowly digested starch, essential fatty acids, and micronutrients like iron, zinc, and vitamins. It also boasts a low glycemic index and is naturally gluten-free; c). High yielding hybrids: offers significant yield advantages compared to traditional varieties through the utilization of cytoplasmic male sterility (CMS) systems (Burton 1965; Athwal 1966). Despite its numerous benefits, pearl millet cultivation area has declined in recent decades (Fig. 1). However, currently, a significant increase in production and productivity of pearl millet has been noticed (Fig. 1). With its high nutritional value and increasing awareness, it has the potential to regain its importance. Increasing the adoption of high-yielding and adaptable varieties and hybrids can further enhance its contribution to food security and nutrition.

Origin and domestication

Pearl millet's wild ancestor is believed to be *P. glaucum* subsp. *monodii*, native to the Sahelian region of Africa (Harlan 1975; Brunken 1977). The exact location and timing of its domestication are still debated, with some suggesting multiple events in the region (Harlan 1975; Portères 1976). Evidence suggests the earliest domestication occurred around 3000 BC in northern Ghana (D'Andrea and Casey 2002). Following domestication, it is hypothesized that migrating populations in sub-Saharan regions contributed to the crop's secondary diversification in the eastern Sahel (Tostain et al. 1987; Tostain 1992). Genetic analyses using isozymes and simple sequence repeats (SSRs) suggest a single origin (monophyletic) for domesticated pearl millet, with cultivated and wild forms sharing many similarities (Mariac et al. 2006a, 2006b; Oumar et al. 2008; Kapila et al. 2008). However, molecular profiling also reveals that 81% of alleles and 83% of genetic diversity found in wild pearl millet are absent in cultivated varieties (Oumar et al. 2008). This decrease in diversity is likely a consequence of domestication selection favoring specific traits. Interestingly, some studies (Robert et al. 2011) suggest that gene flow between domesticated and wild populations may have helped maintain genetic diversity within the domesticated gene pool.

Agro-climatic zones of pearl millet in India

There are three zones named as Zone A1, A and B. Descriptions are as follows:

- Zone A1: This zone covers the drier regions of Rajasthan, Gujarat, and Haryana with light sandy soils, high temperatures, and drought conditions. The average yearly rainfall in this zone is less than 400 mm. Pearl millet cultivars grown here need to be early maturing and drought-tolerant. This zone encompasses over half of India's total pearl millet cultivation area.
- Zone A: This zone includes parts of Rajasthan, Gujarat, Haryana, and northern regions like Uttar Pradesh, northern Madhya Pradesh, Punjab, and Delhi. The average yearly rainfall in this zone exceeds 400 mm. The soils range from sandy to sandy loam, and some areas have irrigation facilities. This zone accounts for around 25% of the total pearl millet plantation in India.
- Zone B: This zone covers the southern states of Andhra Pradesh, Tamil Nadu, Telangana, Maharashtra, and Karnataka. The average yearly rainfall in this zone also exceeds 400 mm. The zone has relatively thick soils and a milder climate compared to zones A1 and A. The days in this zone are shorter than those in zones A1 and A. Zone B represents nearly 25% of India's total pearl millet acreage.

Brief history of pearl millet breeding in India

Pearl millet breeding in India began in the 1930s, utilizing traditional landraces and simple mass selection to improve existing genetic diversity. The establishment of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in the 1970s marked a shift towards systematic breeding. ICRISAT facilitated access to a vast germplasm collection, particularly from Africa (Gill 1991; Witcombe 1999). This diversity allowed breeders to create populations with broad genetic bases and diverse breeding lines, developing several new varieties and composites (Rai and Anand Kumar 1994; Rai et al. 2006). While heterosis (increased vigor in hybrids) was observed in pearl millet, its exploitation was initially hampered by the hermaphroditic nature of flowers (Athwal 1966). This hurdle was overcome in the 1950s with the discovery of cytoplasmic male sterility (CMS) in the US (Burton 1965). This, combined with the identification of suitable fertility restorers from Indian germplasm, paved the way for the development of commercial pearl millet hybrids. Studies on different CMS systems (A1, A4, and A5) have been crucial for efficient hybrid development and seed production. Research on inheritance patterns continues to improve this process (Yadav et al. 2010; Chandra et al. 2022; Gupta et al. 2012a, 2018; Jorben et al. 2020; Thribhuvan et al. 2021). Alongside hybrid development, Indian and African germplasm have been valuable resources for improving various traits. These include early maturity, tillering ability, panicle size, grain weight and color, disease resistance, and fertility restoration (Andrews and Anand Kumar 1996; Rai et al. 2009a; Yadav et al. 2012c; Patil et al. 2020).

Different phases of pearl millet improvement in India

Pre-hybrid phase (1950-1966)

Prior to 1950, farmers used local landraces, and few attempts were made to improve them through simple mass selection. The selections, namely, Vansari, Kopargaon Local, N 28-15-1, Co 1, K 1, Co 2, Co 3, AKP 1, AKP 2, RSJ, RSK and T 55 were made available for cultivation; a few of them, such as S 530 and Pusa Moti were developed using simple mass selection in African populations. Some non-commercial "chance hybrids" arose during this period, showing yield potential, but lacked proper seed production and adaptability. This phase saw the development of 13 improved cultivars (3 hybrids and 10 OPVs) with an average productivity increase of only 4.5 kg ha-1 per year.

Second phase (1967-1983)

The discovery of cytoplasmic male sterility (CMS) and compatible fertility restorers revolutionized breeding. The availability of male sterile lines, Tift 23A, Tift 18A, L 66A and L 67A facilitated the hybrid development. Male sterile lines like Tift 23A enabled the development of the first commercial hybrid, HB 1, followed by others like HB 3. This phase also saw the release of 13 new varieties and 16 hybrids. Widespread adoption of hybrids led to production reaching a record 8.0 million tonnes in 1970, compared to 3.5 mt in 1965. The ICRISAT initiated work on developing OPVs and population improvement alongside hybrid breeding (Kumara et al. 2014). This phase saw an average productivity increase of 6.6 kg ha-1 per year.

Third phase (1984-2000)

This phase emphasized diversifying parental lines and improving their downy mildew resistance. New male sterile lines, like 5071A, were developed to combat susceptibility in existing hybrids, but faced limitations. Lines 5141A and 5054A offered better resistance and were widely used in hybrids like BJ 104, BK 560, and CJ 104. Private sector involvement began in the mid-1980s, leveraging breeding materials from research institutions. ICRISAT shifted focus from OPV development to hybrid parent development to align with regional and commercial interests. However, some challenges and concerns still remain, which include: a). While downy mildew incidence was reduced, lack of diversity in parental lines remained a concern; b). Reliance on a few male sterile and pollinator lines like Tift 23A, 5141A, and J 104 contributed to vulnerability; c). This highlighted the need for diverse genetic backgrounds in future breeding programs;

d). The average productivity increased significantly to nearly 19.0 kg ha-1 per year during this phase.

Fourth phase (2001 onwards)

This phase has seen a strong focus on using a wide range of diverse parental lines in large numbers. This strategy aims to develop hybrids specifically adapted to different agro-climatic zones. Over the last two decades, this approach has led to the release of 20 new varieties and a remarkable 105 hybrids. The involvement of diverse male sterile lines and pollinators has been crucial. Commercial seed companies have played a role in increasing the genetic diversity of pearl millet hybrids. This diversified approach has effectively controlled downy mildew outbreaks, leading to a significant productivity jump to 31.1 kg ha-1.

Breeding for biotic stresses in pearl millet

Downy mildew, caused by the fungus *Sclerospora graminicola* (Sacc.) J. Schröt., is the most significant threat to pearl millet production, causing yield losses of 20-80% (Singh 1995; Wilson et al. 1996). This disease severely impacted high-yielding hybrids introduced in the late 1960s (Singh 1995). The first widespread outbreak in 1971 drastically reduced grain yield of the widely adopted hybrid HB 3 by 4.6 mt (Singh 1995).

Utilizing diverse parental lines has proven crucial in reducing downy mildew outbreaks. This strategy was implemented in the fourth phase of breeding (2001 onwards) with great success. Researchers have identified dominant genes and quantitative trait loci (QTLs) associated with downy mildew resistance. This knowledge informs breeding programs to incorporate resistant germplasm from sources like 834B, IP 18294-P1, and IP 18298-P1 (Chandramani et al. 2018). The lines, 834B and IP 18294-P1 exhibited resistance that is controlled by a single dominant gene, while IP 18298-P1 possesses two dominant genes. Interestingly, one of these dominant genes in IP 18298-P1 is allelic to the resistance gene in 834B, while the other is allelic to the resistance gene in IP 18294-P1 (Chandramani et al. 2018).

While historically considered minor, blast, caused by the fungus *Magnaporthe grisea*, has emerged as a significant concern in recent years. Though downy mildew resistance has previously been a higher priority, breeding programs are increasingly incorporating blast resistance screening due to its growing prevalence. This effort is aided by the identification of single dominant resistance genes (Gupta et al. 2012b; Mallik et al. 2021).

Ergot, caused by the fungus *Claviceps fusiformis*, is a significant disease of pearl millet in India. It reduces yield by replacing grains with toxic, alkaloid-containing sclerotia and renders the grain unfit for consumption (Yadav and Rai 2013). These soil borne and local weather conditions heavily influence airborne disease. Understanding resistance is crucial for managing ergot. Research suggests the genetic control of ergot resistance is complex, potentially involving interactions between the nucleus and cytoplasm, while initial concerns linked ergot susceptibility to the A1 cytoplasm used in male-sterile lines, further studies revealed the association lies with cytoplasm-mediated male sterility itself, not the A1 cytoplasm specifically (Yadav and Rai 2013). Additionally, ergot resistance is a polygenically controlled recessive trait, making it challenging to breed for resistance.

Limited availability of ergot-resistant lines necessitates creative breeding strategies. Researchers have successfully developed resistant lines by selecting and interbreeding moderately resistant/less susceptible lines (Yadav and Rai 2013). Over time, these lines have demonstrated high resilience in various regions of Western Africa and India. Researchers assessed the agronomic traits and disease response of around 300 ergot-resistant inbred lines and populations to further combat ergot. This facilitated the development of ergot-resistant composites and paved the way for ergot-resistant male-sterile lines, crucial for producing hybrid seeds in ergot-prone areas. Through pedigree breeding, ergot resistance has been successfully introduced into the genetic backgrounds of agronomically elite crops, resulting in the development of ergot-resistant male-sterile lines like ICMA 91333, ICMA 91444, and ICMA 91555 (Yadav and Rai 2013).

Similar advancements have been made in breeding for smut resistance. The pedigree-bulk breeding method has proven successful in introducing resistance from previously unsuitable materials into economically viable male-sterile lines (Yadav and Rai 2013). The first smut-resistant male-sterile line developed using this method was ICMA 88006, highlighting the effectiveness of this approach. Furthermore, ICRISAT has developed additional smut-resistant male-sterile lines, demonstrating the continued success of this breeding strategy (Yadav and Rai 2013). The resistance mechanism involves a simple recessive “tr” allele, which conditions trichome lessness on most above-ground plant parts, including the stigmas, thereby providing a useful level of smut resistance.

Rust, caused by *Puccinia substriata* var. *pencllariae*, is generally a minor problem in pearl millet, appearing late in the grain filling stage. However, early infections can significantly impact grain yield and fodder quality. Published research reports suggested variable severity and yield impacts across regions. Wilson et al. (1996) observed rust severity from 0 to 33%, whereas in late plantings, severities drastically increased (36 to 96%) with substantial yield losses. This highlights the impact of environmental factors on disease progression. Rust also diminishes fodder quality by causing premature leaf desiccation or death (Monson et al. 1986). Efforts to understand rust resistance are ongoing. Both single dominant genes (Andrews et al. 1984) and duplicate genes (Pannu et al. 1996) have been proposed. Alternatively, polygenic systems leading to quantitative horizontal resistance are also possible. The accessions demonstrating resistance to both rust and downy mildew exist within pearl millet germplasm, providing valuable resources for breeding programs.

Breeding for abiotic stresses

Over 90% of pearl millet cultivation in India occurs in rainfed, arid, and semi-arid regions with limited and erratic rainfall, ranging from 150 to 750 mm annually between June and September (Harinarayana et al. 1999). This uneven distribution makes pearl millet highly vulnerable to drought stress, with variable conditions arising both within and between seasons due to the annual rainfall's coefficient of variation ranging from 20 to 30% (Harinarayana et al. 1999). Therefore, developing pearl millet cultivars adapted to these diverse rainfall environments (high, moderate, and low) is crucial for sustaining grain yield.

Average air temperatures in India during the rainy season peak around 35°C, with lows of 25°C. Early in the season, however, maximum air temperatures can reach 43°C (Harinarayana et al. 1999). In the Indian desert zone, soil surface temperatures during germination can even soar to 60-62°C (Harinarayana et al. 1999). Drought during the seedling stage significantly reduces production due to poor plant stands, whereas drought during the vegetative stage can slightly decrease yield, a compensatory mechanism often comes into play, with an increase in panicle number (Bidinger et al. 1987; van Oosterom et al. 2003). However, drought stress at the grain filling stage drastically reduces both grain quantity and size (Fussell et al. 1991).

Utilizing physiological characteristics as selection criteria for drought tolerance in breeding nurseries has proven challenging. In drought-prone regions of northwest India, breeders have successfully employed early maturity as a strategy to escape terminal drought, effectively utilizing the available genetic variation for different morphological and agronomic traits in breeding programs. The importance of adapted germplasm for breeding drought tolerance has also been emphasized, highlighting the potential of landraces and novel gene combinations to achieve high productivity under stressful environments (Yadav et al. 2009, 2012c; Yadav and Rai 2011; Patil et al. 2020). Pearl millet thrives in temperatures between 33-34°C, but rising temperatures threaten its growth at both seedling and reproductive stages. Climate change projections predict a 6-17% decline in pearl millet yields by 2050 in South Africa and Sub-Saharan Africa due to heat stress (Knox et al. 2011).

Seedlings are most susceptible during the first 10 days because soil surface temperatures in affected regions often exceed 45°C and can reach 60°C, leading to poor plant stands (Peacock et al. 1993). Selecting for tolerance to high soil surface temperatures using artificial screening techniques has proven effective (Soman and Peacock 1985; Lynch 1994). Laboratory techniques based on membrane thermal stability are being explored but progress has been slow (Howarth et al. 1997). Reproductive heat tolerance is a crucial breeding target. High air temperatures (>42°C) during the growing season can cause reproductive sterility, reducing seed set and yield (Gupta et al. 2015b; Djanaguiraman et al. 2018). Field and controlled environment screening procedures have been developed for targeted ecosystems (Gupta et al. 2015b). Studies reveal significant genetic variation for heat tolerance, with stigma being more sensitive than pollen (Gupta et al. 2016, 2019). Heat tolerance appears to be a dominant trait, with the boot-leaf stage being more susceptible than the panicle-emergence stage (Gupta et al. 2016, 2019). High-yielding hybrids and other populations demonstrate an accumulation of heat tolerance genes (Gupta et al. 2016, 2019). Mukesh et al. (2021) suggest the potential of transcript profiling for high-throughput screening of heat-tolerant genotypes at the seedling stage. These findings highlight the challenges and potential solutions for breeding heat-tolerant pearl millet varieties, crucial for ensuring future food security in vulnerable regions.

Breeding for improved nutrition

Pearl millet, a highly nutritious cereal boasting high protein and mineral content compared to other major cereals, makes it a valuable crop for food security. However, maximizing both yield and nutritional qualities presents a challenge. While pearl millet exhibits high protein content (up to 19.8% in elite lines, Singh et al. 1987), germplasm lines can reach even higher levels (24.3%, Jambunathan and Subramanian 1988). Unfortunately, there's a negative correlation between protein content and grain yield (Singh and Nainawatee 1999). Breaking this link is crucial for breeding programs.

Recognizing the prevalence of iron (Fe) and zinc (Zn) deficiencies, particularly among women and children, improving grain nutritional qualities has become a major breeding priority (Govindaraj et al. 2019). Studies by Govindaraj et al. (2019) identified diverse seed-mineral dense germplasm, highlighting the genetic potential for increased Fe and Zn content. The research emphasizes the importance of understanding a). Genotype-environment interaction: How environmental factors influence Fe and Zn levels; b). Relationships between minerals and agronomic traits: Potential trade-offs or synergies; c). Genetic control of micronutrients: Identifying inheritance patterns for efficient breeding strategies.

The "iniadi" landrace (Togo type) has emerged as a valuable resource due to its high Fe and Zn levels (Govindaraj et al. 2016). Rai et al. (2016) reported moderate levels (46-56 ppm Fe & 37–44 ppm Zn) in Indian commercial hybrids, highlighting the need for improvement. The Indian National Testing and Cultivar Release Policy (AICPMIP 2018) established minimum standards (42 ppm Fe and 32 ppm Zn) to promote biofortification efforts. Breeding efforts are also being made to increase Fe and Zn contents. Studies by Govindaraj et al. (2013) and Kanatti et al. (2014) suggest additive genetic variance plays a significant role in Fe and Zn levels. This indicates the need to focus on improving parental lines of hybrids. Similarly, lower G×E interaction for Fe and Zn accumulation (Kanatti et al. 2014; Govindaraj et al. 2016) suggests the effectiveness of progeny selection in pedigree breeding for creating lines with higher Fe and Zn density. The potential success of recurrent selection methods in breeding populations with high additive genetic variance (Govindaraj et al. 2019). By combining diverse germplasm resources with appropriate breeding strategies, researchers strive to overcome the yield-protein trade-off and develop pearl millet cultivars with enhanced nutritional value, contributing to improved public health and food security.

Important discoveries have been made regarding the correlation of iron (Fe) and zinc (Zn) content in pearl millet. Studies repeatedly demonstrated a strong positive correlation between these key micronutrients (Govindaraj et al. 2016, 2020; Kanatti et al. 2014; Rai et al. 2014; Pujar et al. 2020; Anuradha et al. 2017; Singhal et al. 2019, 2021; Thribhuvan et al. 2023; Yadav et al. 2023). Moreover, both Fe and Zn are linked to seed size (Gupta et al. 2009; Kanatti et al. 2014; Govindaraj et al. 2016), regardless of color and genetic background (Govindaraj et al. 2018). These correlations create a strong selection criterion for developing Fe and Zn-rich cultivars in conventional breeding programs without focus on specific grain colors. India's biofortification initiatives demonstrate the success of this approach, producing high-yield cultivars with elevated Fe and Zn content (Rai et al. 2014). The challenges include enhancing the shelf-life of the crop. High lipid concentration in pearl millet flour leads to fat acidity, lipolytic activity, and lipid peroxide accumulation, causing rancidity within 7-10 days of milling. Similarly, the removal of anti-nutrients is another challenge. Phytates and polyphenols reduce the digestibility of protein and starch and interfere with mineral bioavailability. These compounds also inhibit digestive enzymes, further impacting nutritional quality. Researchers are exploring various processing methods to address these limitations and develop value-added pearl millet food products with improved shelf-life.

Pearl millet biofortification: Combating malnutrition with iron and zinc-rich varieties

Micronutrient deficiencies, particularly iron and zinc, pose a significant challenge to public health in India and Africa and contribute to widespread malnutrition. These deficiencies are often associated with inadequate dietary intake in populations consuming foods lacking essential micronutrients like calcium, zinc, and iron. In India, the situation is particularly alarming, with the country ranked in the "severe" category according to the WHO-Global Nutrition Targets 2025, with a Global Hunger Index (GHI) score of 27.5 (WHO-Global Nutrition Targets 2025). Nearly 15.3% of the Indian population falls under the under-nutrition category (WHO-Global Nutrition Targets 2025). Moreover, concerning statistics highlight the prevalence of malnutrition in various age groups, such as-: a). Children under five: 35.5% are stunted, 19.3% are wasted, 7.7% are severely wasted, 32.1% are underweight, and 3.4% are overweight; b). Adults: 24.0% of women and 22.9% of men are overweight or obese (Body Mass Index ≥ 25.0), while 18.7% of women and 16.2% of men have BMIs below normal (<18.5) (WHO-Global Nutrition Targets 2025).

Biofortification, a cost-effective and sustainable strategy, offers a promising approach to combat malnutrition in human population (Yadav and Rai 2013). This method involves breeding staple crops to increase their content of essential micronutrients. Pearl millet, a resilient and nutritious cereal, presents a valuable opportunity for biofortification due to its inherent genetic variability for Fe (30–140 mg kg^{-1}) and Zn (20–90 mg kg^{-1}) content (Govindaraj et al. 2019). Significant progress has been made in developing biofortified pearl millet varieties with high grain yield and elevated Fe and Zn levels. Notable examples include Dhanashakti variety and ICMH hybrids (ICMH 1202, ICMH 1203, and ICMH 1301), which boast iron content ranging from 70 to 75 mg kg^{-1} and zinc content between 35 and 40 mg kg^{-1} (Govindaraj et al. 2019). Additionally, a substantial number of biofortified pearl millet varieties and hybrids have been developed in recent years (Table 1), with promising breeding lines undergoing national and international testing for potential release.

Hybrid breeding in pearl millet

Pearl millet hybrid breeding programs prioritize developing high-yielding hybrids resistant to downy mildew. This requires the creation of superior parental lines, categorized as: a). Seed parents (A-lines): Male-sterile lines are unable to produce viable pollen and require crossing with restorer lines for seed production; b). Restorer parents (R-lines): Lines that restore fertility in hybrids when crossed with A-lines, allowing them to produce pollen and set seed. Exotic germplasm, primarily from Africa, is widely used as an A-line due to its high yield potential (Yadav et al. 2021). Similarly, locally adapted Indian material is often preferred as an R-line to ensure adaptability to local conditions (Yadav et al. 2021). The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) plays a vital role in developing maintainer (B) and restorer (R) lines for hybrid production.

So far, a significant number of improved breeding lines and hybrid parents with enhanced yield potential and downy mildew resistance have been developed and disseminated globally, including in India (Yadav et al. 2021). Molecular diversity analysis revealed distinct clusters for A-lines and R-lines, indicating potential for further genetic diversification through strategic breeding (Napolean et al.

Table 1. A list of biofortified hybrids and varieties of pearl millet released in different states of India

Hybrid/Variety	Year of release	Area of cultivation	Nutrient contents		Average yield (q/ha)	Days to maturity	Institution
			Zn (ppm)	Fe (ppm)			
Dhanshakti	2014	Guj.UP, MP, Raj., Har., AP, TN, Mah.	39–48	76-91	24.3	83	ICRISAT
HHB 299	2017	Guj. Del., Pb., MP, Raj., Har., TN, Mah	41	73	32.7	81	CCSHAU, Hisar and ICRISAT
HHB 311	2020	Guj. Del., Pb., MP, Raj., Har., TN, Mah	-	83	31.7	81	CCSHAU, Hisar and ICRISAT
HHB 67 Improved 2	2021	Guj. Raj., Har.	39.6	54.8	20.0	76	CCSHAU, Hisar, and ICRISAT
RHB 233	2019	Guj. Del., Pb., MP, Raj., Har., TN, Mah	46	83	31.6	80	SKNAU, Jobner
RHB 234	2019	Guj. Del., Pb., MP, Raj., Har., TN, Mah	46	84	31.7	81	SKNAU, Jobner
AHB 1200 Fe	2017	Guj. Del., Pb., MP, Raj., Har., TN, Mah	50	73	32.0	78	VNMKVP and ICRISAT
AHB 1269 Fe	2018	Guj. Del., Pb., MP, Raj., Har., TN, Mah	43	91	31.7	82	VNMKVP and ICRISAT
Phule Mahashakti	2018	Maharashtra	71	87	29.3	88	MPKV, Rahuri
ABV 04	2018	AP, Tel., Mah., Kar., TN	63	70	28.6	86	ANGRAU, ARS Ananthpuram
Pusa 1201	2018	Delhi NCR	48	55	28.1	78-80	IARI, New Delhi
GHB 1225	2020	Gujarat	46	76	30.2	83	Jamnagar AU Pearl Millet Res. Centre
GHB 1129	2019	Gujarat	43	72	29.6	80	Jamnagar AU Pearl Millet Res. Centre
Proagro 9450	2019	UP	58	71	38.6	83	Proagro (Bayer)
NBH 4903	2018	AP, Tel., Mah., Kar., TN	63	70	44.44	88	Nuziveedu Seeds Pvt Ltd
Mahabeej 1005 (MH 1852)	2017	Maharashtra	37	62	29.94	80	Maharashtra States Seeds Company Ltd.

Guj. = Gujarat, AP = Andhra Pradesh, Tel. = Telangana, UP =Uttar Pradesh, Mah. = Maharashtra, Pb. = Punjab, Kar. = Karnataka and TN = Tamil Nadu and Har. = Haryana

2012). Studies employing microsatellite markers identified a substantial number of alleles (12.7 per locus) across a collection of 379 hybrid parents, suggesting ongoing genetic diversification efforts (Gupta et al. 2015). Minimal crossover between A-lines and R-lines indicates the existence of two distinct and diverse gene pools within the hybrid parental lines (Gupta et al. 2015).

Key Breeding Objectives for A-lines include: a). High grain yield potential- both as individual lines and in hybrid combinations (combining ability); b). Retention of desirable maintaining genetic variation for yield components (panicle size, 1000-seed weight, tillering), disease resistance, male sterility stability, and pollen abundance across diverse environments; c). Operational efficiency-maturity duration synchronization with R-lines and a d2 dwarf plant height are preferred for efficient hybrid seed production and d). Improved management by giving emphasis on factors like, reduced lodging susceptibility to downy mildew, efficient off-type and pollen shedder roguing for maintaining line purity. Similarly, R-lines' considerations include restorer ability- effective restoration fertility in hybrids crossed with A-lines and plant height, preferably 150-180 cm with desired features like lodging resistance.

Molecular breeding in pearl millet

Molecular breeding techniques have revolutionized crop improvement by enabling the development of stress-tolerant, high-yielding, and nutrient-enriched cultivars. Pearl millet is a prime example of this success story. In 2005, India witnessed the release of HHB 67 Improved, the first pearl millet hybrid developed using marker-assisted selection (MAS). This hybrid marked a significant milestone in pearl millet breeding due to the role of MAS in incorporating downy mildew resistance. There are accelerated achievements through molecular tools and techniques. For example, the transfer of the downy mildew resistance gene from ICML 22 to the female parent (843A/B) using conventional backcrossing methods took almost nine years (1991-1999). However, utilizing SSR markers, MAS facilitated the transfer of the same resistance gene from ICMP 451 to the male parent (H 77/833-2) in just over three years from 1997-2000 (Taunk et al. 2018). MAS accelerated the breeding process by effectively identifying plants carrying the desired traits, leading to more rapid development of resistant cultivars. Similarly, HHB 67 (Improved) incorporated three downy mildew resistance loci (QTLs) using this efficient MAS approach. The subsequent cycle of improvement, HHB 67 Improved 2-7, demonstrated superior performance in multi-location trials across various pearl millet growing regions. The HHB 67 (Improved 2) has been successfully released in several Indian states, while GHB 538 (Maru Sona), an EDV (Essentially Derived Variety) hybrid resistant to downy mildew, has been introduced in Gujarat. Thus, molecular technologies like MAS in pearl millet breeding hold immense potential for: a). Facilitating further genomic selection and breeding for improved parental lines and b). Enhancing predictive ability in pearl millet breeding may lead to the development of more efficient and successful cultivars. Thus, molecular technology must be encouraged to facilitate genomic selections to improve parental inbreds (Jarquin et al. 2019).

Future prospects and the way forward

Improved pearl millet cultivars have played a transformative role in India, leading to a six-fold increase in productivity compared to the 1950s. This remarkable achievement is even more significant considering that 90% of pearl millet cultivation occurs in rainfed conditions, and India contributes nearly 45% of the global production. However, the challenges include-a). Combating Downy Mildew- the development and deployment of resistant cultivars have successfully controlled the devastating downy mildew disease; b). Parental Line Development- utilizing diverse germplasm resources, including wild relatives and exotic materials, has fostered the creation of robust parental lines for hybrid development; c). Climate Change- adapting to unpredictable weather patterns and resource scarcity is crucial; and d). Malnutrition- addressing widespread malnutrition calls for increased pearl millet production and improved nutritional profiles. The Strategies for the Future includes- a). Breeding for Diverse Environments- developing open-pollinated varieties and hybrids tailored to various ecological conditions can further enhance total production and ensure stability; b). Heterotic Group Development- intensifying breeding efforts to create diverse heterotic groups and improve parental inbred lines hold immense potential for yield improvement; and c). Embracing New Technologies- integrating high-throughput molecular technologies, speed breeding, and precision breeding approaches can accelerate the exploitation of available genetic variation. By actively pursuing these strategies and leveraging the power of innovation, pearl millet research can continue to play a vital role in ensuring food security and alleviating malnutrition in the future.

Sorghum

Sorghum [*Sorghum bicolor* (L.) Moench], the world's fifth most important cereal crop, is mostly cultivated in the arid and semi-arid tropics because of its better adaptation to drought, heat, salinity and flooding. The genus Sorghum has chromosome numbers of 2n=10, 20, 30, or 40; with these, about 25 species have been classified. The cultivated species, *S. bicolor*, is a self-pollinated diploid (2n = 2x = 20) with a natural range through Africa and South Asia. *S. bicolor* and *S. propinquum* are both 2n = 20 species that are chromosomally similar (de Wet, 1978). Hybrids of *S. bicolor* and *S. propinquum* are meiotically regular with ten bivalents (Doggett, 1988). *Sorghum halepense* (2n = 40) is a tetraploid (allopolyploid), in which one genome is common and the other may be divergent or reorganized (Endrizzi, 1957; Tang et al. 1988; Rooney, 2000).

Origin and domestication of sorghum

Sorghum is believed to have been domesticated in northeastern Africa, potentially along the Egyptian-Sudanese border, approximately 5000 to 8000 years ago. Africa is considered the primary center of origin, exhibiting the greatest diversity of both wild and cultivated sorghum (de Wet 1967; Doggett 1988; Kimber 2000). The Indian sub-continent represents a secondary center of origin (Vavilov 1992; Damania 2002). This extensive geographical distribution and the varied climates these regions encompass likely contributed to sorghum's significant morphological diversity (Doggett 1988).

Taxonomy and classification

Sorghum belongs to the grass family Poaceae, within the tribe Andropogoneae and subtribe Sorghinae. Its genus is Sorghum Moench. Harlan and de Wet (1972) established a system classifying cultivated sorghum into five basic, cross-compatible races: *Bicolor, Kafir, Caudatum, Durra, and Guinea*. An additional ten intermediate races represent hybrid combinations, resulting in a total of 15 distinguishable cultivated sorghum races identifiable by spikelet morphology and grain qualities. The *Bicolor* is considered the most primitive race, while *Durra* represents the most evolutionarily advanced.

Distribution and cultivar types

Indian sorghums primarily consist of Durra, Caudatum, Guinea, and Guinea-Kafir races, alongside limited bicolor cultivation (Prabhakar et al. 2022). *Kafir-Caudatums* dominate American grain sorghum production. Nigerian Kauras are classified as *Durra-Caudatum*, while Zerazeras and Hegaris belong to the *Caudatum* race. Sudanese Feteritas exhibit a range from *Guinea-Caudatum* through *Caudatum* to

Durra-Caudatum. Broomcorns, sorgos, and Sudan grass are categorized within the bicolor race.

Status of production and productivity

Sorghum is cultivated in a wide range of countries, with 109 countries reporting production in 2021 according to FAOSTAT (2023). Global sorghum production in 2021 was 61.41 mt, with an average yield of 1,500 kg/ha. The United States has the highest average sorghum grain yield at 4,330 kg/ha, while India is the second largest producer of sorghum globally. In India, sorghum was one of the major cereal staple during 1950s, occupying an area of 17.21 m ha (1951-56), but has come down from 10.99 m ha in 1951-52 to 4.79 m ha currently during 2016-21 (www.angrau.ac.in). But there is an increase in productivity from 381 kg/ha in 1951-52 to 1099 kg/ha in 2020-21 due to concerted research efforts in varietal development and agronomic packages (Fig. 2). However, it is known that India's sorghum yield is the lowest amongst the major sorghum-producing countries, averaging 840 kg/ha, which is significantly lower than the world average. The productivity enhancement has been noticed to the tune of 28.6% in *kharif* sorghum and 24% in *rabi* sorghum during the last six years (Prabhakar et al. 2022). The coverage of sorghum with high-yielding varieties (HYVs) is nearly 80% in *Kharif*, and the potential for under-moderate input is also high (4-6 t/ha). This is despite sorghum cultivation in India occupying a substantial area during the 1950s, accounting for 40 to 45% of the major cereal crops at that time (www.angrau.ac.in).

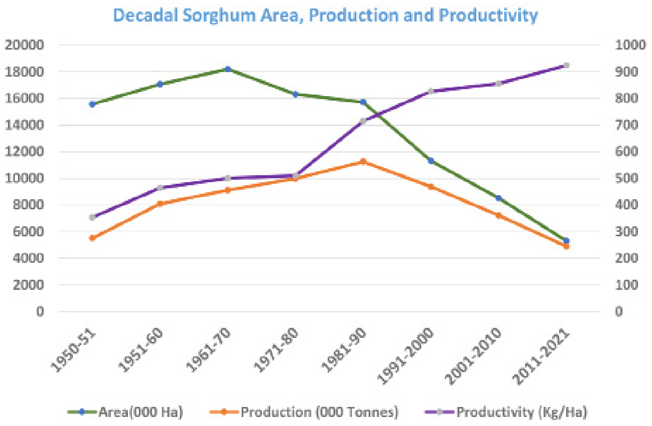


Fig. 2. Figure depicting area, production and productivity from 1951-2021

Genetic improvement of sorghum

Sorghum is primarily a self-pollinated crop, but it can also experience some cross-pollination (often cross-pollinated), ranging from 5 to 15% with an average of about 6% (Poehlman 1987). This mixed breeding system allows breeders to use techniques suitable for both self-pollinated and cross-pollinated crops. They can develop homozygous lines as varieties or exploit heterosis (hybrid vigor) to create high-yielding hybrids.

Sorghum improvement programs have successfully increased grain yields over time (Miller and Kebede 1984; Doggett 1988), allowing sorghum cultivation to spread to diverse agroecosystems worldwide. These programs are led by sorghum-growing countries and the CGIAR systems. In general, the breeding goals for sorghum typically focus on-yield and yield stability, stress resistance and quality aspects. Breeders achieve these goals by identifying and improving yield-contributing traits such as grain number, grain size, test weight, and harvest index. These traits and other morpho-physiological traits that influence yield are the targets for sorghum improvement efforts.

Utilization of genetic diversity in breeding programs

The world's sorghum germplasm collections offer a vast resource for genetic diversity, presenting significant opportunities for improvement (Dahlberg et al. 1996). The two largest collections, held by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (https://www.icrisat.org/) and the United States Department of Agriculture's National Plant Germplasm System (USDA-NPGS) (https://www.ars-grin.gov/), house over 41,000 accessions that can be utilized to discover new genes for sorghum improvement. However, assessing the exact number of germplasm lines employed in global sorghum breeding programs remains challenging (Aruna and Deepika 2018). For illustration, the combination of the *kafir* race with *durra* from eastern Africa established the foundation for the nuclear-cytoplasmic male sterility system, enabling the exploitation of hybrid vigor in sorghum. Additionally, yield genes were identified in *caudatum* and *durra*, while the Guinea race from West Africa contributed resistance to grain mold, and the bicolor race played a role in breeding forage sorghum (Kameswara Rao et al. 2004). Further analysis suggests the presence of genes resistant to shoot fly and drought within Indian *durras*. Grain sorghum is inherently a short-day plant and generally photoperiod-sensitive, although genotypes exhibit varying degrees of sensitivity to different photoperiods and temperature regimes (Childs et al. 1997; Doggett 1988). *Kharif*-adapted lines are predominantly photoperiod-insensitive, whereas *rabi* lines are photosensitive.

Conventional breeding approaches for development of cultivars

Prior to the 1960s, sorghum improvement relied on selecting from local landraces. These varieties were often tall, photoperiod-sensitive, matured late after monsoon season, and adapted to specific regions. Initially, breeding efforts only involved pure line selections from farmers' varieties and landraces. The discovery of cytoplasmic-nuclear male sterility (CMS) in sorghum revolutionized breeding by enabling large-scale hybrid seed production using the three-line system (A, B, and R lines). This facilitated the commercial cultivation of hybrids. To develop high-yielding hybrids, breeders create diverse parental lines exhibiting strong heterosis (hybrid vigor). Notably, the R lines developed in this process become valuable candidates for breeding open-pollinated varieties (OPVs).

India's Accelerated Hybrid Sorghum Project, launched by the ICAR in 1962 and later evolving into the All-India Coordinated Research Project on Sorghum, significantly expanded germplasm resources. This included male steriles, converted lines, and tropical varieties from India and Africa. These efforts have driven substantial improvements in sorghum over the last 60 years. This is demonstrated by developing and releasing roughly 60 national varieties (CSV 1 to CSV 60) and over 250 state-level cultivars for grain, forage, and sweet sorghum production.

Organized sorghum research programs have been essential to India's agricultural success. These programs, carried out through five-year plans, focus on high-yielding varieties and supporting production and protection technologies. Strategic manipulation of plant height and maturity, combined with the use of exotic germplasm (House et al. 1996), has significantly boosted sorghum grain yields. Under favourable conditions, released hybrids achieve yields of 3.0 to 4.2 t/ha, while varieties produce 2.8 to 3.8 t/ha, illustrating their high genetic potential.

Post-rainy sorghum (*rabi)* primarily relies on receding soil moisture, leading to post-flowering drought stress and lower yields (784 kg/ha) compared to rainy-season sorghum (Patil et al. 2013). The popular *rabi* variety M35-1, released in 1969, has been favored for its stability and quality, but focused *rabi* sorghum breeding began in the early 1970s. Most improved varieties stem from pure line selection within local varieties and their crosses. Nationally, the first dedicated *rabi* variety, CSV 7R, was released in 1974, followed by a dozen others. Additionally, states like Maharashtra, Karnataka, Gujarat, and Andhra Pradesh have released varieties exceeding M35-1's yield and maintaining or improving roti-making quality. Soil depth is crucial in rabi sorghum environments. Recent breeding efforts target specific soil situations (shallow, medium, and deep). This has led to the release of varieties like Phule Maulee (shallow to medium), Phule Chitra, Phule Suchitra (medium), Phule Vasudha (deep), Phule Revati (medium to deep) and CSV 26R, Phule Anuradha (shallow) (Prabhakar et al. 2015).

Exploiting heterosis in sorghum

The discovery of cytoplasmic male sterility in sorghum (Stephens and Holland, 1954) opened the door to exploiting hybrid vigor (heterosis). While Indian sources like "Maldandi" and "Vijayanagaram" were known to induce male sterility, the US-discovered "milo" cytoplasm became the foundation of the Indian hybrid program.The "Combined Kafir (CK) 60A" CMS line, an exotic source, facilitated the development of the first commercial hybrids, CSH 1 and CSH 2, released in 1964 and 1965, respectively (Rao 1970). This led to a series of "CSH" hybrids (up to CSH 54) utilizing promising parental lines. These hybrids achieve average yields of 3.0-4.2 t/ha in the rainy season, showcasing a genetic gain of 18.5 kg/ha/year.

Hybrids consistently outperform improved varieties and landraces in diverse conditions. Compared to limited niches for local varieties, the widespread adoption of CSH 1 in the rainy season demonstrates the superior adaptability of hybrids (Rao 1970, 1982). This highlights the ongoing pursuit of developing stable hybrids across environments. However, exploiting heterosis in the rabi season remains a challenge, despite the release of a few hybrids with limited genetic gain (Rakshit et al. 2014). While offering advantages in yield and other traits, rabi sorghum hybrids face a consumer preference for bold, round, and lustrous grains like those of the local "Maldandi" variety. Attempts to incorporate this trait into hybrids using "Maldandi" haven't yielded successful results. Early hybrids like CSH 7R, CSH 8R, and CSH 12R, derived from rainy season lines, lacked desirable grain characteristics and resistance to pests and lodging.CSH 13, though superior to local varieties in yield, couldn't match M35-1 in grain quality. Later hybrids like CSH 15R, CSH 19R, and CSH 39R, based on *rabi*-adapted parental lines, show some improvement in this aspect.

Genomics and sorghum improvement

Trait-based approaches to sorghum improvement can leverage cutting-edge molecular biology technologies to develop high-performing genotypes under stress and with enhanced quality traits. The availability of the whole genome sequence (Paterson et al. 2009) revolutionized our understanding of sorghum genomics, evolution, and biology. Since then, the development of various molecular markers, including Simple Sequence Repeats (SSRs), Intron Length Polymorphisms (ILPs), Insertion-Deletions (Indels), and Single Nucleotide Polymorphisms (SNPs), has progressed significantly. These markers have facilitated the identification of Quantitative Trait Loci (QTLs) associated with key economic traits, currently targeted for marker-assisted breeding in sorghum. QTL mapping has identified numerous QTLs for agronomic traits, resistance to biotic and abiotic stresses, but validation of these QTLs is ongoing across various institutions (Madhusudhana 2018). Furthermore, techniques like gene introgression, transformation, and development of transgenic sorghum hold significant promise for further improvement.

Population improvement

Using recurrent selection procedures, population improvement offers an ideal approach to incorporate QTLs controlling multiple traits. These improved populations serve as a continuous source of new lines for breeding programs (House 1985). The process fosters random crossing between selected individuals, crucial in sorghum as it's primarily self-pollinated. Recessive genetic male sterile systems (ms3, ms7) are used to achieve this. At ICRISAT, Hyderabad, recurrent selection was employed to improve grain yield and stability, grain quality, agronomic traits, and resistance to key diseases (grain mold, charcoal rot, leaf diseases) and pests (shoot fly, stem borers, and midge) (Reddy et al. 2006). This approach successfully improved grain mold resistance, with the B population's score dropping from 7.0 to 5.6, and the R population's score decreasing from 6.5 to 5.4 (Aruna et al. 2021). Population breeding has resulted in several cultivars released for cultivation in Ethiopia, China, and Myanmar. Notably, a male sterile line (421 A) developed through this method facilitated the development and release of numerous hybrids in China (Reddy et al. 2006).

Deciphering the sorghum genome for trait improvement

Understanding the genetic basis of various qualitative and quantitative traits in sorghum is crucial for formulating effective breeding strategies. This knowledge encompasses Enhancing yield potential in varieties and hybrids; strengthening resistance to diseases, studying genetic parameters like heritability, and identifying, locating, and mapping genes. While sorghum breeding and genetic research lagged compared to other crops like rice, wheat, and maize, recent advancements have identified numerous genes and Quantitative Trait Loci (QTLs) influencing key agronomic traits. Early work on sorghum trait genetics was reported by Doggett (1970). Rapid developments in gene identification, mapping, sequencing, and phenotyping technologies have facilitated the identification of important genetic loci and genes controlling agronomic and adaptive traits in sorghum. These advancements, primarily through Genome-Wide Association Studies (GWAS), QTL mapping, and mutant analysis, are documented in earlier reports (Zhang et al. 2018; Hao et al. 2021; Takanashi 2023).

Flowering time

Sorghum is a short-day plant, meaning it flowers when days become shorter. Several genetic loci (Ma1-Ma6) influence flowering time and photoperiod sensitivity (Quinby 1967, 1974; Rooney and Aydin 1999; Thurber et al. 2013). Ma1 and Ma6 act as repressors in long days, while Ma2, Ma4, and Ma5 determine photoperiod responsiveness (Murphy et al. 2014). Additional QTLs for flowering time have been discovered on chromosomes 2, 6, and 9, explaining 6-11% of phenotypic variation (Sukumaran et al. 2016). While tropical types dominate these loci, recessive alleles can enable adaptation to temperate zones (Doggett 1988). Several genes have been identified and cloned:- *Ma3*: encodes phytochrome B (Childs et al. 1997); *Ma1*: likely encoded by a gene for pseudo-response regulator protein 37 (PRR37) (Murphy et al. 2011); *Ma6*: encodes the CONSTANS, CO-like, and TOC1 (CCT)-domain protein SbGhd7, which delays flowering (Murphy et al. 2014)

Plant height

Plant height is controlled by four partially dominant genes, Dw1-Dw4 (Karper and Quinby 1947). The recessive alleles (dwdw) at any locus result in a brachytic dwarfing effect, reducing internode length without affecting other traits like maturity. Each gene has an independent additive effect, with the absence of a single dominant gene potentially reducing height by 50 cm or more. Major QTLs for plant height have been linked to these qualitative loci:Dw1 on chromosome SBI-09, Dw2 on SBI-06, Dw3 on SBI-07. Recently, a new gene, Dw7a, encoding an R2R3 type MYB transcription factor, was identified to influence plant height (Hashimoto et al. 2021).

Plant and grain coloration

Several genes influence the coloration of different plant parts in sorghum.

- Green parts (Leaves, Stems, Glumes)

The P gene controls the presence of purple pigment, with pp plants appearing tan; the Q gene modifies the shade of purple; q allele produces a purplish-black hue; Q or q alleles result in reddish-purple.

- Glumes

P and Q genes also control glume color: P- alleles produce dominant black or red glumes; pp results in recessive mahogany or sienna glumes.

- Grain color

Different sets of genes determine the pigmentation of the pericarp, testa, and endosperm, leading to a variety of grain colors like brown, yellow, white, or purple. These genes include Ce, B1, B2, S1, Y, Bw1, Bw2, M, Pb, and Pt.The Wx gene affects the starch composition in the endosperm. Its dominant allele (*Wx*) maintains a normal balance of amylose and amylopectin starch, while the recessive allele (*wx*) produces a waxy endosperm rich in amylopectin. The *Su* controls sugar content: the dominant allele (*Su*) maintains normal levels, while the recessive allele (*su*) leads to high sugar content. The *Z* governs endosperm hardness: the dominant allele produces a hard endosperm, while the recessive allele results in a chalky appearance. Additionally, quantitative loci might influence the presence of yellow pigment in the endosperm.

Male sterility

Genetic factors primarily control male sterility in sorghum. Several recessive genes, ms1 to ms7 and al, have been identified to cause this trait (Reddy et al. 2005). Recently, ms9 was discovered as an additional nuclear-male sterility gene (Chen et al. 2018). Previous research also documented the inheritance pattern of cytoplasmic male sterility. Two independent recessive genes with duplicate effects were reported (Stephen and Hollend 1954; Maunder and Pickett 1959; Pi and Wuu 1962; Doggett 1964). The *ms* gene, when present with the milo cytoplasm found in kafirs, leads to pollen sterility. Among these genes, *ms3* exhibits the most stable and consistent expression of male sterility across environments and is widely used in breeding programs. Other genes like *ms2* and *al* have been found to be applicable in developing composites and hybrids.

Complexities of breeding for high yield

Enhancing sorghum grain yield presents a significant challenge due to the involvement of numerous interwoven factors. These factors, such as panicle length and weight, branch number, grain number per branch, and individual grain weight, are all polygenic, meaning they are influenced by multiple genes (quantitative trait loci, QTLs). Additionally, these genes interact with each other and the environment in complex ways, making breeding for high yield a non-linear process.

Unveiling the genetic landscape

Despite these complexities, significant progress has been made in identifying the genetic basis for grain yield and its components. Researchers have identified over 180 QTLs associated with these traits (Hart et al. 2001; Mace and Jordan 2011; Reddy et al. 2013; Srinivas et al. 2009; Boyles et al. 2016; Sukumaran et al. 2016; Takanashi 2023). Notably, a sorghum gene (Sobic.001G341700) similar to grain size genes in rice (GS3) and maize (ZmGS3) has been found to influence grain length, weight, and protein content (Tao et al. 2017). Sorghum also shows significant variability in grain micronutrient content, specifically iron (Fe) and zinc (Zn), ranging from 12 to 68 ppm and 11 to 44 ppm, respectively (Hariprasanna et al. 2014a, b). Studies have identified a positive correlation between parental performance and offspring inheritance for these traits. Furthermore, additive and non-additive gene actions influence grain Fe and Zn content, with non-additive effects having a stronger influence on Fe and additive effects playing a more prominent role in Zn (Kumar et al. 2013b). Understanding these genetic complexities is crucial for breeding sorghum varieties with enhanced nutritional value.

Breeding for resistance to biotic stresses

Initially, sorghum breeding in India prioritized high-yielding varieties and hybrids. However, the focus gradually shifted towards combining these traits with resistance to insect pests and diseases. This led to the development of comprehensive research programs- a). Germplasm screening- Identifying resistant lines for major biotic stresses like shoot fly, stem borer, midge, aphids, shoot bug, grain mold, charcoal rot, and foliar diseases (Das and Padmaja 2016); b). Resistance traits- Identifying and characterizing traits associated with resistance; c). Inheritance studies- Understanding the genetic basis of resistance, and d). Segregating population development and evaluation- Breeding new lines with improved resistance. These efforts have yielded significant results in developing effective screening techniques and identifying resistant germplasm, paving the way for breeding sorghum varieties with enhanced resilience against biotic stresses.

Grain mold

Grain mold, particularly prevalent during the *kharif* season, remains a major obstacle to sorghum cultivation. Integrating resistance into high-yielding varieties presents a complex challenge due to- a). Multifaceted resistance- Grain mold resistance involves intricate mechanisms often linked to undesirable agronomic traits (Aruna and Audilakshmi 2004); b). Environmental influence- Resistance effectiveness varies significantly based on both the sorghum variety and the environment; and Fungal complexity- The disease is caused by a combination of fungi, primarily *Fusarium moniliforme, Curvularia lunata, Fusarium semitectum,* and *Phoma sorghina*

Despite these challenges, research has identified promising strategies such as a). Resistance factors- Harder grains, influenced by both genetics and environment, offer greater resistance. Additionally, higher levels of seed phenolics like ferulic acid and tannins act as natural inhibitors against pests and pathogens; b). Resistant germplasm- Utilizing Guinea and zera-zera sorghums as sources, 14 resistant genetic stocks have been developed and registered; c). Marker-assisted breeding: Studies have identified two Single Nucleotide Polymorphism (SNP) loci linked to grain mold resistance (Upadhyaya et al. 2013); and d). Breeding approaches- Alongside conventional methods, population breeding has been implemented since 2000 to combat grain mold (Aruna et al. 2021). These advancements offer promising avenues for developing sorghum varieties with enhanced resistance, contributing to improved crop yield and stability.

Foliar diseases

In addition to grain mold, sorghum suffers from several foliar diseases, particularly destructive under warm and humid conditions (Das et al. 2016). These include leaf spots caused by fungi like *Bipolaris sorghicola, Cercospora sorghi*, and *Gloeocercospora sorghi*, anthracnose caused by *Colletotrichum sublineolum*, rust caused by *Puccinia purpurea*, and various viral diseases. These diseases reduce the amount of green leaf area available for photosynthesis, impacting both grain yield and the quality of fodder by lowering protein, zinc, and digestibility (IVDMD).

Breeding for foliar disease resistance has shown promising results. Genes for anthracnose resistance have been mapped to chromosomes SBI-05 and SBI-08 (Perumal et al. 2008). A major quantitative trait locus (QTL) on chromosome SBI-06 has been identified that influences resistance against various foliar diseases, potentially indicating a key gene for broad-spectrum disease resistance (Mohan et al. 2010). Studies have identified genes involved in plant defence mechanisms as potential candidates for anthracnose resistance (Cuevas et al. 2014; Upadhyaya et al. 2013). These advancements offer hope for developing sorghum varieties with improved resistance to foliar diseases, leading to enhanced crop productivity and stability.

Charcoal rot

Charcoal rot, caused by the fungus *Macrophomina phaseolina*, is a major threat to *rabi* sorghum, especially plants susceptible to lodging during grain filling (Marquez et al. 2021). Understanding the complex genetic basis of this disease is crucial for developing resistant varieties. Research suggests various inheritance patterns, including dominance of susceptibility, partial dominance, and polygenic control, making breeding efforts challenging (Indira et al. 1984; Garud and Borikar 1985). Additionally, the low heritability of resistance traits further complicates breeding programs. Despite these challenges, advancements have been made in identifying and utilizing resistance factors, such as- a). Phenolic compounds- These naturally occurring compounds in sorghum plants can inhibit the spread of the fungus during dry periods, contributing to tolerance (Marquez et al. 2021); b). QTL mapping- researchers have identified quantitative trait loci (QTLs) associated with charcoal rot resistance, providing valuable insights for breeding programs (Patil et al. 2012; Adeyanju et al. 2015); c). Marker-assisted selection- new polymorphic markers have been identified to aid in breeding programs, allowing for targeted selection of resistant traits (Kumar et al. 2017); d). Disease prediction models are being developed to predict end-of-season disease severity based on soil and stubble inoculum levels, offering a potential tool for early intervention (Dante 2023); and e). Additional management strategies- cultural practices like crop rotation and residue management can also be beneficial in reducing pathogen pressure and improving overall crop health (Singh et al. 2023). By combining these advancements with a deeper understanding of the disease's complex genetics, sorghum breeding programs can develop more robust varieties, ultimately contributing to improved crop health, yield stability, and food security.

Ergot

Ergot, caused by the fungus *Claviceps sorghi*, is a significant concern for sorghum seed production, causing losses ranging from 27% to 60%. However, the severity of infection is heavily influenced by environmental factors. The initial sign of ergot infection is the appearance of sticky "honeydew" droplets on infected florets. This honeydew attracts saprophytic fungi, which often blacken the leaf surface.

Breeding for Ergot resistance is complicated by several factors, including: a). Environmental influence: Ergot expression varies significantly depending on the location and associated temperature, making breeding for resistance complex. Studies have shown significant differences in infection rates between locations, with cooler temperatures favoring the disease (Reed et al. 2002); b). Complex inheritance: Both additive and non-additive genetic effects contribute to ergot resistance, further challenging breeding efforts (Kebede et al. 2022); and c) Limited genetic resources: There are few known sources of strong ergot resistance in sorghum. However, advancement in molecular tools and techniques have strengthened the breeding process with newer approaches, such as: a). QTL mapping- researchers have identified several quantitative trait loci (QTLs) associated with ergot resistance, offering potential targets for breeding programs (Klein et al. 2001; Mohan et al. 2010; Parh et al. 2008), and b). Marker-assisted and transgenic approaches- utilizing marker-assisted breeding and transgenic technologies holds promise for overcoming the limitations associated with conventional breeding and developing more robust ergot resistance in sorghum (Madhusudhana et al. 2919; Baloch et al. 2023). These advancements offer valuable tools for tackling this complex disease. By combining this knowledge with ongoing research efforts, scientists can develop sorghum varieties with enhanced ergot resistance, contributing to improved seed production and overall crop health.

Insect-pests

Shoot fly

The sorghum shoot fly (*Atherigona soccata*) is a major insect pest, causing significant yield losses across both *kharif* and *rabi* seasons. While large-scale germplasm screening has identified moderately resistant sources, incorporating this resistance into high-yielding cultivars remains challenging due to the complex, quantitative nature of the inheritance (Riyazaddin et al. 2016). Despite these challenges, advancements have been made in understanding and managing shoot fly. For example, accessions like IS 18551 have been identified as potential sources of resistance. Researchers have also noted that morphological traits like leaf glossiness, trichome density, and seedling vigor can deter egg-laying by the shoot fly (Dhillon et al. 2005). Researchers have identified major quantitative trait loci (QTLs) associated with resistance-related traits, paving the way for targeted breeding approaches (Satish et al. 2009; Aruna et al. 2011). Further, combining favorable alleles through population improvement, and marker-assisted selection (MAS) are being explored to enhance resistance (Aruna et al. 2011). Besides, the marker-assisted backcrossing (MABC)technique has successfully been used to transfer

QTLs controlling tolerance traits into sorghum varieties, improving shoot fly resistance in post-rainy sorghum (Gorthy et al. 2017). Recent studies suggest that susceptible varieties may emit volatile compounds that attract shoot flies, offering potential avenues for developing repellence strategies.These advancements provide valuable tools and knowledge for breeders to develop sorghum varieties with enhanced shoot fly resistance, contributing to improved crop protection and yield stability.

Stem borer

Stem borer (*Chilo partellus*) is another significant pest of sorghum, causing "deadhearts" and leading to substantial yield losses. While sources of resistance were identified as early as 1949 (Trehan and Butani 1949), understanding the complex nature of resistance has been crucial. Progress in the research has given insights into the resistance mechanisms in the plant against stem borer. For instance, genotypes like ICSV700 and IS2205 demonstrate lower susceptibility to larval damage compared to susceptible varieties (Vashisth et al. 2022). Certain features like shoot length and days to panicle initiation were also observed to be linked to resistance (Vashisth et al. 2022). Studies suggest a combination of tolerance, antibiosis (inhibiting larval development), and antixenosis (deterring egg-laying) contribute to resistance (Singh and Rana 2011; Singh and Verma 2011).

Factors, such as- a, challenge breeding for stem borer). Inheritance patterns: Research indicates that resistance is likely polygenic (controlled by multiple genes) and partially dominant, with different inheritance patterns for various damage types (Singh and Rana 2011; Singh and Verma 2011); b). Gene action: Both additive and non-additive gene effects and epistatic interactions contribute to the complex inheritance of resistance (Muturi et al. 2019); c). Combining ability: Studies suggest dominance gene action for certain traits like stalk length, while other traits like leaf feeding score may be governed by additive gene action (Sharma et al. 2007). Besides genetic factors, biochemical factors have also been identified, highlighting that defensive enzymes, secondary metabolites like tannins and phenols, and fiber content may play a role in the resistance mechanism (Vashisth et al. 2022). In addition to the conventional approaches, transgenic approaches using the Bt gene from *Bacillus thuringiensis* have also been adopted to breed for resistance (Girijashanksar et al. 2005). Thus, it can be said that addressing stem borer requires a comprehensive approach. Combining resistant germplasm, understanding the complex inheritance patterns, and exploring diverse strategies like conventional breeding, marker-assisted selection, and potential transgenic approaches hold promise for developing robust sorghum varieties with enhanced resistance and improved yield stability.

Sorghum midge

The sorghum midge (*Contarinia sorghicola*) is a major concern for sorghum cultivation worldwide. Several countries, including India, have reported sources of resistance within their germplasm collections. Studies have identified lines like TAM 2566 and IS 10712 as potential resources for breeding programs (Sharma et al. 1993). Understanding the inheritance of resistance is crucial for breeding strategies. While some reports suggest recessive gene control (Boozaya-Angoon et al. 1984), most evidence points towards polygenic inheritance with both additive and non-additive gene action (Patil and Thombre 1983). This implies the involvement of multiple genes and the importance of resistance in both parents for hybrid development. Researchers have also identified quantitative trait loci (QTLs) associated with resistance mechanisms. Two QTLs on chromosomes SBI-03 and SBI-09 are linked to antixenosis (deterring egg laying), while another on SBI-07 is associated with antibiosis (inhibiting larval development) (Tao et al. 2003).

Breeding for tolerance to abiotic stresses in sorghum

Drought and heat tolerance

Despite its relative drought tolerance, sorghum still faces significant yield losses due to drought, particularly, during the critical post-flowering stage. Additionally, moisture stress during germination can hinder plant establishment and growth (Younesi and Moradi 2009). Sorghum's diverse genetic makeup, adapted to various environments, holds immense potential for breeding drought and heat tolerance. Identifying key traits and understanding the underlying physiological and genetic mechanisms are crucial for effective breeding strategies. Remarkable progress has been made in this direction. Studies have shown a positive correlation between chlorophyll content and stay-green characteristics, indicating its role in delaying senescence and maintaining higher yield (Enyew et al. 2022). Similarly, researchers have identified several QTLs associated with stay-green, providing valuable targets for breeding programs. These QTLs explain a significant portion of the phenotypic variation (Xu et al., 2000; Subudhi et al., 2000; Haussmann et al. 2001). Efforts are underway to transfer identified QTLs, such as Stg3a and Stg3b, from tolerant lines into high-yielding cultivars, using marker-assisted introgression (Madhusudhana 2018). Similarly, utilizing genomic selection techniques offers the potential for even more precise breeding and faster development of drought-tolerant varieties.

Cold tolerance

Compared to other cereals, sorghum has higher susceptibility to low temperatures, impairing seed germination, growth, and seed set, particularly in the *rabi* when low temperatures often coincide with flowering. Understanding the physiological, metabolic, and molecular mechanisms underlying cold tolerance is crucial (Hernandez et al. 2023). Genetic variation in low-temperature germination response is the key for identifying sorghum genotypes suitable for early sowing in semi-arid areas, potentially resulting in higher biomass production in cooler climates (Patane et al. 2021). Breeding efforts should also consider resilience as an important component of cold tolerance (Emandack et al. 2021). Genetic mapping has identified several QTLs associated with cold tolerance:- Two QTLs for germination on SBI-03 and SBI-07 influence performance in both cold and optimal temperatures (Knoll et al. 2008); - A major QTL on SBI-01 contributes to seedling emergence and vigor in early and late plantings; - A QTL on SBI-02 influences seedling emergence timing; - New sources of cold tolerance, like PI610727, are being used to identify further genomic regions linked to cold tolerance traits. These discoveries offer valuable targets for breeding programs aiming to improve sorghum's cold tolerance, which can ultimately lead to better-adapted varieties and expanded cultivation into cooler environments.

Sorghum as a forage crop

Sorghum serves as a crucial forage crop during the kharif and summer seasons, either as a single-cut option (primarily rain-fed in kharif) or a multi-cut option (common in northern states during summer and *kharif*). Various varieties and hybrids of single-cut, multi-cut, and dual-purpose types have been developed and released for fodder use. The introduction of Sudan grass from Africa significantly impacted breeding efforts. Since the 1950s, Sudan grass has been hybridized with other sorghum subspecies to boost forage production and productivity. Two primary types of Sudangrass hybrids exist globally:

- True Sudangrass hybrids: Produced using male sterile lines and fertility restorers, these hybrids resemble the common Sudangrass in growth and agronomic characteristics. However, they are taller with a larger stem diameter, leading to higher forage yields.
- Interspecific hybrids: Created by crossing sorghum (*S. bicolor*) with Sudan grass (*S. sudanense*), these hybrids are known for their vigor and height. They produce larger stems and coarser leaves but yield significantly more forage (2-3 times) at the flower and milk stages, making them ideal for green chop and silage production (Snyman and Youbert, 1996; Paknejad et al. 2001).

By hybridizing Sudan grass (*S. sudanense*) with sorghum, a superior forage sorghum variety, SSG 59-3, was developed. This hybrid combines desirable traits like yield, leafiness, digestibility, regrowth, disease resistance, and low prussic acid content. Recent progress has led to the release of single-cut varieties like CSV 30F, CSV 32F, etc., and multi-cut hybrids like CSH 43MF and CSH 46MF. These cultivars offer improvements in resistance to leaf spot diseases, stem borers, and seed yield. Notably, the multi-cut hybrid CSH 24MF enjoys high popularity and widespread demand. A few privately developed multi-cut forage hybrids have also gained traction in the market (Prabhakar et al. 2015).

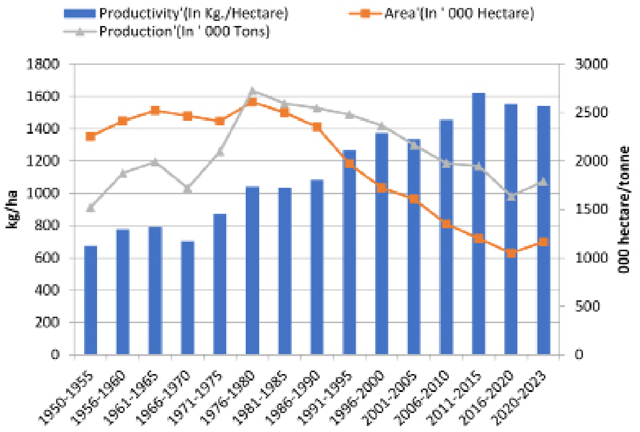
Sweet sorghum: a potential bio-fuel crop

Distinct from its grain counterpart, sweet sorghum accumulates significant amounts of fermentable sugars in its dry pithy stalk (Mathur et al., 2017). This characteristic, reaching 15-23% soluble sugar content (compared to 14-16% in sugarcane), makes it a promising bio-ethanol feedstock. The entire plant biomass can also be used for lignocellulosic ethanol production (second generation bio-fuel). Sweet sorghum exhibits substantial genetic diversity in stem water content, evident at morphological, molecular, and genomic levels. Early studies (Rangaswami et al. 1937; Hilson 1916) attributed juiciness to a single locus ("Dry" or D), with dry stem being dominant over the juice-rich trait. Recent research by Zhang et al. (2018) identified the *Dry* gene as a specific plant NAC transcription factor, mutated or deleted in sweet sorghum varieties. Additionally, they identified 23 ancestral *Dry* haplotypes associated with dry stems in wild sorghum and related species.

Functional and comparative analysis of natural populations and those developed through NAM, MAGIC, and mutagenesis have revealed significant genetic variation and identified key genetic loci and genes influencing agronomic and adaptation traits (Hao et al. 2021). Six sweet sorghum varieties and two hybrids have been released for ethanol production and green/dry fodder use. Recent releases include CSV 49SS, CSV 52SS, and CSH 47. Brown mid-rib (bmr) sorghum varieties (CSV 43 BMR and CSV 59 BMR) and a hybrid (CSH 54 BMR) offer superior digestibility due to lower lignin content, making them ideal high-yielding fodder options. These, along with high biomass sorghum hybrid CSH 47 and varieties JaicarUrja- CSV 48 and CSV 54 HB, showcase the diversification of sorghum breeding from food to industrial uses.

Finger millet

Like other millets, finger millet (*Eleusine coracana* L.) thrives in harsh environments, making it a popular crop in Africa and Asia's arid and semi-arid regions. For instance, over one million hectares were dedicated to finger millet cultivation in India in 2019-2020, producing roughly 1.8 million tonnes (Wafula et al. 2016; Davis et al. 2019). The area, production, and productivity of finger millet in the past 7 decades is represented in Fig. 3. Even in drought-prone and rainfed areas, its productivity rivals that of sorghum and pearl millet (Chetia and Malleshi 2007; Upadhyay et al. 2011). Rainfed finger millet boasts impressive nutritional qualities, containing high levels of calcium (300-350 mg/100g), iron, amino acids, fiber, polyphenols, and antioxidants (Upadhyay



Source: Ministry of Agriculture & Farmers Welfare, Govt. of India (ON2740) & Past Issues

Fig. 3. Area, production and productivity of finger millet based on five year mean

et al. 2011). Additionally, its straw and haulm serve as a valuable source of fodder due to their high nutrient digestibility (60%).

While several high-yielding finger millet varieties have been developed, their success can be attributed to factors like blast resistance, improved biomass allocation, and better sink size (Megha et al. 2023). However, finger millet yield improvement has shown a concerning decline in recent years (Adugna et al. 2011; Megha et al. 2023). This is likely due to an overemphasis on yield alone in breeding programs, neglecting other crucial traits for resilience against frequent droughts and rising temperatures (Krishna et al. 2021). To enhance finger millet's productivity and production in the future, advanced breeding methods are needed alongside the exploration of new cultivation niches.

Domestication of finger millet

The exact origins of finger millet remain a subject of debate. While some researchers, like Greenway (1945), point to an African origin with its wild ancestor being Eleusine africana, others like Vavilov (1951) suggest independent domestication in both Africa and India based on similar genetic diversity. More recent studies provide clues that support the African origin theory. The presence of several wild diploid *Eleusine* species with similar ribosomal DNA (rDNA) sites as cultivated finger millet, the possibility of interbreeding between them, and the greater genetic diversity found in African finger millet germplasm compared to Asian varieties all suggest an African origin (Bisht and Mukai 2001, 2000; Hilu and De Wet 1976).Evidence also suggests domestication around 5,000 years ago in eastern Africa, followed by introduction to India roughly 3,000 years ago (Hilu and De Wet 1976; Hilu 1979). Genetic analyses using SSR markers further support this theory, indicating an African origin before introduction to India (Dida et al. 2008). This movement is thought to have begun in the African highlands, then progressed to the southern lowlands before reaching India. This aligns with the discovery of carbonized finger millet seeds from the Iron Age in Zimbabwe (Summers 1958). Despite its long history of cultivation in India, the finger millet varieties there are considered to be a secondary center of diversity due to the unique characteristics developed through generations of human selection (Padulosi et al. 2009).

Cytological studies: Unveiling the secrets of plant evolution

Krishanswami and Ayyangar (1935) reported differences in the haploid chromosome number of various *Eleusine* species, including *E. indica* (n=9), *E. coracana* (n=18), *E. brevifolia* (n=18), and *E. aegyptica* (n=17). These variations suggest distinct evolutionary lineages within the genus. Further studies by Bisht and Mukai (2001) confirmed these findings and also reported the diploid chromosome number for these species. Additionally, they analyzed the 2C DNA content of *E. indica*, finding it to range from 1.51 to 2.65 pg, while the polyploid species *E. coracana* ssp. coracana and *E. coracana* ssp. *africana* exhibited a higher range of 3.34 to 3.87 pg (Mysore and Baird 1997). Researchers have also employed techniques like genomic *in situ* hybridization (GISH), ribosomal DNA sequences, and plastid DNA sequences to explore the phylogenetic relationships among *Eleusine* species (Bisht and Mukai 2001; Liu et al. 2011, 2014; Neves et al. 2005; Agrawal et al. 2014). These studies revealed the polyploid origin of the *Eleusine* genome and identified the diploid *E. indica* as the primary maternal donor of the A genome in the cultivated tetraploid *E. coracana*.

Early efforts and progress in finger millet breeding

Finger millet improvement through conventional breeding began relatively late in India. In 1913, Leslie C. Coleman at Hebbal farms, Bangalore identified a few pure lines, including Hullubele and Gidda. He later developed and released the popular cultivar H-22 in 1918, followed by several others. Recognizing the potential of hybrid vigor and adaptation to monsoonal variations, Ayyangar (1932) encouraged the use of hybridization strategies in finger millet breeding. C.H. Lakshmanaiah pioneered recombination breeding by crossing Indian cultivars with high-yielding African ecotypes like Indaf. Similar efforts emerged in Africa. In 1985, a collaborative research program on finger millet improvement was initiated by SADCC (Southern African Development Coordination Conference) and ICRISAT (Gupta et al. 1986). This led to the development and release of several early-maturing, blast-resistant, high-yielding cultivars like Engeny, Gulu E, Serere 1, Pese 1, Seremi 1-3, SX 8, SEC 915, and SEC 934 (Alimu, 1985).

In India, the All India Coordinated Research Project (AICRP) on Small Millets plays a key role in breeding improved cultivars. They have released numerous blast-

Table 2. Genetic variability (values in range) for some nutrient composition in finger millet

Nutrient parameters/content	Values in range
Moisture	9.35–18.67 g/100g
Fat	0.86–2.69 g/100g
Protein	4.85–14.38 g/100g
Carbohydrates	67.2–77.8 g/100g
Fibre	4.46–19.1 g/100g
Energy	323. 5–365.1 kcal/100g
Phenol	5.6–25.7 mg/100g
Flavonoid	2.85–40.13 mg/100g
Vitamin C	7.15–77.2 µg-1
Antioxidant	2.0– 6.2%

resistant varieties like GPU-26, GPU-28, GPU-45, GPU-48, GPU-66, KMR-204, and KMR-340, with average yields of 2-4 t/ha. Additionally, the AICRP released the semi-dwarf, non-lodging cultivar GPU-67, suitable for wider adoption. Notably, around 45% of finger millet cultivars released in India, totaling about 145 varieties, from which about 45% have been developed through hybridization and selection (https://www.seednet.gov.in/; Nagaraja et al. 2022).

Genetic improvement of finger millet: Conventional breeding approaches

Finger millet improvement traditionally involves selecting superior genotypes from landraces and natural populations. Hybridization, however, is challenging due to the small floral structures. Breeders overcome this by intertwining female and male panicles in a cover or using hot water emasculation for the female parent (Nagaraja et al. 2023; Raj et al. 1984). However, seed set remains a challenge. While genetic male sterility lines exist (Gupta et al. 1997), their maintenance is complex. Wide hybridization with diverse germplasm, including exotic materials and related species, offers an avenue for introducing valuable traits (Dwivedi et al. 2008).

Modern breeding efforts combine improved grain yield, resistance to abiotic and biotic stresses, and enhanced nutritional qualities. Two distinct finger millet gene pools, African and Indian, offer diverse traits. Several researchers have reported that finger millet possess tremendous amount of genetic variability including quality traits particularly micronutrients (Table 2). Indian accessions generally have compact ears, higher yield potential, and better fodder characteristics, while African accessions possess diverse ear types, disease resistance, but also limitations like poor threshability and late maturity (Naik et al. 1993; Gowda et al. 1986). Introgression of desirable traits from African germplasm into Indian cultivars has been highly successful, particularly in southern India. This approach has increased finger millet productivity by over 50% (Gowda et al. 1986).

Modifying plant architecture in finger millet holds promise for yield improvement. However, knowledge on the genetic basis of key traits remains limited. Existing studies indicate simple or dominant gene inheritance for traits like plant pigmentation, glume size, and grain color (Ravikumar and Seetharam 1990; Shanthakumar 1988; Shanthakumar and Gowda 1997). Inheritance of head shape seems to involve multiple genes, with separate ones controlling shape and finger curvature (Owere 2013). Blast resistance, however, appears to be quantitatively inherited, requiring further investigation for appropriate breeding strategies (Seetharam and Ravikumar 1993; Owere 2013). The advent of DNA marker technology has shifted the focus towards molecular breeding approaches for further enhancing finger millet, aligning with trends in other crops.

Intensive selection efforts are required to effectively select novel variants from complex population crosses (like MAGIC). Understanding the correlations between traits helps identify suitable donors for specific breeding goals. In finger millet, improved grain yield typically depends on positively correlated traits like biomass, harvest index, mean ear weight, and threshing percentage. Studies indicate a negative correlation between yield and grain protein/calcium content, implying that improving both simultaneously might be challenging (Lule et al. 2012; Kumar et al. 2012). Path coefficient analysis highlights the significant positive impact of traits like productive tillers, thousand-grain weight, finger length/number, ear weight, grains per spikelet, and culm diameter on finger millet yield. This suggests that focusing genetic improvement efforts on these traits would directly enhance productivity. Importantly, mean ear-head weight should be prioritized as a selection trait for yield improvement due to its strong negative correlation with ear-head number (Chaithra and Nanja Reddy 2023). Combined with the threshing percentage, this can form the foundation for a successful finger millet genetic improvement strategy.

Conventional breeding approaches have been used to identify blast-resistant lines, such as interspecific crosses between wild E. kigeziensis and E. africana and cultivated finger millet (Akech et al. 2016). Additionally, trait-targeted gene bank breeding has successfully identified high-quality cultivars, such as Jigu 21, Chaozaoshu 2, and Jigu 32, by leveraging the additive effects of genes from the gene bank (Zhengli and Zhengli 2005; Li et al. 2014). Exploiting hybrid vigor, a significant yield booster in many crops, has been limited in finger millet due to the challenges of hybridizing its tiny florets. Studying floral morphology to improve hybridization techniques offers a promising research avenue for overcoming this limitation (Nagaraja et al. 2023). Developing male sterile lines, a key component of hybrid seed production, could potentially unlock this potential. While some lines exist, like the ICRISAT-developed INFM 95001 and the PS 1 mutant, their seed set and hybrid recovery rates require further improvement (Gupta et al. 1997; Manjappa 2017).

Mutagenesis has proven successful in developing improved finger millet varieties. Notable examples include the X-ray-derived cultivar Hagari-1 (Krishnaswami and Ayyangar 1941) and later, the gamma-irradiation-derived cultivars CO-3 (dwarf), Dibyasinha (early maturing), and K-6 (dwarf, early maturing). These were released commercially in 1942, 1976, and 1982, respectively. Further gamma-irradiation of cultivar HES 927 yielded the promising high-yielding, blast-resistant mutant M21 (Goud et al. 1969, 1971). Extensive studies have demonstrated the effectiveness of mutagenesis in generating desirable traits in finger millet, including dwarfism, early maturity, and high tillering, in cultivars like PR 202, HR-911, Indaf-8, and TNAU-294 (Goud et al. 1969, 1971; Tikka 1985). China has also achieved success with mutagenesis, developing high-yielding mutants like 21 (Chen and Wei 1992), Longfu 93-076 (Yi et al. 2002), and Chigu 4 (Li and Jiang 1990).

Breeding for disease resistance

Finger millet faces various biotic stresses, significantly impacting yield. Fungal diseases are major concerns, including downy mildew, blast, leaf blight, leaf spot, and sheath blight. Among these, blast, caused by *Pyricularia grisea*, is particularly devastating, causing yield losses exceeding 50% in wet seasons and potentially reaching 90% (Esele and Odelle 1995; Vishwanath et al. 1986; Ekwamu 1989).

Breeding for blast resistance, a major constraint in finger millet production caused by *Magnaporthe grisea*, is crucial for sustainable yield improvement. The rapid evolution of virulent pathogen strains necessitates careful selection of resistance genes from diverse germplasm resources (Mbinda and Masaki, 2020).Studies have identified numerous resistant and moderately resistant germplasm lines within India (Babu et al. 2013; Manyasa et al. 2019) and globally (Dida et al. 2020). Wild relatives often exhibit superior resistance, highlighting their potential as breeding resources (Dida et al. 2020).Marker-assisted selection is emerging as a powerful tool for identifying and incorporating resistance genes. Babu et al. (2014b) identified 19 markers associated with blast resistance, paving the way for targeted breeding efforts. Additionally, the development of high-yielding and blast-resistant varieties like GPU-28 demonstrates the success of resistance breeding (Gowda et al. 2014).

Molecular Breeding approach for finger millet improvement

Despite lagging behind other cereals in terms of advanced biotechnology, finger millet research is embracing modern tools. These include molecular markers, SSRs, ESTs, gene expression profiling, genome-wide association studies, and genome editing (Dida et al. 2020; Mbinda and Mosaki 2020; Sood et al. 2019).Recent studies have successfully identified QTLs associated with agronomic traits and blast resistance using various techniques. Pendergast et al. (2021) identified eight significant QTLs for five key traits, while Ramakrishnan et al. (2016) identified seven QTLs linked to blast resistance and other desirable features. These findings provide valuable resources for marker-assisted breeding programs aiming to develop finger millet varieties with improved yield, pest resistance, and climate resilience. Challenges like *in-vitro* regeneration due to the plant's recalcitrant nature are being addressed with new protocols offering potential solutions (Babu et al. 2018; Ngetich et al. 2018).

Genomics-assisted breeding

This approach leverages tools like SSRs, ESTs, and genome-wide association studies to exploit the extensive genetic diversity within the species (Dida et al. 2007; Ramakrishnan et al. 2015). Initial research by Dida et al. (2007) and others revealed high levels of polymorphism (genetic variation) within finger millet germplasm, ranging from 35% to 100% (Fakrudin et al. 2004; Babu et al. 2007). This diversity offers valuable resources for breeding programs. Similarly, the comparative genomics studies have further enhanced understanding. These studies, like those by Srinivasachary et al. (2007) and Lata (2015), established a high degree of shared genetic material between finger millet and rice, suggesting potential for cross-breeding and marker development.

Functional genomics, particularly transcriptomics, plays a key role in identifying genes associated with valuable traits in finger millet. Transcriptome profiling has been successful in identifying calcium sensor genes and their potential role in calcium transport (Mirza et al. 2014; Sood et al. 2016; Kokane et al. 2018). Functional validation of genes involved in drought tolerance, including *EcDehydrin7, EcGBF3, CIPK31*, and *TAF6*, has been conducted using qRT-PCR (Singh 2014; Ramegowda et al. 2017; Hittalmani et al. 2017; Parvathi and Nataraja 2017; Parvathi et al. 2019; Li et al. 2021). RNA-sequencing is used to study the expression patterns for drought tolerance, high calcium content, and other important features (Kumar et al. 2016a,b). Similarly, research has identified a salinity tolerance regulatory gene (Rahman et al. 2014). Advances in genomic resources, including a validated genome assembly, will significantly enhance molecular-level research and the discovery of genes impacting important agronomic and nutritional traits in finger millet.

Genetic transformation

Genetic transformation, a powerful tool for crop improvement, remains underexplored in finger millet compared to other major cereals. Challenges like *in-vitro* regeneration have hindered progress, although recent protocols offer some promise (Dosad and Chawla 2016; Babu et al. 2018; Ngetich et al. 2018).

Despite limitations, significant advancements have been made in developing transformation protocols using both *Agrobacterium* and biolistic methods (Vetriventhan et al. 2020; Bhatt et al. 2021). This has paved the way for research on transgenic finger millet resistant to blast disease (Latha et al., 2005; Ceasar and Ignacimuthu 2009), drought and salinity (Hema et al. 2014), with improved herbicide tolerance (Bayer 2014) and zinc content (Ramegowda 2013).

Challenges in finger millet breeding

Finger millet breeding faces several challenges, including:

- Limited genetic diversity: Conventional breeding relies on diverse germplasm, which can be limited in finger millet. This necessitates exploring wild relatives and incorporating resistance genes from broader sources.
- Biotic stresses: Diseases like blast, downy mildew, and leaf blight significantly impact yield. Linking identified resistance genes with yield traits poses a challenge due to complex interactions and data analysis.
- Climate change: Changing weather patterns can exacerbate diseases, especially in high-yielding varieties under intensive cultivation.
- Abiotic stresses: Drought and salinity are major constraints, requiring the development of tolerant varieties.
- Heritability: Complex trait inheritance with varying levels of heritability can hinder efficient selection of desired phenotypes.
- Stacking desirable traits: Combining resistance to multiple stresses with high yield and improved nutritional content requires advanced breeding techniques.

Beyond these challenges, market demands, processing efficiencies, and incentives for farmers also limit finger millet's mainstream adoption. Addressing these challenges is crucial for increased production, productivity, and farmer adoption of this valuable crop.

Other millets

Generally referred as minor or small millets include foxtail millet, proso millet, little millet, barnyard millet, kodo millet and browntop millet. However, the detailed information on phylogeographic and evolutionary history and to estimate their gene pool range than shall aid in genetic improvement and breeding is very limited. Therefore, significant research attention to explain various aspects of origin, domestication, cultivation etc., are needed.

Foxtail millet boasts a wealth of carbohydrates, with double the protein content of rice. It also provides essential minerals like copper and iron. Additionally, foxtail millet is a good source of ferulic acid, an antioxidant (Goudar et al. 2023). Kodo millet is another nutritional star, offering 11% protein, exceptional fiber content (14.3%), and rich B vitamins. It also contains valuable phytochemicals like alkaloids, flavonoids, and phenolics (Goudar et al. 2023). Proso millet takes the crown for protein content (12.61% per 100g) and calcium among millets. It's also known for its heart-protective properties, potentially lowering cholesterol and reducing heart disease risk (Goudar et al. 2023).

Generally, millet is gluten-free and has a low glycemic index, making it a good dietary choice (Muthamilarasan et al. 2016). However, a drawback exists: the presence of anti-nutrients like tannins, polyphenols, and phytic acid can limit the absorption of essential nutrients from millets (Samtiya et al. 2021). Millets typically contain 0.2–0.3% polyphenols, 0.48% phytates, and 0.61% tannins, with phytic acid being the most concerning due to its impact on nutrient bioavailability (Sheethal et al. 2022). Barnyard millet stands out for its abundance of micronutrients, particularly iron and fiber. Despite these limitations, research highlights millets, also known as nutri-cereals, as a valuable source of macro and micronutrients compared to staple crops. They are rich in dietary fiber, essential amino acids, minerals, antioxidants, trace elements, protein, fats, and carbohydrates (Geervani and Eggum 1989; Muthamilarasan et al. 2016; Jaiswal et al. 2019; Dey et al. 2022). Their superior nutritional profile and climate resilience make them a promising alternative food source.

Foxtail millet *(Kangni or kakum) Setaria italica syn. Panicum italicum L., 2n=2x=18*

Morphological and molecular analyses have indicated that cultivated foxtail millet was domesticated from green foxtail millet (*Setaria viridis*) (Doust et al. 2009; Wang et al. 2010). Two phylogenetic lineages, which are evolutionarily different, are put forth by the researchers that depend on at least two independent domestication events in foxtail millet (Kawase and Sakamoto 1984, 1987; Jusuf and Pernes 1985; Fukunaga et al. 1997, 2002, 2006; Nakayama et al. 1998; Benabdelmouna et al. 2001; Kawase et al. 2005), followed by genetic introgression from green foxtail millet (Darmency et al. 1987). Chloroplast, isozyme and nuclear genes were used for phylogenetic analysis, indicating that foxtail millet and green foxtail millet were close relatives (Doust et al. 2007). The primary gene pool constitutes *S. italica* and *S. viridis* designated as AA genome with $2n = 2x = 18$ (Benabdelmouna et al. 2001), the secondary gene pool comprises of *S. faberi* (giant foxtail millet) and *S. verticillata* (bristly grass) with AABB genome and tertiary gene pool includes the landraces of *Setaria* viz.,*grisebachii*, *queenslandica*, *pumila* and *pallide-fusca* (Lata et al. 2013).

A rich genetic diversity exist in cultivated and wild foxtail millet for various phenotypic traits including plant height, productive tillers, panicle length, growth habit, flowering period, inflorescence and seed phenology. Phenotypic characterization has indicated that foxtail millet germplasm is highly diverse (Li and Wu 1996; Reddy et al. 2006). Further, Jusuf and Pernes (1985) suggested that the wild species collected from Europe and China established novel genetic variability among cultivated types and wild relatives.

Significant improvement in foxtail millet yield was achieved in China with the development of new cultivars like, Yugu 1 and Zhaogu 1. Lateon, the focus shifted from breeding high yielding foxtail to high quality traits (Pan et al. 2012; Sang 2011; Wang 2008). A novel foxtail millet genotype 'Super Early Maturation No.2' developed by Institute of Millet Crops, China with super early maturity within 63 days, increased iron content (54.1 mg/kg^{-1}), high crude fat (6.24%) and protein content (14.36%) is also available. India has also released about 40 varieties of foxtail millet, which are currently in cultivation. Only 22% of these varieties are developed through hybridization and selection. Although, foxtail millet research began with the development of male sterile lines through hybridization of *Setaria verticillata* with *Setaria italica* to enhance heterosis (Zhu et al. 1991), but success in hybrid seed production could not be achieved up to economic level due to some unknown factors. Zhi et al. (2007) identified a cytoplasmic male sterile (CMS) line from a cross between green and cultivated foxtail millet. Likewise, various researchers (Cui et al. 1979; Du and Wang 1997) have attempted the usage of male sterile lines to develop hybrid cultivars like Suanxi 28 × Zhangnong 10 and Jigu 16. A high degree of cross transferability of SSR markers, Intron-length polymorphic markers, through in silico mining of foxtail sequences to barnyard millets (Pandey et al. 2013; Kumari et al. 2013; Prasad and Muthamilarasan 2015). Further, single nucleotide polymorphic markers, microsatellites, expressed sequenced tags, and sequences of miRNA-based and transposable elements-based markers have also been developed in foxtail millet that could be used in breeding high-yielding and disease-resistant genotypes. The genetic analysis has determined the genes, B, I and K controlling seed colour viz., BB produces gray seeds, two homozygous genes produce deeper color, whereas KK produces dark yellow seeds (Wang et al. 1998). The genotype carrying BBIIKK genes produces black seed color. Different loci control the traits, basal and axillary branching. Many primer pairs were designed from microRNA sequences mapped to the foxtail millet genome (Yadav et al. 2014). Efficient methods for genetic transformation systems and to generate transgenic plants in foxtail millet and its wild relative *Setaria viridis* have been established (Jency et al. 2016, 2020; Jia 2013).

Proso millet *(Chenna/Barri) Panicum milliaceum L., 2n=4x=36*

Proso millet was first domesticated around 10,000 years ago in China (Hunt et al. 2014; Lu et al. 2009) and from there it had spread to Central Eurasia and to Eastern Europe (Miller et al. 2016). Evolutionary studies are limited due to the dissimilarity between the cultivated proso millet with its wild relatives (*P. miliaceum* subsp. *ruderale*) and weedy forms. Hunt et al. (2011) highlighted two distinct gene pools, "Eastern" and "Western," based on genetic diversity and phylogeographic studies. Central Asia and Eastern Europe are the secondary centers of origin of proso millet, but needed resolve the chronological inconsistencies.

The basic chromosome number of proso millet is x=9 in descending order from chromosome number $x = 10$ basic (Hiremath et al. 1990). Chromosomal *in situ* hybridization with genomic DNA and phylogenetic data supported the allotetraploid origin of proso millet, with *Panicum capillare* as a close relative and *Panicum repens* as an ancestor (Hunt et al. 2014). Several subspecies of diploid and tetraploid nature, such as, *P. sumatrense, P. psilopodium, P. capillare P. repens* have evolved through speciation involving inter-specific hybridization as also revealed by molecular analysis. The studies have indicated allotetraploid origin of *P. miliaceum* and *P. capillare* (or a close relative) as the maternal ancestor *Panicum milliaceum*.

The development of high-yielding genotypes through hybridization and selection is are 29% of a total of 30 released and cultivated in India but only a few have entered the seed chain. Diverse proso millet genotypes, including landraces and cultivars, have been genotyped using polymorphic SSR markers and linkage map are constructed for application in molecular breeding approaches (Cho et al. 2010; Rajput and Santra 2016a). The cluster analysis resulted in different groups based on geographic origin, pedigree and agronomic traits, variable heterozygosity, and short geographical distance between groups (Flajsman et al. 2019). Advanced molecular analysis using genic-SSR motifs identified huge unigene sequences and different repeat motifs, di-, tri- and tetra-nucleotide repeat (Desai et al. 2021) in proso millet. Identifying chloroplast genome sequence and de-novo reference-guided assembly should facilitate determining more DNA markers for that could be used as barcodes, genetic diversity, evolution and the phylo-geography (Cao et al. 2021).

Kodo millet *(Kodo), Paspalum scrobiculatum L., 2n=4x=40*

Kodo millet is an annual grain that is grown in India, Nepal, Southeast Asia, and West Africa. It is grown as a minor crop in most of these areas, except for the Deccan plateau in India, where it is grown as a major food source. The presence of *Paspalum scrobiculatum* var. *commersonii*, a wild variety indigenous to Africa, and occurrence of *P. scrobiculatum* in wild as a perennial in West Africa, where it is eaten as a famine food reflect that Kodo millet originated in tropical Africa. It probably traveled to the Indian subcontinent across the Indian Ocean, possibly through natural processes like wind (Porteres 1976). It was domesticated in India some 3000 years ago (Kajale 1977) and is still being domesticated in the Deccan Plateau, where it has become a major food crop. Under artificial inoculation, the performance of 25 pre-release and 13 released cultivars of kodo millet was evaluated for Striga, an obligate hemiparasitic root parasite, resistance. Resistance was found in eight cultivars *viz.,* KOPN 21, RPS 594, RPS 531, KOPN 8, RPS 745, RBK 155, RPS 630 and KOPN 22 (Jain et al. 2018). Nagaraja et al. (2022) reported that about 40 varieties of kodo millets have been released in India.

However, the detailed information on phylogeographic and evolutionary history and to estimate their gene pool range that shall aid in genetic improvement and breeding is very limited and hence, significant attention to explain various aspects of origin, domestication, cultivation etc.

Barnyard millet *(Sanwa), Echinochloa spp. , 2n = 6x = 36*

Barnyard millet, an allohexaploid, whose origin is traced back to its wild form *E. colona* (L.) (Jungle rice) and exhibits a parallel line of evolution in India and Africa. Among the cultivated and wild species of barnyard millet, two most popular species are *Echinochloa frumentacea* (Indian barnyard millet) and *Echinochloa esculenta* (Japanese barnyard millet) (Sood et al. 2015). The four races of *Echinochloa frumentacea* that are widely cultivated in Central Africa, India, Malawi, Nepal, Pakistan and Tanzania are *stolonifera, intermedia, robusta* and *laxa* (Upadhyaya et al. 2014). The *Echinochloa esculenta* is believed to be originated from wild *E. crusgalli* (*L.*) (Barnyard grass) and was domesticated 4,000 years ago in the temperate regions of Japan (De Wet et al. 1983; Doggett 1989).

The worldwide barnyard millet germplasm collection is maintained in Japan, India, China and the United States. The collection is maintained in India at the National Bureau of Plant Genetic Resources, All India Coordinated Research Project (AICRP) on Small Millets, and ICRISAT (Gomashe 2017). High level of genetic diversity in barnyard millet germplasm for morphological and agronomic traits (Dhanalakshmi et al. 2019; Raju et al. 2022; Nandini et al. 2020; Nilavarasi et al. 2020; Deepak et al. 2023; Vanniarajan and Chandirakala 2020; Kuraloviya et al. 2022; Joshi et al. 2015; Sood et al. 2015; Mehta et al. 2005), grain micro-nutrient content (Prabha et al. 2017), salinity tolerance (Williams et al. 2019), shoot fly resistance (Padmaja et al. 2022; Rawat et al. 2019), grain smut resistance (Joshi et al. 2015) and stem borer (Rawat et al. 2019) is observed. Superior trait specific donors are also identified (Williams et al. 2019; Sood et al. 2015;; Padmaja et al. 2022; Geethanjali et al. 2023; Kuraloviya et al. 2022) for utilization in barnyard improvement.

A high level of genetic diversity for yield and related traits in barnyard millet has been witnessed (Vikram et al. 2020). Subsequently, various researchers have also identified high-yielding varieties coupled with high zinc and iron (Renganathan et al. 2020; Renganathan et al. 2018), and high-yielding coupled with grain smut resistance (Rawat et al. 2020) containing segregating barnyard millet lines. A novel barnyard millet genotype B29 with 42–146.4% faster de-hulling percentage relative to other check varieties is registered by Gupta et al. (2014). About 23 varieties of barnyard millet have been released, but only five are occupying the area under barnyard cultivation in India. Therefore, in addition to the focus on higher grain yield, millet breeding programs should also include the registration strategy for unique traits observed in landraces, germplasm, or rejected entries from the evaluation trials.

Little millet *(Moraiyo, Kutki/shavan; Panicum sumatranse, 2n=36)*

Little millet (*Panicum sumatrense* Roth. Ex Roem. & Schult.), also known as Kutki, is a self-pollinating tetraploid crop cultivated across India, Nepal, and Myanmar (Manimozhi et al. 2015). A neglected crop like other minor millets, little millet thrives in the tropics and subtropics, particularly on light red soils and hillsides, where it is traditionally grown by tribal farmers as a rainfed crop. Due to its drought tolerance and ability to withstand harsh climatic conditions, little millet can provide food and nutritional security in areas where other crops fail. Similar to other millets, it is a rich source of vitamin B, minerals like potassium, phosphorus, iron, zinc, and magnesium (Manimozhi et al. 2015). The nutritional profile of little millet includes proteins (9.80–12.49 g/100 g), fat (2.87–5.09 g/100 g), ash (0.98–4.78 g/100 g), crude fiber (0.49–8.72 g/100 g), and carbohydrates (62.25–76.59 g/100 g) (Chandel et al. 2014). Notably, a study by Chandel et al. (2014) using molecular markers identified little millet line RLM-37 to be high in iron (32.20 ppm) and zinc (32.40 ppm). Additionally, being gluten-free, little millet has become a natural choice for people with celiac disease or wheat allergies and intolerances (Satunui et al. 2010). Despite its potential, little millet remains the least studied among small millets. Research on the genetic diversity of Indian little millet (*P. sumatrense*) has been limited to morphological traits (Arunachalam et al. 2003; Selvi et al. 2015).

Origin and domestication

Little millet originated and was likely domesticated in India (de Wet et al. 1984). It's considered a domesticated complex of the weedy grass *Panicum psilopodium*, which is thought to be the wild ancestor of the cultivated subspecies *Panicum sumatrense* subsp. *sumatranse*. Interestingly, these two subspecies can interbreed where they overlap geographically, creating fertile hybrids. These hybrids can sometimes become weeds within cultivated little millet fields (de Wet et al. 1984). Today, little millet is widely grown across India, Nepal, and western Myanmar. In India, it's particularly important in tribal agriculture, especially in the Eastern Ghats region.

Genetic and molecular improvement of little millet

Despite a reported fair amount of ecological genetic diversity in Indian little millet (*Panicum sumatrense*) (Arunachalam et al. 2005; Upadhyaya et al. 2014), its potential for genetic improvement in yield remains largely untapped. While researchers have conducted morphological characterization and evaluation of little millet germplasm (Nirmalakumari et al. 2010), concerted breeding efforts have been limited, particularly for little millet compared to other small millets. About 38 varieties have been released, but most cultivated varieties are simply selections from landraces. Scattered research attempts using conventional approaches, interspecific hybridization, and mutagenesis have yielded limited success. For example, attempts have been made to induce mutations using gamma radiation, but with modest results.

However, there are promising avenues for future research. An *in vitro* regeneration protocol has been established for little millet (Vasanth and Jayabalan 2003), opening the door for exploring transgenic work to introduce genes for stress resistance. Additionally, researchers have made progress in understanding the genetic makeup of little millet. Sivakumar et al. (2006) reported the cloning and structural analysis of an Indian little millet zein-like storage protein, and Chandel et al. (2017) identified and characterized a grain micronutrient-related *OsFRO2* rice gene ortholog from micronutrient-rich little millet.

Furthermore, determining relationships among little millet populations is crucial for utilizing plant genetic resources and implementing genetic improvement through molecular technologies. Molecular markers have already been used to identify genotypes with desirable traits, as evidenced by Tiwari et al.'s (2018) report of high molecular diversity in a large collection of little millet germplasm. Desai et al. (2021) recently published research on genic microsatellite marker characterization and development in little millet using transcriptome sequencing, offering another tool for future genetic improvement efforts.

Browntop millet *[Brachiaria ramose (L.) Stapf. = Urochloa ramosa (L.) T.Q. Nguyen]*

Browntop millet, commonly known as pedda-sama and korne, is a small-seeded annual grass cultivated as grain crop, primarily on the marginal lands in dry areas in temperate, sub-tropical and tropical regions. It is domesticated in South India, Deccan region and distributed across the USA and India. It is a nutritionally rich crop with content of Calcium (28.0mg), Iron (7.72mg), Phosphorus (276mg), Potassium (60mg), Magnesium (94.5mg), Manganese (1.99mg), Sodium (7.70mg), Zink (2.50mg), Copper (1.23mg), etc. The carbohydrate, crude fiber, and fat is available at 71.32 gm, 8.06–16.08%, 1.89 gm, respectively. The protein content in the seeds of browntop millet ranges from 11.64% to 10.72% (Singh et al. 2022). Besides, it contains phytochemicals such as flavonoids, quinones, tannins, and resin. However, the phylogeographic information on browntop millet is hitherto unavailable. Therefore, emphasis should be given to explain its evolutionary history and to estimate its gene pool range for effective genetic improvement and breeding.

Future prospects for minor millets

Minor millets hold immense potential due to their rich genetic diversity for protein and micronutrients. However, their production and productivity currently lag behind major millets (Dwivedi et al. 2020). Despite possessing adequate genetic variation in germplasm collections, breeding efforts in minor millets have primarily focused on selecting desirable genotypes from landraces and releasing them directly as cultivars. These crops are often cultivated on marginal lands with harsh environments and limited resources. In addition, their inherently low yield potential and a historical lack of focus on genetic improvement for yield and desirable traits has contributed to a decline in the cultivation area of minor millets since the Green Revolution.

To re-popularize minor millets, a two-pronged approach is needed. First, creating sustained consumer demand with awareness about nutritional value is crucial. Second, ensuring the availability of quality seeds for farmers is essential. Seed availability is a persistent challenge across many crops, with demand often exceeding supply. Farmers often resort to growing traditional varieties and landraces instead of potentially higher-yielding improved varieties. Addressing this issue requires a multi-stakeholder approach. Very few out of released varieties of minor millets have entered the seed chain. Public and private seed agencies, along with farmers' organizations, should be encouraged to participate in producing breeder, certified, and foundation seeds for minor millets. Additionally, seed requirement assessments based on standard procedures and the inclusion of recently released high-yielding varieties into the seed chain are necessary steps. Finally, timely placement of breeder seeds with production agencies and proper integration into the production chain are crucial for ensuring a functional seed system and the availability of quality seeds for farmers.

It's important to note that new breeding techniques like marker-assisted selection and genomic selection are being explored for minor millets. These techniques have the potential to accelerate genetic improvement and develop cultivars with enhanced yield, stress tolerance, and other desirable traits.

Pseudocereals

Pseudo-cereals are a group of seeds made up of higher bran fraction to endosperm than common cereals. These seeds are also consumed like cereals but come from different plants belonging to the non-graminaceous section. Some of the most popular pseudo-cereals include quinoa, amaranth, chia seeds, and buckwheat. These ancient grains are a good protein, fiber, vitamins, and minerals source. One of the biggest advantages of pseudo-cereals is that they are naturally gluten-free. Their mild, nutty flavor makes them a versatile ingredient that can be enjoyed in various dishes. From breakfast bowls and salads to baked goods and savory main courses, pseudo-cereals can add a unique taste and texture to our meals. India hosts various pseudocereals; however, for brevity, we will review only two of them here, i.e. Amaranth and Buckwheat.

Amaranth *(Amaranthus hypochondriacus L., 2n= 32)*

Amaranth, a promising pseudocereal, stands out for its superior nutritional profile compared to traditional cereals. It boasts a higher content of fiber (8%), essential minerals (calcium, magnesium, iron), and vitamins (C, β-carotene, folic acid) (Gupta et al. 2005). Additionally, amaranth offers a complete protein source, containing 22.5% protein and all but 3 of the essential amino acids, particularly lysine (Schmidit et al. 2021; Anuradha et al. 2023). This gluten-free grain is also rich in bioactive compounds like vitamin C, amaranthine, rutin, and carotenoids, and boasts valuable grain oil with squalene, vitamin E, phytosterols, and fatty acids (Schmidit et al. 2021; Bressani et al. 1992). Beyond its impressive nutritional content, amaranth is a hardy plant requiring minimal inputs and thrives under stress, drought, and salinity conditions. Similar to other millets, it exhibits high genetic variability. However, progress in developing high-yielding varieties is slow due to limited research, shortage of genomic resources, and easy accessibility of the germplasm resources.

Origin and history

The genus Amaranthus likely originated in the Americas, with a much higher number of native species there (60 nos.) compared to the Old World (15 nos.) (Brenner et al. 2000). Grain amaranths primarily self-pollinate but can occasionally outcross (up to 34%) (Hauptli and Jain 1985; Brenner et al. 2000). These species have unique flowers with both male and female parts (compound monoecious) and a specific arrangement of clusters called glomerules (Brenner et al. 2000).

Domestication and geographic distribution

Three main Amaranthus species belonging to Amaranthaceae are cultivated for their edible seeds: *A. cruentus* L. and *A. hypochondriacus* L. from Central and North America (Mexico and Guatemala) and *A. caudatus* L. from South America (Andean regions) (Sauer 1967; Santra et al. 2024). Genetic analysis suggests a common ancestor (*A. hybridus*) for these three species (Clouse et al. 2016). Interestingly, phylogenetic studies reveal separate domestication events in different regions. *A. hybridus* from South America appears closer to *A. quitensis* and *A. caudatus*, while the Central American *A. hybridus* is closer to the two northern crop species (Stetter and Schmid 2017). This suggests independent domestication events based on geographic distribution (Stetter and Schmid 2017).

Amaranth is a highly adaptable crop, thriving in both temperate and tropical climates. Cultivated varieties within the three main species exhibit significant genetic diversity. This diversity provides a valuable resource for breeders to develop improved lines with traits suited for modern grain production.India has a widespread cultivation of amaranth, utilizing it for its grain, green leaves (as a vegetable), and ornamental purposes (Brenner et al. 2000).In recent decades, its potential as a nutritious food ingredient and source of pharmaceutical compounds has sparked renewed interest (Barba de la Rosa et al. 2009). Furthermore, amaranth's resilience to environmental stresses like high temperatures, drought, and low-input conditions makes it a valuable crop (Barba de la Rosa et al. 2009). Its exceptional nutritional value and oil quality further enhance its appeal. However, by the mid-20th century, global amaranth cultivation had dwindled to small plots in Mexico, the Andean highlands, and the Himalayan foothills of India and Nepal (Kauffman 1990). Even today, some traditional farmers are replacing local amaranth landraces with higher-yielding modern crops. Fortunately, recent recognition of amaranth's nutritional prowess and broad adaptability has reignited cultivation efforts. While other cereal crops have established genetic improvement standards, amaranth lags behind (Kauffman 1990). Therefore, focused efforts using novel breeding technologies are crucial to improve agronomic and physiological traits like seed size, pest and disease resistance, seedling vigor, reduced seed shattering, lodging tolerance, uniform maturity, easy threshing, low saponin content, adaptation to local photoperiods, and overall nutritional quality.

Genomic constitution and ploidy level

Amaranth species exhibit variation in chromosome number. Notably, *A. dubius* has 32 chromosomes (n = 32) compared to the more common n = 16 or 17 in other species. Species like *A. cruentus* and *A. hypochondriacus* have n = 16, while *A. tricolor, A. spinosus*, and others have n = 17 (Brenner et al. 2000). The total genome size is estimated to be around 500 Mbp (Lightfoot et al. 2017; Stetter and Schmid 2017). Polyploidy has also been observed, with *A. dubius* being an example (2n = 64) (Khoshoo and Pal, 1972). Interestingly, grain amaranths are believed to be paleo-allotetraploids. However, crosses between *A. tricolor, A. cruentus*, and *A. dubius* are incompatible (Brenner et al. 2000).

Genetic and molecular improvement in grain amaranth

Germplasm collections in gene banks have played a vital role in breeding advancements for minor millets and pseudocereals. A prime example is the Rodale Research Center (RRC) collection in Pennsylvania, USA. This collection significantly strengthened amaranth breeding programs in North America and China, with most released cultivars in these regions sharing RRC germplasm lines (Joshi et al. 2018). The well-known 'Plainsman' cultivar, derived from RRC lines, exemplifies successful germplasm utilization. Its lodging resistance, shattering resistance, and early maturity have made it the dominant grain amaranth in the United States (Stallknecht and Schulz-Schaefer 1993). National gene banks play a crucial role in conserving diversity. For example, India maintains about amaranth accessions from 11 countries (Joshi et al. 2018). *Amaranthus hypochondriacus* dominates these collections, followed by *A. caudatus*. India also demonstrates the value of germplasm resources. A total of nine varieties of amaranth have been released so far. The 'Annapurna' cultivar, a direct selection from a local hilly region line (Pauri, Uttarakhand), showcases the potential of local varieties. Unlike minor millets, hybridization in pseudocereals like amaranth is challenging due to the small florets and difficulty in emasculation. Traditional breeding methods like mass and pure-line selection are more prevalent. However, advancements like hot water emasculation techniques have enabled the development of some hybrid varieties using the pedigree selection method.

Mutation breeding has shown promise in improving traits like 1000-seed weight and lysine content in amaranth (Keckesova et al. 2012; Hricová et al. 2016). Additionally, interspecific hybridization remains largely unexplored to tap into the valuable genetic diversity of wild pseudocereals. However, a successful example exists where researchers transferred genes for reduced seed shattering from *A. powellii* to cultivated amaranth species (*A. hypochondriacus* and *A. cruentus*) (Brenner 2002).

Scientists have also identified genes controlling various morphological and agronomic traits in amaranth. Studies have revealed the genetic control of flowering time (Kulakowand Jain 1985), seed coat color, and leaf pigmentation (Gupta and Gudu 1990), as well as seedling and inflorescence color (Kulakowand Jain 1985). Okunu and Sakaguchi (1982) even pinpointed a single major gene influencing starch content.Another breakthrough involves male sterility, a desirable trait for breeding purposes. Researchers identified a single recessive gene (*ms)* governing male sterility in *A. hypochondriacus* (Peters and Jain, 1987; Gudu and Gupta 1988). Similarly, herbicide tolerance has been successfully transferred from *A. hybridus* to cultivated amaranth species (Trucco et al. 2006). The complete genome sequence of *Amaranthus hypochondriacus* L. opens new avenues for identifying genes responsible for valuable traits. Only a few genes have been identified, including those for squalene synthase (SQS), vitamin C synthesis (VTC2), and lysine synthesis.

Looking ahead, advancements in breeding techniques like CRISPR/Cas, TILLING, and RNA interference (RNAi) hold immense potential for targeted genetic improvement in pseudocereals. The availability of the complete genome sequence further accelerates this process by enabling the identification of key genes. Additionally, research utilizing diverse molecular markers has successfully estimated genetic variation, established phylogenetic relationships, and identified markers linked to agronomic traits (Ramakrishnan et al. 2016).

Amaranth's resilience positions it as a valuable crop in a changing climate. Its adaptability to diverse environments makes it a perfect candidate for diversifying cropping systems and fostering resilience (Barba de la Rosa et al. 2009). The growing awareness of its exceptional nutritional value, health benefits, medicinal uses, and industrial applications is already fuelling renewed interest in amaranth cultivation. Furthermore, the rich genetic diversity within the amaranth gene pool offers a significant advantage. Breeders can leverage this variation to develop improved cultivars with enhanced nutritional profiles, potentially reviving widespread amaranth cultivation (Joshi et al. 2018).

Buckwheat *(kuttu, Phaphar/Oggal), 2n=16*

Buckwheat (*Fagopyrum esculentum* Moench., 2n=2x=16) is a flowering plant belonging to the Polygonaceae family. The genus *Fagopyrum* comprises about 30 perennial and annual species, with chromosome numbers varying from diploid (2n=2x=16) to hexaploid (2n=6x=48). Only two diploid species, *Fagopyrum esculentum* (common buckwheat, kuttu) and *Fagopyrum tataricum* (tartary buckwheat), are cultivated. *F. esculentum* thrives in temperate regions of the northern hemisphere (Eastern Europe to Japan), while *F. tataricum* is adapted to high altitudes (Rana, 2004; Zhou et al. 2018). In India, buckwheat cultivation is widespread in the Himalayan foothills, from Ladakh to Arunachal Pradesh. Tartary buckwheat, on the other hand, is primarily grown in the mountainous regions of China and the Himalayas (Zhou et al. 2018).

Nutritional status

Buckwheat grains are a rich source of nutrients, boasting 13.3% protein with a balanced amino acid profile, gluten-free flour, 17.8% dietary fiber, 7.4 g of fat, and 72.9 g of carbohydrates per 100 g grain (Krkoskova and Mrazova, 2005). They are also a good source of minerals like calcium (1101 mg), iron (4.0mg), magnesium (390 mg), phosphorus (330mg), manganese (3.4 mg), zinc (0.8 mg), and potassium (450mg), and vitamins like thiamine (3.3 mg), riboflavin (10.6 mg), and possess high antioxidant properties (Krkoskova and Mrazova, 2005; Chrungooand Chettry, 2021). Buckwheat flour and groats are used to make various dishes like noodles, dumplings, pancakes, porridge, and soups.

Adaptability and genetic diversity

Buckwheat is a short-season crop maturing within 70-90 days. It thrives under diverse environmental conditions, including marginal lands, rocky soils, and low-input settings with minimal tillage. It is mainly cultivated in India at high altitudes with low temperatures and strident conditions in the Himalyas and part of Nilgiris. Recently, a variety Him Phaphra was released from germplasm line IC341589 of F. tataricum (Chandora et al. 2022).

The protein content in buckwheat flour surpasses that of rice, wheat, millet, sorghum, and maize. Buckwheat protein is rich in lysine and arginine, essential amino acids often limiting in other cereals. Buckwheat's nutraceutical properties position it as a healthy food crop. However, seed shattering due to weak pedicels and self-incompatibility challenges yield maximization (Chrungoo and hettry 2021).

Over 10,000 buckwheat accessions are maintained worldwide, with nearly half residing in gene banks located in East and South Asian countries (Zhou et al. 2018). Sustainable utilization of this genetic diversity is crucial for optimizing buckwheat production. Studies on morphological traits of *Fagopyrum* species from the Indian Himalayas revealed that accession IC13145 belongs to *F. esculentum*, and IC13141, previously identified as *F. tataricum*, is likely *F. esculentum* as well (Rout and Chrungoo, 2007). This highlights the diverse nature of buckwheat germplasm. Further research using protein profiles supports a close relationship between *F. esculentum* and *F. tataricum* (Rout and Chrungoo, 2007; Yabe et al. 2008).

Challenges and opportunities for genetic improvement

Yield instability due to flower abortion and seed shattering is a major challenge in buckwheat cultivation. Seed shattering is attributed to weak pedicels controlled by two complementary dominant genes and the formation of an abscission layer. Research suggests a possible link between seed shattering and the number of vegetative nodes on the main stem (Matsui et al. 2004; Wang et al. 2005). Several shattering-resistant buckwheat varieties have been developed (Suzuki et al. 2012).

Despite a long history of cultivation, conventional breeding for buckwheat improvement has achieved limited success, likely due to its complex floral structure and self-incompatibility. While research has focused on bioactive molecules, development of molecular markers and resources for quantitative trait loci (QTLs) remains limited. Recent advancements in whole genome sequencing pave the way for integrating phenomics and genomics tools to improve buckwheat quality. Wide hybridization with self-compatible wild species like *F. homotropicum* using backcrossing and embryo rescue techniques offer possibilities for overcoming self-incompatibility (Woo and Adachi, 1997). Studies have identified genes controlling self-incompatibility and developed markers to differentiate between genotypes (Adachi et al. 2000; Nagano et al. 2000; Yasui et al. 2016). Thus, Buckwheat offers a unique combination of nutritional value, adaptability, and potential health benefits. By addressing challenges related to yield and harnessing the power of modern breeding techniques, buckwheat can be positioned as a valuable crop for sustainable food security.

Bottlenecks in minor millets and pseudocereals breeding

Despite adequate genetic variation reported in crop germplasm repositories (Joshi et al. 2023a), breeding efforts in minor millets and pseudocereals have primarily focused on selecting desirable genotypes from landraces and directly releasing germplasm lines as cultivars. This approach has limitations: 1). Intricate floral structure of these species makes artificial hybridization more challenging compared to other crops (Joshi et al. 2023a); 2). Effectively incorporating valuable traits from exotic germplasm into breeding populations is cumbersome. Hybridization often results in very few viable seeds (≤ 1%), necessitating improved methodologies (Bhinda et al. 2023). While minor millets and pseudocereals boast rich nutritional profiles, they are not well-suited to modern agricultural systems. Therefore, breeding programs should prioritize traits like: Synchronized flowering for efficient management; Increased grain size for improved yield; reduced seed shattering for minimized harvest losses; reduced plant height to facilitate mechanical harvesting and prevent lodging; reduced levels of anti-nutritional factors and allergens for enhanced safety (Joshi et al. 2018, 2019; Sood et al. 2019). Diseases, insects, and weeds significantly impact minor millets, causing yield reductions exceeding 30% (Burkill 1985). Isolated fields can suffer complete yield loss due to bird predation (Sood et al. 2015). Compared to minor millets, pseudocereals generally face fewer pest and disease pressures. However, frost susceptibility is a major production constraint for quinoa (F. esculentum) (Zhou et al. 2016). Therefore, developing biotic and abiotic stress tolerant cultivars including herbicide tolerance could be beneficial.

How to popularize millets

Millets, also known as "nutri-cereals," are powerhouses of nutrition, providing essential energy, protein, healthy fats, minerals, vitamins, and fiber. Their low glycemic index makes them ideal for blood sugar management, and they're naturally gluten-free, a boon for those with dietary restrictions. Dieticians recommend millets for everyone, from infants and children to lactating mothers, the elderly, and those recovering from illness, due to their immune-boosting properties. Despite their high nutritional value, millets haven't received the recognition they deserve. To change this, we need to educate people about the exciting world of millets. To achieve this goal, the United Nations has declared the year 2023 as 'International Year of Millets (IYM)". Govt. of India took special initiatives to make millets popular and household food for all.It has rechristened millets as 'Shree Anna', a highly valued food. The program of IYM could rejuvenate global attention generatingspecial interest on various millets.

Each variety boasts unique characteristics and regional specialties. Simple preparation methods can unlock their versatility in modern cuisine. Chefs worldwide are already creating innovative recipes using techniques like boiling, steaming, toasting, and even fermenting.Ready-to-eat options like millet cookies, flour, rotis, batter mixes, noodles, and even chocolate bars can further increase their appeal. Traditional dishes like nasi goreng (Southeast Asian fried rice) can be made healthier with kodo millet, and familiar favorites like *vadas* can be reimagined using the same grain. From breakfast staples like upma (made with little millets) to comforting winter meals like bajra rotis (flatbreads) in North India, millets offer endless possibilities. Different millets cater to seasonal needs. Jowar (sorghum), ragi, and bajra (pearl millet) are rich in carbohydrates and micronutrients, perfect for winter's higher energy demands. In contrast, kodo millet's cooling properties make it ideal for summer, while ragi, a South Indian staple, offers a variety of delicious options like *mudde*, porridge, and *dos*a. Foxtail millet adds a delightful crunch to salads, and Amaranth makes a unique and nutritious crust for fried fish. The possibilities are endless! The journey towards incorporating millets into our daily lives has begun. Hotels and restaurants are leading the charge by introducing innovative millet-based dishes. Millets offer a fantastic opportunity to supplement our reliance on rice, wheat, and maize. While they may not completely replace these staples, they can be a valuable addition to creating more balanced and nutritious diets, especially for children consuming excessive carbohydrates. Millets aren't just good for consumers; they're also a boon for farmers. These hardy grains are naturally drought-resistant, require minimal water (often rainfed), and are less susceptible to pests and diseases compared to other cereal crops. Their longer shelf life makes them ideal for storage and reduces post-harvest losses. To create wider awareness; engaging advertising campaigns can highlight the health benefits of millets. Additionally, voluntary services teaching people how to cook delicious and diverse millet dishes can further increase their popularity.

Beyond food, millets offer a wealth of other uses. They can be used as animal fodder, a source of sugar, and even biofuel, providing farmers with additional income streams. With their low cultivation costs, millets have the potential to significantly improve farmer profitability.

Authors' contribution

All the authors' have contributed equally.

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