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REVIEW

The role of phenomics and genomics in delineating the genetic basis of complex traits in millets

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Abstract

Millets, comprising a diverse group of small-seeded grains, have emerged as vital crops with immense nutritional, environmental, and economic significance. The comprehension of complex traits in millets, influenced by multifaceted genetic determinants, presents a compelling challenge and opportunity in agricultural research. This review delves into the transformative roles of phenomics and genomics in deciphering these intricate genetic architectures. On the phenomics front, high-throughput platforms generate rich datasets on plant morphology, physiology, and performance in diverse environments. This data, coupled with field trials and controlled conditions, helps to interpret how the environment interacts with genetics. Genomics provides the underlying blueprint for these complex traits. Genome sequencing and genotyping technologies have illuminated the millet genome landscape, revealing diverse gene pools and evolutionary relationships. Additionally, different omics approaches unveil the intricate information of gene expression, protein function, and metabolite accumulation driving phenotypic expression. This multi-omics approach is crucial for identifying candidate genes and unfolding the intricate pathways governing complex traits. The review highlights the synergy between phenomics and genomics. Genomically informed phenotyping targets specific traits, reducing the breeding size and cost. Conversely, phenomics identifies promising germplasm for genomic analysis, prioritizing variants with superior performance. This dynamic interplay accelerates breeding programs and facilitates the development of climate-smart, nutrient-rich millet varieties and hybrids. In conclusion, this review emphasizes the crucial roles of phenomics and genomics in unlocking the genetic enigma of millets.

1 | INTRODUCTION

Millets, a group of small-seeded cereal grains, have garnered increasing attention in recent years due to their significant importance in agriculture and their potential to address various global food and nutrition challenges (Rachie, 1975; Vetriventhan et al. 2020). With an ever-expanding world population, millets play a crucial role in addressing food security, dietary diversity, malnutrition, human health, fuel, and climate change. The major millets (prominent types) encompass sorghum (*Sorghum bicolor*), pearl millet (*Cenchrus americanus*, synonym *Pennisetum glaucum*), and finger millet (*Eleusine coracana* (L.) Gaertn.), while the minor millets (lesser-known ones) include kodo millet (*Paspalum scorbiculatum* L.), barnyard millet (*Echinochloa crusgalli* (L.)), proso millet (*Panicum miliaceum* L.), little millet (*Panicum sumatrense* Roth. Ex. Roem. & Schult), and browntop millet (*Brachiaria ramosa* (L.)). These small millets are also called “wonder cereals.” Often referred to as “Nutri-Cereals” (or Shree anna in India), millets have earned these titles due to their exceptional nutritional and health benefits (Barretto et al. 2021).

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Millets play a crucial role in promoting sustainable and resilient farming systems in agriculture. These hardy, drought-resistant crops are well-suited to a range of agro-climatic conditions, making them a valuable option for farmers facing climate change-induced uncertainties. Millets require less water compared to major cereals like rice and wheat, reducing the pressure on water resources (Sharma et al. 2021). Moreover, they exhibit a shorter growth cycle, allowing for multiple harvests in a year, enhancing food security and income generation for small-scale farmers. Millets are also excellent rotational and intercropping options, helping to improve soil health and reduce pest and disease pressures in crop fields. Their efficient use of nutrients and minimal need for synthetic inputs contribute to more sustainable and environmentally friendly farming practices.

Beyond agriculture, millets have gained recognition as a highly nutritious dietary choice. They are rich in essential micro- and macronutrients, including dietary fiber, vitamins, minerals, and antioxidants (Table 1). In addition, millets and minor millets are rich in phytochemicals, viz., alkaloids, flavonoids, phenolics, and saponins (Rao et al. 2011). Millets are gluten-free, making them a valuable dietary option for individuals with gluten sensitivity or celiac disease (Deshpande et al. 2015; Vetriventhan et al. 2020). For example, Kodo millet has the maximum content of phenolic compounds (10.3%), and finger millet is rich in reducing sugars (391.3 mg g^{-1} each) (Rao et al. 2011). Ferulic acid, predominantly identified as free phenolic fractions, was recorded highest in kodo millet (99.35 mg/100 g), followed by finger millet and foxtail millet with 57.04 mg/100 g and 54.65 mg/100 g of ferulic acid, respectively (Goudar et al. 2023). Similarly, proso millet is the richest source of protein (12.610 mg/100 g) among the millets (Goudar et al. 2023). It is also noteworthy to mention that finger millet has the highest source of calcium among cereals (>300 mg/100 g), which is believed to help alleviate calcium deficiency in Asia and Africa (Maharajan et al. 2021, 2022).

The dietary versatility of millets is another remarkable feature. They can be incorporated into a variety of culinary preparations, from porridges and bread to dosas, and are often used in traditional dishes in different parts of the world (Dewan et al. 2022; Deshpande et al. 2021). The diversity of millet species, including pearl millet, finger millet, and foxtail millet, ensures a wide range of flavors and textures, catering to diverse tastes and preferences (Goyal et al. 2021; Alavi et al. 2019). Overall, millets are indispensable in both agriculture and human diets. Their role in promoting sustainable farming practices, mitigating climate change impacts, and improving food and nutrition security makes them a valuable asset in addressing the complex challenges facing our planet today. Recognizing the importance of millets and promoting their cultivation and consumption can contribute significantly to building a more resilient and healthy food system for the future (Ceasar and Maharajan, 2022; Mustafa et al. 2021).

2 | HISTORY AND THE NEED FOR OMICS TO STUDY MILLETS

Staple crops like rice, maize, and wheat (Farooq et al. 2022; Syed et al. 2022) are particularly vulnerable to climate-induced risks, threatening global food production. Abiotic stresses such as extreme temperatures, nutrient imbalances, precipitation changes, and issues like salinity, waterlogging, drought, and land degradation (Mahmood et al. 2021; Raza et al. 2021a) pose significant threats. Climate change also amplifies the impact of biotic constraints like insects and fungi, further reducing crop yields and impacting global economies (Vaughan et al. 2018). Food security, a paramount concern since the advent of agriculture, has propelled plant breeding as a fundamental practice to meet escalating food demands. Originating with early human civilizations, crop cultivation and selection have focused on taste, nutrient content, high yield, and resistance to environmental challenges (Dossa et al. 2017). Mendel's laws marked a turning point in 1866, introducing pedigree breeding based on hybridization principles (Mendel, 1866). The revelation of DNA structure in 1953 revolutionized plant breeding, ushering in molecular techniques like marker-assisted selection (MAS) and genetically modified (GM) approaches (Shen et al. 2022), transforming selection from phenotype-based to a combination of genotype and phenotype selection.

Studying omics techniques in plants is a crucial endeavor that has revolutionized the fields of plant biology and agriculture. Omics refers to a set of high-throughput technologies that allow researchers to

TABLE 1 Various millets and their grains' nutritional profiles per 100 g with a moisture level of 12% compared to rice and wheat (Source: Ingle et al. 2023).

Millets	Protein (g)	Fats (g)	CHO (g)	Fibre (g)	Minerals (g)	Iron (mg)	Phosphorus (mg)	Calcium (mg)	Thiamine (mg)	Riboflavin (mg)	Niacin (mg)
Barnyard millet	6.2	2.2	65.5	9.8	4.4	15.2	280	11	0.30	0.1	4.2
Finger millet	7.5–11.7	1.3	72	3.6	2.7	3.6–6.8	283	376–515	0.42	0.19	1.1
Foxtail millet	11.2	4	63.2	6.7	3.3	2.8	290	31	0.59	0.11	3.2
Kodo millet	8.3	1.4	65.9	9	2.6	0.5	188	27	0.33	0.09	0.2
Little millet	7.7	4.7	67	7.6	4.5	9.3	220	17	0.3	0.09	3.2
Pearl millet	8.5–15.1	2.7–7.1	58–70	2.6–4.0	1.6–2.4	70–180	450–990	10–80	0.38	0.21	2.8
Proso millet	12.5	3.1	70.4	7.2	1.9	0.8	206	14	0.41	0.28	4.5
Sorghum	10.4	3.1	70.7	2	1.6	3.4	520	25	0.38	0.15	4.3
Rice	6.8	2.2	78.2	0.2	0.5	0.7	160	45	0.41	0.04	4.3
Wheat	11.8	1.5	71.2	1.2	1.5	5.3	306	41	0.41	0.1	5.1

analyze and understand the complete set of structures and functions of molecules within a plant or biological system (Dai and Shen 2022). Advances in next-generation sequencing (NGS) have paved the way for a new generation of omics. These techniques, which include genomics, resequencing, functional genomics, transcriptomics, proteomics, metabolomics, and more, have revealed each corresponding molecular biological facet integrated with plant systems (Figure 1) (Salt et al. 2008; Houle et al. 2010; Talukdar and Sinjushin, 2015; Wu et al. 2017; Muthamilarasan et al. 2019). An understanding of gene functions and networks under physiological and environmental stress could be gained by integrating several omics techniques (Singh et al. 2013). Multi-omics studies, facilitated by next-generation sequencing technologies, enhance the understanding of metabolic pathways, molecular regulators, and gene functions under various stresses. Comprehensive multi-omics techniques were utilized to identify key factors influencing senescence, stress response, and harvest index in crucial crops like rice, wheat, soybeans, rapeseed, and maize (McLoughlin et al. 2018; Peng et al. 2020; Uchida et al. 2020; Ma et al. 2021; Raza et al. 2021b). The integration of multi-omics data holds promise for interpreting gene functions and networks under diverse environmental stresses.

2.1 | Background of omics techniques in plant breeding

Crop production plays a vital role in feeding the growing global population. To ensure food security, it is essential to improve crop yields, resilience, and nutritional quality. Understanding the genetics of crops is fundamental to achieving these goals. Conventional plant breeding has been the primary method for crop improvement for centuries. It involves selecting plants with desirable traits and crossing them to develop improved varieties. However, this process is time-consuming and often imprecise. Omics technologies are powerful tools that allow us to study the biological systems of living organisms on a global scale. These technologies include genomics, transcriptomics, proteomics, metabolomics, and ionomics each of which focuses on a different

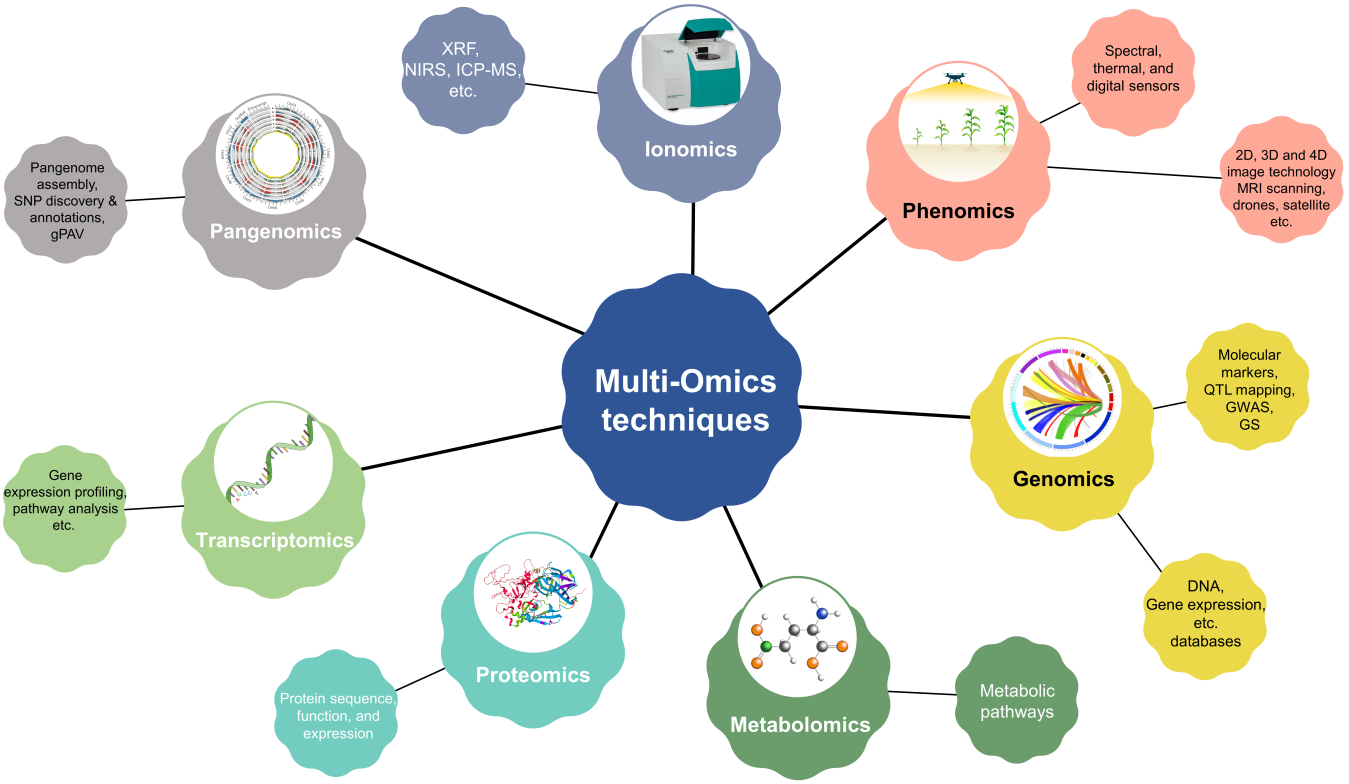

FIGURE 1 **An overview of omics techniques used in plant breeding to improve crops**. Phenomics symbolizes the study of the phenotypic expression of plants using several high-throughput phenotyping platforms. Genomics identifies and characterizes genes responsible for desirable traits, metabolomics represents the study of a complete set of metabolites within a plant, proteomics and transcriptomics explains the entire set of proteins expressed by an organism, and gene expression patterns and pathway analysis, respectively. Pangenomics represents a systematic study of entire genomes so that it can present the entire gene repertoire of a species, including core and accessory genes. Ionomics is a scientific discipline on the cutting edge that employs high-throughput platforms to analyze the elemental composition of plant species comprehensively. This methodology helps facilitate the development of agriculturally important crop varieties equipped with improved nutritional profiles. Integrating data from multiple omics approaches allows researchers and breeders to gain a holistic understanding of the plant's biology. This integrated knowledge can lead to the development of improved crop varieties with enhanced yield, resilience to environmental stresses, and nutritional content. Additionally, it enables precision breeding strategies that are more targeted and efficient in achieving desired outcomes. Created using Adobe Photoshop software.

Box 1 Key omics approaches in plant breeding

1. Genomics: Genomics is the study of the genes and genome, which focuses on the complete set of DNA, structure, function, evolution, mapping, epigenomic, mutagenomic, and genome editing aspects (Muthamilarasan et al. 2019). Genomics can play a vital role in elucidating genetic variation, which may enhance crop breeding efficiency and subsequently result in the genetic improvement of crop species. Structural genomics encompasses sequence polymorphism and chromosomal organization and enables the construction of physical and genetic maps to identify traits of interest for plant biologists. In contrast, functional genomics provides insights into the functions of genes with regard to the regulation of traits of interest. At the genome level, when epigenetic changes occur in the form of histone modifications, DNA, or small RNA methylations, the phenomenon is known as epigenomics. The epigenetics known for heritable changes other than those in the DNA sequence (Strahl and Allis, 2000, Novik et al. 2002). The amalgamation of epigenetics and genomics is referred to as epigenomics, which has arisen as a new omic technique in order to understand genetic regulation and its contribution to cellular growth and stress responses (Callinan and Freinberg, 2006). Mutagenomics deals with mutational events that orchestrate genetic modification in mutant traits. However, pangenomics is defined as the sum of a core genome, shared by all individuals, plus a dispensable genome, partially shared or individual-specific (Tettelin et al. 2005). The pangenome concept refers to the full genomic makeup of a species, which can be divided into a set of core and dispensable genes. The sets of core genes are shared by all individuals, whereas sets of dispensable genes (also known as accessory genes) are individual-specific and/or present in some individuals but not all (Tettelin et al. 2005). Mutagenomics and pangenomics have emerged as recent omics approaches focused on mutagenesis and the pangenome in crop sciences, respectively (Golicz et al. 2016; Goh, 2018; Muthamilarasan et al. 2019).

2. Transcriptomics: Deals with transcriptome, which focuses on the complete set of RNA transcripts that are produced by the genome of an organism in a cell or tissues (Raza et al. 2021a). Transcriptome profiling is dynamic and has emerged as a promising technique to analyze gene expression in response to any stimuli over a certain period of the time (Duque et al. 2013; El-Metwally et al. 2014).

3. Proteomics: A Technique involved in the profiling of total expressed protein in an organism and is categorized into four different parts, including sequence, structural, functional, and expression proteomics (Mosa et al. 2017; Aizat and Hassan, 2018).

4. Metabolomics: Metabolomics is the comprehensive study of metabolites that participate in different cellular events in a biological system. By studying the metabolome of crops, one can identify important metabolites synthesized through metabolic pathways in the plant system (Fiehn, 2002; Baharum and Azizan, 2018).

5. Ionomics: This category of omics deals with ionomes, which refer to the total mineral nutrient and trace elemental composition and represent the cellular inorganic components of plant systems (Salt et al. 2008; Satismruti et al. 2013). In ionomics, the elements that make up an organism are measured quantitatively, and changes in mineral composition are found in response to different physiological stimuli, genetic changes, or developmental conditions.

aspect of the cell's molecular machinery (Weckwerth, 2011; Muthamilarasan et al. 2019; Yang et al. 2021). For a brief overview of the key omics approaches used in plant breeding, refer to Box 1. By studying all these components together, omics techniques can provide a holistic understanding of how genes and proteins interact to produce complex phenotypes, such as crop yield (Naeem et al. 2022), nutritional quality (Paine et al. 2005), drought tolerance in Sorghum (Spindel et al. 2018), rice (Guo et al. 2018), and maize (Shikha et al. 2017), and disease resistance.

2.2 | Significance of omics technologies in crop genetics

Omics techniques have had a profound impact on crop genetics research, with several key implications: 1. Accelerated Breeding: Omics techniques facilitate marker-assisted breeding, a process where specific genetic markers associated with desired traits are used to accelerate the breeding process. This leads to the faster development of new crop varieties with improved characteristics (Mahmood et al. 2022). 2. Precision Agriculture: Genomic information allows for the development of precision agriculture practices, enabling farmers to tailor their crop management strategies based on the genetic makeup of their crops. This can lead to more efficient resource use, increased yields, and reduced environmental impact (Bohra et al. 2020). 3. Resilience to Climate Change: With a better understanding of the genetic basis of stress tolerance, researchers can develop crops that are more resilient to climate change-induced challenges such as drought, extreme temperatures, and increased biotic stress tolerance (Zenda et al. 2021). 4. Nutritional Enhancement: By identifying the genes, proteins, and metabolites responsible for nutritional content in crops, omics techniques can help in biofortification efforts. This is particularly significant in addressing global malnutrition and health concerns (Kudapa et al. 2023). 5. Pest and Disease Resistance: Omics techniques can uncover genetic markers associated with pest and disease resistance, enabling the development of crops that require fewer pesticides, reducing environmental impact and production costs (Sai Reddy et al. 2022). 6. Biodiversity Conservation: Genomic studies can aid in the conservation of crop biodiversity by identifying valuable genetic resources within various plant populations (Thakur et al. 2024). Thus, multi-omics techniques play a pivotal role in enhancing breeding practices across various domains. Multi-omics technologies can transform breeding techniques, promote sustainable agriculture, and address global concerns by leveraging the power of complete molecular data to generate crops with superior phenotypes and resilience to environmental biotic and abiotic stresses. In this context, this review discusses current trends in phenomics and genomics tools and their applications for major and minor millet improvements. Furthermore, it also discusses the success stories, future aspects, and potential risks of these techniques in breeding programs for improvement in millets.

3 | MILLET PRODUCTION, DIVERSITY, DISTRIBUTION, AND DOMESTICATION

3.1 | Millet production

India stands as the global leader in millet production and is the fifth-largest exporter of these grains (www.pib.gov.in, Ministry of Commerce & Industry, India, 2022). With a rapidly increasing demand for millets, India's exports have experienced exponential growth. Millets serve as a valuable resource not only in the food sector but also in the production of fuel and animal feed. Millets have the potential to be a source of biofuel, contributing to sustainable energy production. The global millet market is experiencing substantial growth. From a value of $11.02 billion in 2023, it is estimated to reach $13.80 billion by 2028, growing at a Compound Annual Growth Rate (CAGR) of 4.60%. The exports of millets worldwide have seen remarkable expansion, increasing from $400 million in 2020 to $470 million in 2021. In the context of India's trade, the nation exported millets worth $75.46 million in the 2022–2023 fiscal year, a notable increase from the $62.95 million recorded in the preceding year (www.apeda.gov.in; Sachan et al. 2023). While the potential of millets is undeniable, challenges related to quality, supply chain efficiency, and processing persist. However, with concerted efforts from all stakeholders, these challenges can be overcome. Millets, often regarded as the future of food and farming, are poised to play an increasingly pivotal role in addressing various global challenges and fostering sustainable agricultural practices (Simmons et al. 2020; Ye and Fan, 2021).

3.2 | Diversity, distribution, and domestication

Millets, including major millets and minor millets, belong to the *Poaceae* family with different genera. Millets are grown in various regions worldwide, especially in regions with semi-arid to arid climates. They are popular in India, Africa, China, and parts of Europe. Millets were among the earliest crops domesticated by humans, dating back thousands of years. The domestication process has varied across different regions, with some types being more prevalent in specific areas due to their adaptability to the local environment and soil conditions.

Sorghum ($2n = 20$) is the fifth-most cultivated popular cereal crop in the world and a staple food for more than 500 million people in Asia, and Africa (Xin et al. 2021). The genus Sorghum includes 23 or 24 species, although the taxonomy of that genus is still debated (Ananda et al. 2020; Ohadi et al. 2018). *S. bicolor* (L.) Moench subsp *bicolor* includes all cultivated sorghum cultivars derived from the wild ancestor *S. bicolor* subsp *verticilliflorum* (formerly subsp *Arundinaceum*), which is widespread in Africa (Berenji et al. 2011; DeWet and Harlan 1971; De Wet and Huckabay 1967). It is estimated that sorghum was cultivated as a food source in the Sahel zone of Africa and was originally domesticated in central eastern Sudan about 6000–4000 years ago (Winchell et al. 2017). Although some questions are still debated, it is generally accepted that sorghum originated in Africa around 7500 BC, based on evidence from archaeological finds (Ananda et al. 2020). Some studies have reported the possible evolutionary history and distribution route of domesticated sorghum (Burgarella et al. 2021; Fuller and Stevens 2018; Venkateswaran et al. 2019; Winchell et al. 2018). It has been suggested that sorghum was first domesticated in the eastern Sahel around 4000 BC. And spread to South Asia about 1000 years later (Winchell et al. 2017, 2018). Sorghum was then introduced to China and domesticated as Chinese kaoliang (Zhang and Ping 2022).

Pearl millet, commonly known as bulrush millet ($2n = 14$), also classified as *P. tyhoides*, *P. dentifica* or *P. spicatum*, is a cultivated small-grained C4 tropical cereal grass. Pearl millet originates from West Africa, where the oldest finds in Mauritania date back to 1000 BC. Fuller et al. (2021) reported that *Pennisetum glaucum* may have been undergoing domestication shortly after the sorghum in the western Sahel, as finds of fully domesticated pearl millet were present in southeastern Mali by the second half of the third millennium BC, and present in eastern Sudan by the early second millennium BC. The dispersal of the latter to India took less than 1000 years, according to present data.

Finger millet ($2n = 36$) was first cultivated in western Uganda and the Ethiopian highlands around 5,000 years ago. It made its way to India roughly 3,000 years ago (Dida et al. 2008). The inflorescence of finger millet appears to have a human finger-like structure, the distinct appearance of the inflorescence helps distinguish between its two subspecies, *dentifi* and *coracana*, each further divided into various races (Dida and Devos, 2006). This crop is an allotetraploid, and likely received its “A” genome from *Eleusine indica* and *Eleusine trisachya* (Liu et al. 2014). However, the identity of the elusive “B” genome remains a mystery, possibly originating from an extinct ancestor (Liu et al. 2014). It ranks fourth in importance among millets in the world after sorghum, pearl millet, and foxtail millet. Finger millet was often regarded as a “poor man's crop,” but in the last ten years, its dietary value and resistance to climate change have brought it back into favor.

Named for its bushy and tail-like appearance, foxtail millet (2n =18) has received promising research. Domesticated approximately 8700 years ago in China, and it is considered the oldest crop in the world and second in total world millet production. The history of foxtail millet is more complicated. The sequence diversity of 250 Chinese genotypes was found to be quite high, with an average of 20.9 alleles per locus when examined with 77 SSRs (Wang et al. 2012). The alleles clustered in two geographic centers of diversity, suggesting the possibility of two domestication events in China; More work is needed to confirm this hypothesis (Wang et al. 2012). Additionally, it has been argued that foxtail millet was independently domesticated in Europe based on archaeological evidence (Jusuf and Pernes, 1985; Hunt et al. 2008; Hirano et al. 2011). After its domestication in China, foxtail millet spread throughout Asia, Europe, and finally, North America (Jusuf and Pernes, 1985). Its wide range has given rise to three distinct breeds, each with several subbreeds. *Moharia* is common in Europe, Russia, and the Middle East. *Maxima* is found in eastern China, Georgia, Japan, Korea, Nepal, northern India, and the United States, where it was introduced as animal feed. *Indica* is dominant in South India and Sri Lanka (Jusuf and Pernes, 1985). An interesting feature of modern foxtail millet diversity is the global distribution of two phenotypically distinct cultivars, *waxy* and *non-waxy* grain types (Van et al. 2008).

Kodo millet (2n = 40) was domesticated about 3000 years ago in India, which is now the only country where it is harvested in significant quantities as a cereal, mostly in the Deccan Plain (De Wet et al. 1983b). It is believed that kodo millet was mostly first harvested as a weed alongside other cereals like rice, resulting in multiple domestication events across its current range (De Wet et al. 1983b). This practice continues in parts of Africa, where weeds are sometimes harvested during times of famine (De Wet et al. 1983b; Neumann et al. 1996; Ogie-Odia et al. 2010). In Africa, Kodo is called black rice or bird and bird grass (M'Ribu and Hilu, 1996). Analysis of limited molecular markers has shown that millet genotypes cluster according to African and Indian origin (M'Ribu and Hilu, 1996). Kodo millet is divided into three races (*regularis*, *irregularis* and *variabilis*) based on panicle morphology (De Wet et al. 1983b). In southern India, small seeded (*karu varagu*) and large-seeded (*peru varagu*) varieties are known, often grown together in the same field (De Wet et al. 1983b). Overall morphological variation is high, and large differences have been reported in many phenotypic parameters such as flowering, number of cultivars, and yield (Subramanian et al. 2010; Upadhyaya et al. 2014). Kode millet is a crop that can be described as incompletely domesticated, with some authors calling this cereal "pseudo-cultivated" (De Wet, 1992; Blench, 1997). Systematic breeding of domestic millet is thus neglected, but limited efforts have shown promise.

Proso millet (2n = 36), also called broom and common millet, was domesticated in Neolithic China as early as 10,000 years ago (Lu et al. 2009). Proso millet sequence diversity provides evidence for a single site of domestication in the Loos Plateau of China (M'Ribu and Hilu, 1994; Hu et al. 2008, 2009). Proso millet spread to Eurasia and was introduced to North America in the 18th century, where it is currently used mainly as fodder and bird seed (Bagdi et al. 2011). It is also referred to in classical European and Near Eastern sources as a true millet, and called "milium" by the ancient Romans (Smith, 1977). Archaeological evidence of prose in Eastern Europe 8000 years ago raises the possibility of secondary independent domestication, but further research is needed to confirm this finding (Hunt et al. 2008, 2011). Cultivated proso millet is divided into five races, *viz*., *miliaceum*, *patentissimum*, *contractum*, *compactum*, and *ovatum*, with different morphological characteristics of infloresence (Reddy et al. 2007).

Barnyard millet (2n = 36) consists of two separate species belonging to the genus *Echinochloa*. *Echinochloa esculenta* (syn. *Echinochloa utilis*, *Echinochloa crusgalli*) is cultivated in Japan, Korea and Northeast China, while *Echinochloa frumentacea* (syn. *Echinochloa colona*) is cultivated in Pakistan, India, Nepal and Central Africa (Yabuno, 1987; Wanous, 1990). Both species have overlapping morphological features that make differentiation problematic. Visual identification is possible only on the basis of the presence or absence of awn and slight differences in the sharp and adhesive morphologies (De Wet et al. 1983c). Japanese barnyard millet is categorized into two races *utilis* and *intermedia* (Upadhyaya et al. 2014), whereas Indian barnyard millet consists of four morphological races viz., *laxa*, *robusta*, *intermedia*, and *stolonifera* (De Wet et al. 1983c).

Little millet (2n = 36) is cultivated to a limited extent in India, Sri Lanka, Pakistan, Myanmar, and other Southeast Asian countries (Hiremath et al. 1990). In India, it is important to the tribes of the Eastern Ghats and is cultivated together with other millets (Hiremath et al. 1990). Little millet is a domesticated form of the weed *Panicum psilopodium* (De Wet et al. 1983a). Chromosomes of *Panicum sumatrense* and *P. psilopodium* hybrids pair almost perfectly with only one tetravalent, indicating that the divergence of the two species may have originally arisen through a single reciprocal translocation (Hiremath et al. 1990). This millet is categorized into two races on the basis of panicle morphology, viz., *nana*, and *robusta*. The domestication, distribution, and diversity of millets are not only a significant part of agricultural history but also crucial in addressing modern-day challenges such as food security, nutritional deficiencies, and sustainable agriculture.

4 | PHENOMICS APPROACHES IN CROP ANALYSIS

4.1 | Introduction and importance of phenomics techniques

The term 'phenome' describes the entire phenotype, or the expression of a trait's genome in a particular environment (Soul, 1967). In contrast, phenomics provides high-dimensional phenotypic data on a wide scale for an organism. In general, phenomics is used as an analogy to genomics; however, it differs from the latter. Phenomics utilizes advanced technologies such as high-throughput imaging and data analysis to collect and analyze vast amounts of data on plant characteristics, from the molecular level to the whole-plant level. However, the phenotypic expression of a trait varies depending on the environmental conditions, making it challenging to complete the characterization of the phenome (Houle, 2010).

4.2 | Applications of phenomics techniques

Advancements in biotechnology and next-generation sequencing have resulted in an abundance of genomic data. However, there is still a significant gap in fully annotating phenotypes and functions. To tap into the vast reservoir of genomic data, it is imperative to quantitatively characterize crop performance and establish connections with genomic information. Phenomics studies show ways to quickly sort through large populations and pick out a specific phenotype by using advanced robotics, sensors, imaging systems, and powerful computers. Plant phenomics relies on three main steps: (1) detection of a target trait, such as a physiological process or specific stress; (2) extrapolation of data from devices (i.e., imaging analysis) to quantitative measures or qualitative categories; (3) computation, aiming to give a biological response from retrieved data and to support decision-making.

To decode the complexities within vast sets of phenotypic data, advanced bioinformatics tools play a pivotal role. They enable the analysis of extensive data collected through phenotyping. Through an integrated approach that combines genotyping and phenotyping, it becomes possible to gain deeper insights into gene functions and how they respond to different environmental conditions. Therefore, using sophisticated phenotyping approaches can lead to a stronger link between plant performance, environmental response, and gene function.

A computational framework for image-based plant phenotyping has been developed to understand plant morphometric and functional changes (Das Choudhury et al. 2019). In other words, the phenomena facilitate the decoding of plant genetic information in phenotypic characters such as growth architecture, speed, and biomass (Tackenberg, 2007). Image-based plant phenotyping offers tremendous opportunities to understand functional traits and evaluate complex traits such as yield and their interactions with adverse environmental conditions (van Eeuwijk et al. 2019). During the past decade, this technology has been a highly sought-after tool for the accurate interpretation of abiotic stress responses in crops such as wheat, barley, rice, mung bean, and safflower (Golzarian et al. 2011). Sensing devices have a wide range of uses in agriculture, from understanding the primary physiological changes in plants due to external stress to controlling cultivations in the glasshouse, laboratory, and field (Tripodi et al. 2018).

5 | PHENOTYPING PLATFORMS FOR MILLETS

With the rapid development of genetic tools in millets, it is critical to have advanced phenotyping techniques to maximize the value of these resources. Automated high-throughput hardware platforms and corresponding software packages are transforming the field of plant-based phenotyping (Yang et al. 2013; Solimani et al. 2023). Phenotyping applies certain methods and protocols to measure morphological structural traits, physiological functional traits, anatomy, canopy, whole plants, or even populations. However, conventional breeders follow typical conventional phenotyping based on the appearance, touch, and taste of the crop, which is a time-consuming, resource-insensitive, and destructive methods that requires more human resources to sample a large population of crop plants. Nevertheless, currently, fully automated systems use non-destructive sensors to screen thousands of individual plants or field plots and up to hundreds of genotypes; the data is automatically processed and archived for subsequent use (Lorence and Jimenez, 2022; Tardieu et al. 2017; Fiorani and Schurr, 2013; Furbank and Tester, 2011). Automated phenotyping in controlled environments is commonly accomplished by placing sensors on individual plants or by moving sensors to or over the plants (Granier et al. 2006; Nagel et al. 2012). Sensors are also delivered to plants in the field utilizing mobile vehicles, drones, or other aerial platforms that fly over field trials (White and Conley, 2013; Deery et al. 2014; Vargas et al. 2020; Roth et al. 2022). Automation has made it possible to process many more individual plants or plots each day in all of these cases—often by an order of magnitude.

With these platforms, we may use 3D image technology and magnetic resonance imaging (MRI) to quantify the dense canopy, plant size, and leaf area of huge germplasm collections using 2D color images (Poorter et al. 2010). The utilization of fluorescence and hyperspectral analysis facilitates the quick and non-invasive assessment of diverse plant characteristics, enabling the physiological and biochemical characterization of the leaves and roots. However, this method of evaluation is limited to some elements of plant performance. The robotized sensor-actor, an exciting new invention, has expanded phenotyping capabilities by automatically measuring gene expression and/or cellular processes at certain time periods. It does this by destructively sampling important plant parts. Because characteristics that are deemed crucial in a greenhouse may not be as relevant in the field, the applicability of laboratory and greenhouse phenotyping techniques is actually assessed in the field.

For instance, in field conditions, the canopy of a stand matters more than the canopy of a single plant. As a result, while drones or airborne platforms can cover large agricultural areas, mobile platforms, like a tractor fitted with particular sensors to enable larger spatial flexibility, have been developed for mechanistic field phenotyping measurements with high accuracy and repeatability in given plots. Although physical processes can be analysed using multi- and hyperspectral technologies (Rascher and Pieruschka 2008; Comar et al. 2012), there are not many reliable methods for estimating photosynthesis efficiency in the field, such as the laser-induced fluorescence transient (LIFT) approach (Pieruschka et al. 2010). Special field sensors are already used in precision agriculture for nutrient management (Scotford and Miller 2005), and in the near future, they may become important tools for identifying plant diseases (Mahlein et al. 2012). The construction of wireless sensor networks enables continuous monitoring of the environment and crop characteristics and provides valuable information for agricultural management (Ruiz-Garcia et al. 2009).

Fahlgren et al. (2015) studied the drought responses of *Setaria* sp using a pipeline-based platform. Using image analysis, the authors found that *S. viridis* (a wild relative of foxtail millet) grows faster and earlier than foxtail millet (*S. italica*), although later they have similar biomass points. *S. viridis* was also found to respond more quickly to water restrictions than cultivated foxtail millet. In addition to 2D images, 3D images can also be created using scanner-based systems. For example, Vadez et al. (2015) used 3D scanning to characterize differences in leaf area between breeding populations in pearl millet. Substrate properties contribute significantly to crop performance, but there are challenges for the image. Therefore, the methods to get root images are critical. Future advancements in imaging technologies will enable even more detailed analysis of crop responses to environmental stresses like drought, providing insights into the genetic and physiological mechanisms underlying resilience in millets. Integrating multidimensional imaging with genomic tools will accelerate breeding efforts aimed at developing millet varieties with enhanced drought tolerance and productivity.

Rhizotrons are root imaging systems in which there is a thin amount of soil or nutrient medium between two plastic sheets (Neufeld et al. 1989; Rellán-Álvarez et al. 2015; Passot et al. 2016). This system was used for pearl millet to measure root growth (Passot et al. 2016). In the future, rhizotron technology is anticipated to undergo significant advancements, offering unparalleled insights into the intricate root systems of pearl millet and other millets. Enhanced imaging resolutions and automated data analysis will revolutionize our understanding of root growth dynamics, paving the way for tailored breeding strategies aimed at optimizing nutrient uptake efficiency and drought tolerance in millets. Automated pipelines for leaf angle extraction have been developed and tested for sorghum (Kenchanmane Raju et al. 2020), allowing breeders to track variability and distribution in leaf angle over time. Identifying varieties with a desired leaf angle distribution can assist breeders in selecting the varieties best adapted to specific environmental conditions, such as high planting densities where a narrow angle prevents the leaf from being shadowed by others (Pepper et al. 1977; Lambert and Johnson, 1978). In the case of sorghum, Wang et al. (2018) found that the heights measured by the ultrasonic sensor, the LIDAR-Lite v2 sensor, the Kinect v2 camera, and the imaging array had a high correlation with the manual measurements ($r \geq 0.90$), while the heights measured by remote imaging had a good but relatively lower correlation with the manual measurements ($r = 0.73$). Automated pipeline technologies for leaf angle extraction are poised to become even more sophisticated, leveraging advances in machine learning and computer vision algorithms to enhance accuracy and efficiency in millet breeding programs. Integration of a diverse array of sensors and imaging modalities will enable comprehensive phenotypic characterization, facilitating the identification of sorghum varieties with optimal leaf angle distributions for specific environmental conditions.

6 | GENOMICS IN UNCOVERING GENETICS IN MILLET RESEARCH

Genomic techniques in plants have revolutionized agriculture and our understanding of plant biology. Plant genomics research efforts have continuously increased in the past 40 years. These techniques target decoding, characterizing, and studying the genetic (DNA/RNA) compositions, structures, organizations, and functions, as well as the molecular genetic interactions and networks of a plant genome (Stokes and McCourt 2014; Poland 2015). The introduction of genomic technologies has significantly accelerated our ability to decipher genetic information, unravel complex traits such as yield, disease/insect resistance, nutritional quality, etc., and enhance crop improvement strategies. Plant genomics aims to develop large-scale, high-throughput technologies and efficient tools and methodologies to elucidate the basics of genetic traits and characteristics, to understand phenotype × genotype × environmental interactions, to map important loci throughout the genome, and to advance crop breeding and selection on a genome-wide scale.

6.1 | Genomic resources for millets

Exploring genetic and genomic resources is an integral part of millet improvement programs. These include genome sequencing, molecular developments, functional genomic analysis, genome-wide association marker mapping, genomic-assisted breeding, and biotechnological advances. The quest for genetic resources in millet crop improvement is to explore the diversity and identify elite donor genotypes with exceptional traits. Genomic tools with higher precision are the prerequisites for harnessing the trait-associated genomic regions for introgression into elite cultivars through cutting-edge approaches like molecular breeding and genetic engineering. International Crop Research Institute for Semi-Arid Tropics (ICRISAT) has an excellent repertoire of millet germplasms from various parts of the globe. With a total number of accessions of 80,208, including 750 wild germplasm accessions, sorghum shares the maximum proportion of germplasm collection (42869) at ICRISAT, followed by pearl millet (25537), finger millet (7513), foxtail millet (1542), kodo millet (665), little millet (473), proso millet (849), and barnyard millet (749) (http://www.genebank.icrisat.org). The genetic diversity in accessions or within a population can be analyzed through molecular markers such as single nucleotide polymorphisms (SNPs), simple sequence repeats (SSRs), cleaved amplified polymorphic sequences (dCAPS), restriction fragment length polymorphisms (RFLPs), and amplified fragment length polymorphisms (AFLPs).

6.2 | Genomic tools to study millets

Several genomic tools available could be utilized to study the millet genomes and unravel the key traits of millets. The small-sized genome (~515 Mb) of foxtail millet, together with the short life cycle,

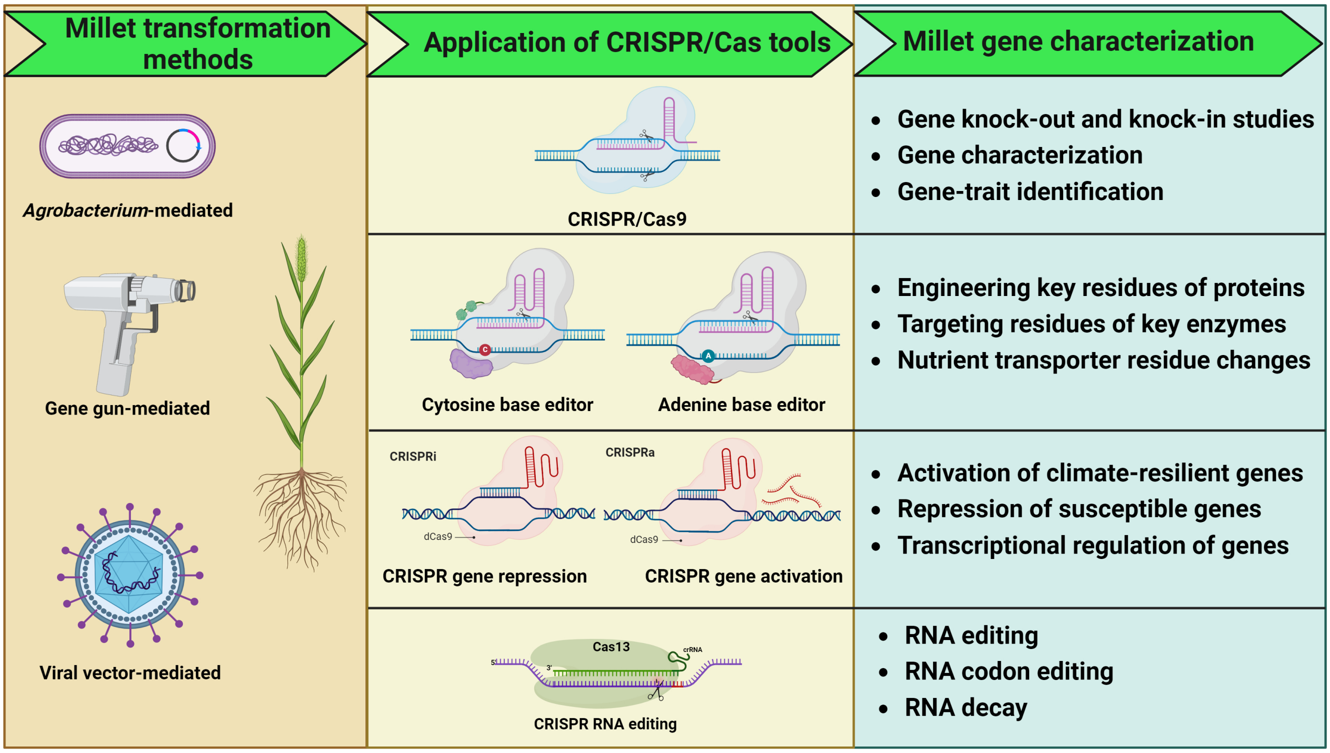

FIGURE 2 **Insights into the application of the CRISPR/Cas system in millets for the characterization millet genes are depicted.** The development and optimization of transformation methods are essential for delivering CRISPR constructs into various millets. Variant CRISPR/Cas tools that could be utilized for gene characterization and trait dissection are illustrated. Gene functions can be identified by CRISPR/Cas9 knock-out and knock-in tools. The key residues of key enzymes and nutrient transporters could be engineered for functional enhancement by CRISPR/Cas base editors. The action of genes could be regulated by gene activation and repression by CRISPR activator (CRISPRa) and CRISPR repressor (CRISPRi) tools. Target RNAs could be edited by the CRISPR/Cas13 system. Created using Biorender.

inbreeding nature, profound seed profile, and extensively available genomic resources, foxtail millet is considered a C_4 model plant for abiotic stress, biofuel trait, and photosynthesis research (Lata et al. 2013). Such genomes allow researchers to dissect climate resilience traits using appropriate genomic tools. Establishing an efficient genetic transformation system is essential for understanding the functions of genes and the genetic improvement of crops. A competent *Agrobacterium*-mediated transformation system has already been developed for pearl millet, foxtail millet, and finger millet (Singh and Prasad 2016; Sood et al. 2019; Ceasar and Ignacimuthu, 2011; Ceasar et al. 2017). Such tools could be used to deliver the constructs and study the specific gene functions. A recently developed system for *Agrobacterium*-mediated genetic transformation of foxtail millet, with a gene integration frequency of approximately 27%, is expected to accelerate the research of millet transgenics to extreme heights (Sood et al. 2020). A foxtail mosaic virus-based gene delivery system has been established for the functional characterization of genes by virus-induced gene silencing (Bouton et al. 2018; Liu et al. 2016; Mei et al. 2016; Mei et al. 2019; Yuan et al. 2020; Zhang et al. 2020; Vinoth and Ravindhran 2017). This system has been shown to be successful in suppressing the expression of candidate genes in both millet and other cereal plants. On the other hand, there are limited reports on the use of other molecular techniques such as RNA interference and genome editing tools such as clustered regularly spaced short palindromic repeats (CRISPR) and CRISPR-associated protein 9 (Cas9), zinc finger nucleases (ZFN) and transcription activator-like effector nuclease. (TALENS) in millets (Ceasar, 2022). Effective application of these tools is necessary to accelerate the biological enrichment and quality improvement of millet grains (Bouton et al. 2018). More specifically, the various tools of the CRISPR/Cas system, such as CRISPR/cas9, CRISPR activation (CRISPRa), CRISPR inhibitor (CRISPRi), CRISPR base editor, and CRISPR RNA editing, might help to dissect the specific roles of genes involved in climate resilience and nutrient fortification in millets (Figure 2).

7 | INTEGRATING PHENOMICS AND GENOMICS

7.1 | Complementary roles of phenomics and genomics

The ample amount of genomic resources available in the public domain remains underutilized due to the absence of precise, accurate, and high-throughput phenotyping tools and techniques. Consequently, there have been concerted efforts to develop advanced phenotyping tools capable of screening morpho-physiological traits linked to both biotic and abiotic stresses. These tools enable the connection of genomic resources in a plant species with physiological and morphological data obtained through contemporary phenotyping approaches deployed at automated phenotyping platforms worldwide. High-throughput phenotyping tools are instrumental in collecting precise and accurate observations, allowing for data analysis to comprehend the entire phenome of a plant under diverse environmental conditions. Similar to genomic platforms, phenotyping platforms contribute to the development of databases such as the Plant Meta-Phenomics Database (Poorter et al. 2010) or the Plant Trait Database TRY (http://www.try-db.org). These databases amalgamate phenotypic responses to the environment across a broad spectrum of plant traits and parameters.

The integration of phenotyping dataset with international genomic databases (such as TAIR, TIGR, and NCBI) and multi-omics information, including metabolomic, proteomic, and transcriptomic data, has emerged as crucial for understanding the genetic architecture of complex traits. Phenomics plays a pivotal role not only in dissecting

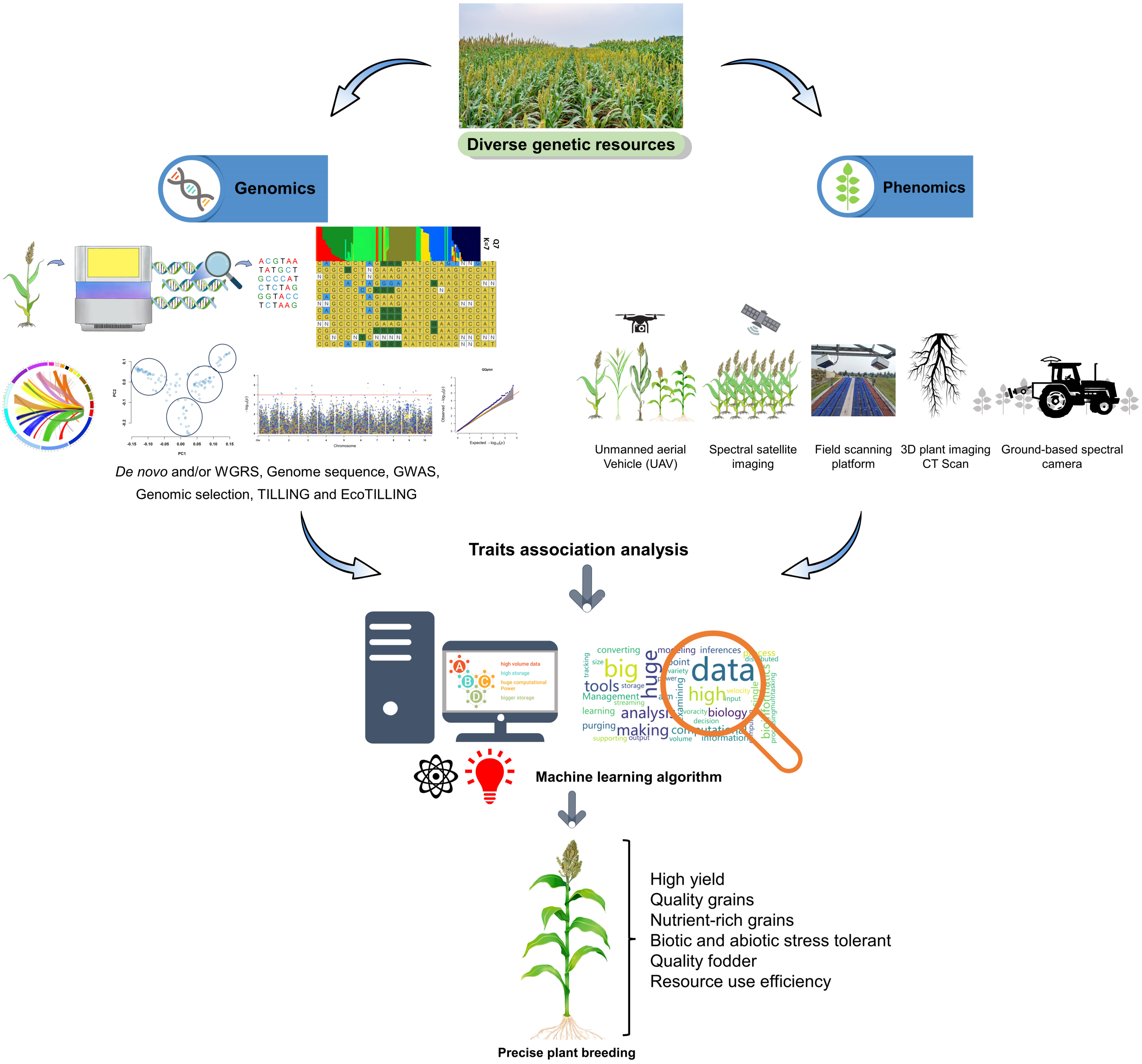

FIGURE 3 **The illustration encapsulates the synergy between phenomics and genomics in millet improvement.** Diverse genetic resources fuel downstream analyses, enhancing the power to identify and improve trait-based future plant breeding. Use of different genomics techniques such as WGRS, GWAS, TILLING, Eco-TILLING, etc., and precision phenotyping platforms such as drones, UAVs, satellites, CT scans, etc., guided by machine learning, yields an ideal millets ideotype. This visual narrative inspires researchers to pursue transformative millet improvement. Created using Adobe Photoshop software.

complex traits through genomics but also in leveraging genomic resources for the discovery of new genes/quantitative trait loci (QTLs), elucidation of gene sequence functions, and enhancing genetic gain for traits with low heritability (Figure 3). This understanding facilitates the simulation and prediction of plant properties, particularly for complex traits like yield or biomass, addressing the paramount challenge of meeting the future needs of a growing human population. Both forward and reverse phenomics approaches can harness the potential of genomic resources. Accurate, cost-effective, and precise phenotyping is essential for fine mapping traits, regardless of the genetic approach used for allelic recombination or assessing variation through re-sequencing technologies.

Phenomics is applicable in reverse genetic studies, aiding in identifying the function of specific genes in the growth and development of crop plants. It can also pinpoint allelic variations to target associated genes, providing valuable insights into the genetic makeup of crops and contributing to advancements in agriculture.

7.2 | Studying the genetic basis of complex traits

The study of an organism's entire set of genes or genome aids in finding key genes responsible for critical agronomic, nutritional, and other relevant aspects in millets. The availability of genome assembly in sorghum (McCormick et al. 2017), pearl millet (Salson et al. 2023), finger millet (Hatakeyama et al. 2017; Devos et al. 2023), and foxtail millet (Wang et al. 2021) is a valuable resource for millets genomic resources. Furthermore, the availability of thousands of genetic stocks of whole genome sequences is the primary genomic resource used to generate additional genomic information, such as the development of molecular markers and the identification of QTLs for target traits, which aids genomics-assisted breeding and genomic selection (Varshney et al. 2005, 2016).

Plant breeding has evolved from conventional to molecular breeding as DNA technology has advanced (Moose and Mumm, 2008). Crop genetic enhancements and breeding strategies have been established using DNA markers, marker-assistant selections (MAS), gene editing, and genetic engineering (Ingle et al. 2023, Narkhede et al. 2022). Second- and third-generation sequencing technologies have improved genomic tools such as genome-wide association studies (GWAS), genome editing (GE), genomic selection (GS), and molecular modules (MMs), as well as high-throughput phenomics. Unlike MAS, GS uses genome-wide marker data to determine whether the target traits are related (Meuwissen et al. 2001), and hence, GS does not require phenotypes and QTL for the breeding population (Xu et al. 2020).

Understanding the genetic and genomic nature of millets could be accomplished through the application of genomics. A deeper understanding of millet domestication and diversification aids in adapting genetic variety from wild progenitors to improved varieties by breeding selection employing genomics and phenomics technology. A diversity study utilizing GWAS in a diverse set of accessions aids in the identification of candidate genomic regions across the targeted lines. To identify and change specific gene(s) controlling certain trait(s), populations such as functional genomics populations, various germplasm panels, and mapping populations could be compiled and used.

The fundamental goal of QTL mapping is to identify the genomic region controlling traits of interest. This can be achieved by finding the genotype–phenotype interaction. In several studies for various millet crop species, an extensive number of DNA marker-trait associations have been revealed to date (Bančič et al. 2023; Srivastava et al. 2019; Rouamba et al. 2023; Habyarimana et al. 2019, 2020). Identification of such marker trait associations (MTAs) can be utilized to boost agricultural output by combining marker-assisted selection with molecular breeding (Ingle et al. 2023, Narkhede et al. 2022). This approach holds promise for the comprehensive understanding and improvement of small millets, ultimately supporting their resilience in the face of challenging climatic conditions. Following are some case studies describing the use of phenomics-genomics technologies in improving millet traits.

QTL mapping has been used in sorghum to study genomics and phenomics. For example, a study utilized a chilling nested association mapping population with 43 K GBS SNPs and uncrewed aircraft system (UAS) high-throughput phenotyping to provide high-resolution chilling tolerance (CT) mapping, addressing weak trait-to-QTL association from previous sorghum CT studies (Marla et al. 2023). UAS-based high-throughput phenotyping offers promising avenues for enhancing millet research and crop improvement. By capturing detailed data on agronomic traits and genotype-environment interactions, UAS technology enables researchers to accelerate breeding efforts, identify resilient varieties, and optimize production practices. As UAS technology continues to advance, future insights in millet research may include the integration of advanced sensors and artificial intelligence algorithms, providing even deeper insights into millet physiology and stress responses. Overall, UAS-based phenotyping holds great potential for driving innovation and sustainability in millet agriculture, contributing to global food security and nutrition.

Similarly, a genome-wide association study (GWAS) identified causal polymorphisms for traits like drought tolerance and biomass yield based on historical recombination events in sorghum by employing a drone (Spindel et al. 2018). The drone was a modified multirotor vehicle with Blue River's proprietary imaging payload (Spindel et al. 2018). The identified candidate genes are related to several proteins, like heat shock proteins, antifreeze proteins, and other domains recognized as important to plant stress responses. This study will be helpful in producing new cultivars with drought tolerance and high biomass traits (Spindel et al. 2018). Furthermore, QTL mapping has been employed to identify genetic variation for agroclimatic traits in sorghum, enabling the dissection of complex traits through QTL analysis. This study indicates that the major tannin haplotypes are present at the *Tan1* locus and the effects of InDels on protein folding (Boatwright et al. 2023). This study could be helpful in precision genomics and breeding by identifying key targets for gene editing and trait integration. The development of improved pearl millet genomes representing the global heterotic pool offers a framework for molecular breeding applications. This includes gene annotation, enrichment analyses, and the identification of structural variations, providing a valuable resource for future breeding efforts (Ramu et al. 2023). Comparative and functional genomics have untangled several loci and genes that regulate adaptive and agronomic traits in pearl millet. The use of high-throughput sequencing technology has boosted pearl millet genomic research, providing insights into its genetic and genomic characteristics (Singh and Nara, 2022). Combined studies of genomics and phenomics in pearl millet have demonstrated achievements in recent years. For instance, Kumar et al. (2021) mapped QTLs for important agronomic traits in an *Iniadi-derived* immortal population of pearl millet, demonstrating the use of QTL mapping through linkage analysis for numerous traits, including stress tolerance and yield-related characteristics. Additionally, another study focused on the genomic dissection of yield and its component traits in pearl millet, identifying multi-environmental QTLs for test weight and seed yield in various agro-climatic zones of India (Singhal et al. 2022).

High-throughput phenotyping platforms (HTPP) are used to reduce the phenotyping bottleneck in breeding programs. HTPPs, such as unmanned aerial vehicles (UAVs) emerged as a powerful tool for genetics research (Kamilaris & Prenafeta-Boldú, 2018; Zhu et al. 2018). UAVs are one of the most popular HTPPs used to track various traits, including plant height, chlorophyll content, and spectral reflectance, by sensing the canopy level using hyperspectral sensors. (Galli et al. 2020; Kamilaris & Prenafeta-Boldú, 2018; Sankaran et al. 2015; Volpato et al. 2021; Buchaillot et al. 2019; Chivasa et al. 2020). Enhanced UAV-based HTPPs equipped with hyperspectral sensors will enable precise monitoring of millet canopy dynamics, facilitating the selection of varieties with optimized height, chlorophyll content, and spectral reflectance for various agroecological contexts. Integration of UAV-based phenotyping into millet breeding pipelines will streamline the selection process, accelerating the development of resilient and high-yielding millet varieties tailored to meet the challenges of future food security. Various HTPP platforms, such as "PHENOPSIS", are used to assess the plant response to water stress conditions in Arabidopsis (Granier et al. 2006); "HyperART" is successfully employed in barley, maize, tomato, and rapeseed and uses for the quantification of leaf traits such as leaf chlorophyll content and disease severity of leaves (Bergsträsser et al. 2015); "PHENOVISION" for tracking the maize crop for drought stress condition (Asaari et al. 2019) etc. Proso millet gains more popularity because of low input demands and drought tolerance nature. The major attribute in the breeding of proso millet is the time of heading. Aerial images captured by UAVs were used as a potential data source to estimate heading percentages and the breeders' visually rated heading percentages in proso millet. It was found that UAV has an accuracy of 92.4% for head initiation (panicle initiation) in proso millet (Zhao et al. 2022). Hence, aerial images captured by using the HTPP could be a potential data source for the detection of panicle and heading percentage estimation in proso millet breeding.

Genomic and phenotypic characterization of finger millet has revealed a complex diversification history, including the geographic structuring of genomic and phenotypic diversity. A high-density linkage map of finger millet has been developed, providing QTL for blast resistance and other agronomic traits (Pendergast et al. 2021). The integration of advanced phenomics methods with genomics data has the potential to enhance the study of the diverse genetic pool of finger millet, contributing to the genetic enhancement of climate-resilient traits. The diverse gene pool, advanced plant phenomics, and genomics methods have enhanced the genetic gain and understanding of important agronomic and nutritional traits in finger millet (Sood et al. 2019). Nutrition deficiency is caused by an improper diet and a low intake of macro- and micronutrients in the food. This could be addressed by consuming nutrient-rich crop varieties. To address this, Puranik et al. (2020) reported 18 MTAs related to grain minerals, viz., iron, magnesium, calcium, potassium, protein, sodium, and zinc in finger millet. After validation, these MTAs could be useful for developing high-yielding, nutrient-rich finger millet varieties to address the nutrition deficiency caused by hidden hunger. More recently, Sood et al. (2023) used GWAS to decipher the genomic regions governing major agronomic traits and neck blast resistance in finger millet, highlighting the importance of genomic resources in understanding the genetic control of agronomic traits. They identified 132 MTAs governing the important traits across multiple years. This indicates a strong association with the trait, and thus, the identified SNPs are important assets for future finger millet breeding. Genomic and phenotypic characterization of finger millet indicates a complex diversification history, highlighting the need for systematic efforts from biologists across the field to better understand the genetics of important traits in finger millet. To achieve this, Bančič et al. (2023) recently used the genome assembly of finger millet to analyze dArTseq single nucleotide polymorphisms (SNPs) at the whole-genome level, providing insights into its genetic diversity and evolutionary history. The findings suggest that finger millet has undergone complex and context-specific diversification, indicative of a lengthy domestication history. Comparative genomics has paved the way for marker-assisted selection, where resistance gene homologs of rice for blast and sequence variants for nutritional traits from transcriptomics studies have provided a preliminary understanding of nutritional variation, drought, and salinity tolerance (Sood et al. 2019).

The genome sequencing of foxtail millet has provided valuable insights for improving the crop, making it an important model crop for functional genomics studies (Krishna et al. 2022). The genome sequence of proso millet has provided essential genetic and genomic resources for improving its agronomic and nutritional traits, contributing to its potential as a promising variety (Pramitha et al. 2023). The genome sequences of barnyard millet (Guo et al. 2017) and proso millet (Zou et al. 2019) are now available for researchers to actively work in the field of breeding. These advances are expected to enhance the prospects of understanding the underlying genomics of millets. However, there remain research gaps in small millets regarding key nutritional and medicinal traits that could be used to revitalize our diets. These results show the wide range of traits that genomics and phenomics research in millets has been looking at. This information is useful for breeding, protecting, and creating climate-resilient and high-yielding varieties.

8 | CHALLENGES AND LIMITATIONS

Genomics and phenomics technologies have significantly advanced the field of millet research, providing valuable tools for understanding the genetic makeup and phenotypic traits of millet crops. However, there are several challenges associated with these technologies, which may include the availability of genetic resources that are suitable for breeding. A vast genetic material with an ample amount of diversity is essential for genomics and phenomics studies to achieve accuracy. The lack of advanced bioinformatics software and tools makes it difficult to study complex tasks like the integration of phenotypic and genotypic data for efficient GWAS in millets. Genome complexity plays an important role in harnessing the outcomes of the study. Millet genomes can be complex, and some species may have large and repetitive genomes. This complexity makes sequencing and assembling the genomes challenging, leading to gaps and errors in the genomic data. Improvements in genome assembly and the application of genomic selection techniques are crucial for harnessing the potential of millet genomes (Sood et al. 2019). Millet production is threatened by various biotic and abiotic stresses, and addressing these challenges through genomics and phenomics studies remains a priority (Choudhary et al. 2023, Krishna et al. 2022). Breeder's strategies for developing new cultivars are crucial in plant breeding.

Developing new breeding strategies that leverage the power of genomics and phenomics data is essential for the development of climate-resilient and nutritionally improved millet varieties (Joshi et al. 2023). A standardized phenotyping protocol set is a key for generating high-throughput phenotypic data for new researchers. Standardized protocols for phenotyping millet traits are essential for comparing results across different studies and environments. The absence of such protocols can lead to inconsistencies in data interpretation and hinder the development of robust breeding strategies (Choudhary et al. 2023). Over-dependence on rice, wheat, and maize to cater to the nutritional requirements of more than 80% of the population poses a challenge in addressing food and nutritional security, hindering research on beneficial traits in minor millets. Millets, despite their importance for food security, have historically received less research funding compared to major cereals. Limited resources can slow down the progress of genomics and phenomics research in millets (Muthamilarasan & Prasad, 2021). A complete and annotated genome is available only for foxtail millet; this hinders the application of genomic tools like CRISPR/Cas to characterize the genes. Millets also need robust transformation protocols with higher transformation efficiency to deliver the constructs. In conclusion, while genomics and phenomics technologies have significantly advanced millet research, challenges such as improper genetic material, software and data integration, genome assembly complexity, biotic and abiotic stresses, breeding strategies, unstandardized phenotyping protocols, over-dependence on major staples, and insufficient funds for research need to be addressed to fully harness the potential of these technologies in improving millets.

9 | FUTURE DIRECTIONS AND EMERGING TRENDS

The exploration of phenomics and genomics in understanding the genetic basis of complex traits in millets holds immense promise for the future of agriculture and food security. Millets, comprising a group of small-seeded grasses, have been pivotal in sustaining human populations for centuries, especially in regions with challenging environmental conditions. Understanding the intricate genetic mechanisms governing their traits is crucial for enhancing their resilience, productivity, and nutritional value. Phenomics, the comprehensive study of an organis's physical and biochemical traits, coupled with genomics, which delves into an organis's complete set of genes, offers a comprehensive approach to dissecting the genetic underpinnings of complex traits in millets. This integrated approach allows scientists to correlate genotype (genetic makeup) with phenotype (observable characteristics), unfolding the intricate relationships between genes and their expressed traits.

One of the primary advantages of phenomics and genomics lies in their ability to identify and characterize specific genes responsible for desirable traits in millets. Traits such as drought tolerance, disease resistance, enhanced nutritional content, and improved yield are complex and multifaceted, influenced by numerous genes interacting with environmental factors. By employing advanced genomic techniques like genomic selection, GWAS or association mapping, breeders can identify these genes and understand their functions, leading to targeted breeding programs for developing improved millet varieties and hybrids.

Furthermore, the utilization of high-throughput phenotyping technologies coupled with other omics, viz., metabolomics, proteomics, etc., allows for the rapid and precise characterization of various traits across large populations of millet plants. This facilitates the collection of extensive phenotypic data, enabling researchers to analyze and correlate these traits with specific genetic markers. Machine learning algorithms and bioinformatics tools play a crucial role in processing and interpreting this vast amount of data, aiding in the identification of key genetic signatures associated with desired traits. The implications of these advancements extend beyond mere scientific exploration. They hold the potential to revolutionize millet research and production by accelerating the development of resilient, high-yielding, and nutritionally enhanced varieties and hybrids. Enhanced understanding of the genetic basis of traits like drought and heat tolerance can be instrumental in mitigating the adverse effects of climate change on millet production and ensuring food security in regions vulnerable to erratic weather patterns.

In the context of millets' short life cycle, genomics and high throughput phenotyping play integral roles in expediting breeding efforts. Complementing genomics, high-throughput phenotyping facilitates the rapid and automated assessment of numerous plant traits, accelerating the evaluation of agronomic characteristics like yield, drought tolerance, and nutritional content. By integrating phenotypic data with genomic information, breeders gain a comprehensive understanding of genotype–phenotype relationships, empowering them to select superior varieties with precision. While initial investments are required, the long-term benefits of these technologies in terms of reduced breeding cycle time, improved crop traits, and enhanced yields underscore their cost-effectiveness, making them essential assets in the quest for resilient and high-yielding millet varieties.

Moreover, improved varieties and hybrids with enhanced nutritional content can address the global issue of malnutrition, a challenge prevalent in many parts of the world. Millets are rich in micronutrients and possess numerous health benefits, making them an invaluable resource for combating dietary deficiencies. As technology continues to evolve and our understanding of genetics deepens, the role of phenomics and genomics in deciphering the genetic architecture of complex traits in millets will undoubtedly expand. This knowledge will not only empower agricultural scientists and breeders but also contribute significantly to global efforts aimed at sustainable agriculture, food security, and human well-being.

10 | CONCLUSION

In conclusion, the integration of phenomics and genomics has emerged as a pivotal approach to unfolding the intricate genetic architecture governing complex traits in millets. The synergistic utilization of these interdisciplinary fields has illuminated the underlying genetic factors influencing various essential characteristics in millet crops, revolutionizing our comprehension of their complex traits. Through phenomics, the comprehensive characterization of phenotypic traits at varying scales has provided a holistic view of millet plants' behavior, allowing for precise trait measurements and detailed trait-to-trait correlations. Concurrently, genomics has enabled the unfolding of the millet genome, identifying key genomic regions, candidate genes, and molecular markers associated with important agronomic traits, facilitating targeted breeding efforts.

This integrative approach not only enhances our fundamental understanding of millet genetics but also holds immense promise for accelerating crop improvement programs. The insights gained from phenomics-genomics integration offer opportunities for the development of millet varieties and hybrids resilient to environmental stresses, enriched in nutritional content, and adapted to diverse agricultural settings, thereby significantly contributing to global food security and sustainable agriculture. As research in phenomics and genomics progresses, continued advancements in technology and analytical tools will further amplify our capacity to decipher the genetic basis of complex traits in millets, fostering a new era of precision breeding and crop enhancement.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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