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REVIEW

Pearl millet a promising fodder crop for changing climate: a review

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Abstract

The agricultural sector faces colossal challenges amid environmental changes and a burgeoning human population. In this context, crops must adapt to evolving climatic conditions while meeting increasing production demands. The dairy industry is anticipated to hold the highest value in the agriculture sector in future. The rise in the livestock population is expected to result in an increased demand for fodder feed. Consequently, it is crucial to seek alternative options, as crops demand fewer resources and are resilient to climate change. Pearl millet offers an apposite key to these bottlenecks, as it is a promising climate resilience crop with significantly low energy, water and carbon footprints compared to other crops. Numerous studies have explored its potential as a fodder crop, revealing promising performance. Despite its capabilities, pearl millet has often been overlooked. To date, few efforts have been made to document molecular aspects of fodder-related traits. However, several QTLs and candidate genes related to forage quality have been identified in other fodder crops, which can be harnessed to enhance the forage quality of pearl millet. Lately, excellent genomic resources have been developed in pearl millet allowing deployment of cutting-edge genomics-assisted breeding for achieving a higher rate of genetic gains. This review would facilitate a deeper understanding of various aspects of fodder pearl millet in retrospect along with the future challenges and their solution. This knowledge may pave the way for designing efficient breeding strategies in pearl millet thereby supporting sustainable agriculture and livestock production in a changing world.

Introduction

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is one of the most important crops that provide food, fodder, feed and fuel to millions of poor families and their livestock. It originated 4900 years ago in Africa and due to evolution under adverse conditions, it can withstand harsh weather conditions in which other major cereal crops fail to grow (Muimba-Kankolongo 2021). Therefore, it is adapted to dry and hot climates and plays a major role in sustaining food security in arid and semi-arid regions (Satyavathi et al. 2021). Pearl millet covers around 30 million hectares globally. It is a significant millet crop in India, cultivated over approximately 7.41 million hectares, with about 0.9 Mha of area dedicated to fodder (Satyavathi et al. 2021 Koli et al. 2018; Directorate of Millets Development 2020). In Africa, pearl millet is grown on approximately 18 million hectares. Limited acreage is allocated to green fodder, as stover is primarily used as fodder instead. (Boote et al. 2022). In the USA, around 60,000 hectares are under cultivation for fodder (Myers 2002; All India Coordinated Research Project on Pearl Millet 2022). It is primarily grown as a grain crop under rainfed conditions, and as a fodder crop in summer and *Kharif* seasons. In Southern India, pearl millet is also grown during the *Rabi* season in the hottest and driest regions. It is an excellent forage crop and has great potential. Its fodder is high in protein, calcium, phosphorus and other minerals, while being low in undesirable components such as hydrocyanic acid and oxalic acid (Gupta 1975). As a fodder crop, it is leafy, nutritious and palatable. It can be fed to animals at any crop stage and is primarily present in two plant morphologies: dwarf bushy type (used for grazing) and tall type (used for green fodder, silage and hay) (Fig. 1) (Hancock et al. 2009). It provides crude protein and total digestible nutrients to cattle at 33% and 66% less cost, respectively, as compared to the concentrated feed (Ravi et al. 2012), making it a valuable feed source for dairy farmers.

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Fig. 1 Plant types in pearl millet: left- dwarf type with shorter internodes and leafiness and right- tall plant type with longer internodes

In India, around 10 million farmers are engaged in the dairy sector, and for many, it serves as their sole source of income (Ministry of Fisheries, Animal Husbandry and Dairying 2022). In the most recent census, 535.70 million livestock population is recorded, reflecting a 4.6% increase from the previous one (Department of Animal Husbandry and Dairying 2019). Therefore, feeding this growing population is going to be a major issue. The lack of fodder increases the cost of concentrated feed and fodder, affecting landless and marginal dairy producers and ultimately raising the costs of dairy products. Moreover, according to UNDESA's 2017 forecast, if the current pace of population growth continues, the world's population will reach 9.8 billion by 2050, which will result in a decline in the amount of cultivable land available for food production. This could result in similar feeding challenges for both animals and humans. Given the anticipated increase in future fodder shortages, proactive measures should be implemented to address this issue. One approach to address this issue is to increase crop production per unit area by developing high-yielding and quality fodder pearl millet varieties/hybrids. This can be achieved by leveraging the available genetic potential in the pearl millet gene pool along with implementing good cultivation practices.

In order to develop fodder cultivars, Dr. Glenn W. Burton initiated traditional breeding activities in Tifton, Georgia, in the 1930s. He has made several contributions to the breeding of pearl millet, including the discovery of the first fodder hybrid, Gahi 1 and CMS source A_1 (Tift 23 A). The dissemination of his material to other parts of the globe has paved the way for the improvement of pearl millet as a grain. The research to evaluate millet as a silage crop started in the 1950s with the development and release of improved varieties of pearl millet and 'Starr' millet was proposed as the first grazing and silage cultivar for dairy cattle (Johnson 1959).

In the USA and Australia, pearl millet is widely used as a forage crop, as Tifleaf and Ghai cultivars were grown on half a million hectares of land in the USA in the 90s and still these are in cultivation (Andrews and Kumar 1992). Also, elephant grass hybrid (*P. purpureum schum)* is a popular perennial forage crop broadly grown in Brazil, East Africa and Southern Africa. Overall, pearl millet is grown in 30 countries in Asia, Africa, America and Australia (Garin et al. 2023). Genetic diversity in *Pennisetum species* for fodder-related traits is present in greater amounts. Over 66,000 distinct accessions representing over 140 species are available at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Research and Development Institute and Global Genebank Information System (GRIN) on a global scale. These accessions are primarily utilized to generate resources for the pearl millet, mainly focusing on grain production. However, there has been limited effort in developing genetic and genomic resources for traits that are valuable for fodder. Consequently, there is a lack of appropriate resources for mapping traits in an advanced mapping population that segregates fodder quality and biomass-related traits and no information is available on key candidate genes and functional SNPs that govern these traits. This information is essential for developing improved fodder cultivars. Therefore, there is a need to develop resources by employing modern genomic tools in combination with conventional breeding approaches. Recently genome sequencing of pearl millet (Varshney et al. 2017) has opened a way to tap into its large genetic diversity to breed varieties and hybrids for future needs. Mapping QTLs at higher resolution and identification of candidate genes for forage quality and biomass-related traits in pearl millet would facilitate the mapping of functionally important genes associated with forage traits in pearl millet. This valuable material will aid in uncovering genomic regions that govern fodder traits and will accelerate the breeding programme for the development of improved cultivars.

This review will explore various aspects of the fodder quality and biomass of pearl millet, as well as its future significance as a fodder crop in regions expected to face water scarcity and drought in the coming years.

Navigating challenges in fodder production for a growing global population

With the global population expected to exceed 9 billion by 2050 (UNDESA 2017), the livestock industry grapples with rising demands for meat and dairy products, straining fodder production systems. Climate change worsens challenges by altering growing seasons, reducing forage yield and increasing vulnerability to pests and diseases. Simultaneously, urban expansion, biofuel production and infrastructure development alter land use, reducing space for fodder cultivation (Kleemann and Riordan 2015). Water scarcity, particularly in arid regions, further complicates fodder production. Therefore, sustainable solutions, including precision irrigation, drought-resistant fodder varieties and improved water-use efficiency, are crucial (Nikolaou et al. 2020).

In arid regions, pearl millet is valued as a staple and gains prominence as a high-quality fodder source (Jukanti et al. 2016). Recent advances in breeding, nutritional enrichment and sustainable cultivation practices highlight pearl millet's potential. Modern breeding methods have hastened the development of improved varieties, emphasizing traits like increased biomass, disease resistance and superior forage quality (Yadav et al. 2021a, b, c). Incorporating genetic diversity from wild relatives holds promise for stress-tolerant and high-yielding varieties, underscoring pearl millet's transformative potential in fortifying livestock production systems and addressing challenges linked to climate change and resource scarcity (Sharma et al. 2021). Therefore, research collaborations are essential to fully unlock pearl millet's potential as a sustainable and nutrient-rich fodder resource. The available resources along with avenues and approaches to generate novel resources for improving pearl millet fodder are discussed further.

Breeding for fodder pearl millet

Pearl millet has the potential as a promising fodder crop due to its nutritional composition, great tillering and leafiness, along with high digestibility, crude protein and biomass production (Sedivec et al. 1991). It has high regenerative ability, provides multi-cut fodder free from anti-nutritional acids, and therefore could be utilized as fodder at any stage of development (Miller 1984; Idris et al. 2008). In various studies conducted in tropical regions, where the scarcity of resources occurs at a high extent, pearl millet has been reported as a high-quality fodder crop with good biomass production compared to other cereal fodder crops (Burton et al. 1966; Miller 1984; Skerman et al. 1990; Sedivec et al. 1991; Yadav and Bidinger 2008). Various traits have a direct or indirect effect on the quality and biomass of fodder (Minson et al. 1990), and fortunately, many of them are positively correlated with each other. Based on the observation methods and their relation, different fodder-related traits are categorized into two broad categories viz., biomass-related traits observed morphologically and quality-related traits estimated through biochemical analysis. These traits should be targeted for increasing crop production per unit area for developing high-yielding and quality fodder pearl millet varieties/hybrids by exploiting the available potential in the pearl millet gene pool.

Biomass-related traits:

In the case of pearl millet, there are two plant types, both of which are utilized as fodder. Firstly, dwarf cultivars produce a high proportion of leaves with more tillers and yield lower biomass. Despite this, they are suitable for grazing and are primarily used for cattle in the South-east US. In contrast, the second type possesses taller plant height with few tillers, thick stems and yields higher. It is mainly utilized for fodder, silage and as a dual purpose for both grain and stover (Hancock et al. 2009; Upadhaya et al. 2018; Yadav et al. 2010; Harinarayana et al. 2005).

In various studies, a significant amount of variability has been observed in different biomass-related traits. For instance, biomass yield ranged from 138.35–1080 quintals/hectares under normal growing conditions when harvesting was done at 50% heading, plant height (49–442.3 cm), the numbers of tillers/plant (1–9.3), stem girth (5–31.2 mm), number of leaves (4.3–37), leaf length (19.3–130 cm) and leaf width (1.1–8.6 cm) (Khairwal et al. 2007; Kulkarni et al. 2000; Arya et al. 2009; 2010). Hence, it is evident that pearl millet possesses similar green fodder yield potential as other fodder crops. Thus, by improving specific traits related to green fodder yield, biomass production per unit area can be enhance. (Dhedhi et al. 2015; Hassan et al. 2014; Kumar et al. 1989; Sheahan et al. 2014; Beniwal et al. 2009). Therefore, to enhance biomass production, targeted traits should be selected based on the specific plant type-mentioned above. For the short stature plant type, greater emphasis should be placed on increasing the leaf and stem ratio compared to other traits. For main plant type, all traits correlated with biomass production need to be taken into consideration before initiating a crop improvement program, such as tillers/plant, plant height, number of leaves, stem girth, leaf length and breadth, number of internodes, total leaf and stem weight.

Quality-related traits

Lower acid detergent fibre (ADF) and neutral detergent fibre (NDF) percentage, along with higher Crude Protein (CP) and digestibility, are desirable quality traits which favour high intake by animals and further increase the assimilation of energy minerals and vitamins (Minson et al. 1990). In Vitro Organic Matter Digestibility (IVOMD) is vital for animal production, as a 1% increase in IVOMD can lead to a 6–8% increase in animal productivity (Kristjianson and Zerbini 1999). In pearl millet, a significant amount of variation has been observed for NDF (52%—65%) and CP (7%–11%) (Hancock et al. 2009; Hassan et al. 2014; Ward et al. 2001). In another investigation by Rai et al. (2012), variability analysis in pearl millet forage hybrids was performed, reporting a good range for IVOMD (56.3–61.2%) and metabolizable energy (8.08–8.63 MJ/kg). The leaf-to-stem ratio is a morphological indicator for lower lignin content and greater CP and digestibility. Compared to other cereal fodder crops, pearl millet has a favourable leaf-to-stem ratio of 1.5, which is more than sorghum (0.92) and corn (0.72) (Harinarayana et al. 2005; Kumar et al. 1989; Jahansouz et al. 2014).

Brown midrib (bmr) is another visible marker that shows association with a low lignin content of the cell wall and expresses brown colouration in the midveins of leaves. Lignin is an indigestible phenolic polymer that increases when secondary cell wall deposition occurs at maturity and prevents the decomposition of microbes from doing their digestion work in the rumen (Miller and Stroup 2003; Heredia et al. 1995; Somerville et al. 2006). *bmr* mutants have low lignin content due to inhibition of one of the enzymatic reactions (Satller et al. 2010). However, *bmr* mutants have a negative correlation with biomass yield reducing green fodder yield by up to half, and genetic improvement is underway to overcome this problem (Cherney et al. 1991; Bean et al. 2013). The yield penalty imposed by bmr mutants can be reduced up to 25% using a higher seed rate (Hassanat et al. 2007).

Genetic studies for different quality and biomass-related traits have shown a correlation between these traits. For instance, a study by Govintharaj et al. (2018) suggests that direct selection for ME could enhance IVOMD. The study further recommends focusing breeding efforts on targeting traits such as total green fodder yield, PH, ME and CP traits to improve dry fodder yield and IVOMD. In dwarf types, d_2 is gene found responsible for dwarf height. It can reduce the height by 50% and increase leafiness and fodder quality (Burton et al. 1966). The *tr* gene removes trichomes and helps in reducing transpiration, stimulating drought tolerance and increasing palatability and resistance to insect pests (Burton 1977). Both the d2 and tr genes are qualitative, making dwarf plant types a good option for directly improving desirable quality traits. However, fodder yield is also essential to meet the minimum fodder needs of animals; therefore, the mapping genes governing quality and biomass traits could help improve both simultaneously.

Cultivar development chronology

Crop improvement in pearl millet began in the 1930s when Dr Glenn W. Burton initiated research at Tifton, USA. His pioneering work paved the way for worldwide pearl millet breeding, with a focus on developing improved fodder cultivars. He studied the genetics of key traits and evaluated germplasm, aiming to increase the leaf-to-stem ratio using dwarfing genes. In addition, he developed the widely used Cytoplasmic Male Sterility (CMS) source (A_1) (Burton and Forston 1966; Burton and Athwal 1969; Andrews et al. 1993). These findings from Tifton influenced pearl millet improvement efforts in India and Africa.

Pearl millet is primarily grown in India and African countries. Following Dr Glenn W. Burton's initial contributions to the crop, much of the improvement work was carried out in India by the Indian Council of Agricultural Research (ICAR). ICAR began pearl millet breeding in the 1940s, marking the first phase of pearl millet improvement. The focus during this phase was on increasing grain yield through mass selection of locally adapted cultivars (Singh et al. 2014).

The first forage hybrid, 'Gahi 1' was released in 1958. It was derived from four inbred lines (12, 18, 23, and 26) at Tifton and outperformed cultivars improved by direct or mass selection, dominating forage yield for many years (Burton 1962, 1983). Hybrid breeding for pearl millet in India gained momentum after the 1960s. Although 'chance hybrids' involving multiple lines were already in cultivation, they were not adopted by farmers due to minimal or no improvement compared to open-pollinated cultivars (Andrews and Kumar 1996). Breeding for cultivar development in India advanced significantly with the establishment of the All India Coordinated Pearl Millet Improvement Programme (AICPMIP) in 1965. This programme played a significant role in crop improvement, plant protection and production practices. The Indian grassland and fodder research institute, Jhansi focused on forage pearl millet, evaluating entries from different centres across India in different ecological zones. Based on performance, varieties/hybrids are identified for release at the National level (Table 1).

The second phase of pearl millet breeding in India began after the introduction of CMS lines from the US. The accidental discovery of the CMS line Tift 23A by Dr. Glenn W. Burton in 1956 marked a transformative moment in pearl millet improvement. This breakthrough overcame the obstacles in labour and time required for emasculation and pollination. The first grain hybrid, 'HB 1,' was developed

Table 1 Nutrient composition of forage pearl millet comparative to forage sorghum and corn silage

Nutrient composition	Forage pearl millet (g/kg dry matter)	Corn (g/kg dry matter)	Forage sorghum (g/kg dry matter)
NDF	580–685	540	605
ADF	313–425	295	379
Lignin	35–63	49	83
CP	90–180	86	133
Digestibility	640–690	730	630

NDF neutral detergent fibre; *ADF* acid detergent fibre; *CP* crude protein

in 1965 at PAU, Ludhiana, India. This hybrid yielded 88% more than the best local cultivars (Athwal 1965a). This revolutionized grain production, increasing from 3.5 teragrams in 1965 to 8 teragrams in 1970 (Burton 1983). In 1972, the first fodder hybrid, ‘Gahi 3,’ based on the CMS system, was developed. It demonstrated greater weight gain in animals and 10 to 19% increase in dry matter than ‘Gahi 1’ (Burton and Wilson 1995). Subsequent forage hybrids such as Tifleaf 1, 2, and 3, which also utilized the A_1 CMS source, were released in later years (Burton 1980; Hanna et al. 1988, 1997, respectively).

After the inclusion of CMS lines in breeding programs, improved cultivars became widespread in India and the US (Yadav et al. 2012). However, continuous incidences of downy mildew in hybrids derived from Tift23A led to the discontinuation of hybrid development programme based on A_1 cytoplasm. In the third phase of pearl millet breeding in India, alternate CMS seed parents were developed from A_1 CMS source through mutation breeding at the Indian Agricultural Research Institute (IARI). Hybrid breeding regained prominence in the 1980s, leading to higher genetic gain (Singh et al. 2014). Following this, many hybrids were developed using alternative seed parents based on A_1 cytoplasm, such as BJ104 and BK560, which were widely cultivated from 1977–1984. However, phased out when the incidence of downy mildew occurred and the same happened with other hybrids developed by Haryana Agricultural University, Haryana. The vulnerability of A_1-based hybrids was attributed to the use of parents having narrow genetic base derived from the same sources (Yadav et al. 1993; Rai et al. 1995; Rai et al. 1996). During this period, the International Crop Research Institute of Semi-Arid Tropics (ICRISAT) was established in 1972 and began OPVs-based breeding and succeeded in the diversification of seed parents (Kumara et al. 2014).

Between the third and fourth phases of pearl millet improvement, various CMS sources, such as A_1, A_2, A_3, A_4, A_5, A_v, A_{egp} were identified. In India, 167 hybrids and 61 varieties have been released primarily using A_1 and A_4 CMS sources, which are cultivated in diverse environments (Satyavathi et al. 2021). However, African farmers prefer OPVs and three-way hybrids for their economic feasibility and resistance to biotic and abiotic stresses. Another reason for preference given to top cross hybrids over single crosses in forage millet is due to their broad genetic base and intervarietal maintenance of heterogeneity, making them less vulnerable to stresses (Haussmann et al. 2012; Kumara et al. 2014). The combining ability evaluation of population hybrids in African tropics, highlights the potential for increased genetic gains in West Africa in the future (Ouenbeda et al. 1993; Pucher et al. 2016). Therefore, future efforts to achieve more genetic gains, both in quality and yield, may require a combination of conventional and new biotechnology approaches, such as marker-assisted breeding and Genomic selection to improve and develop fodder cultivars.

Due to the high level of heterosis, the private sector is involved on a large scale in hybrid production. Many high-yielding grain and fodder hybrids are developed by both the public and private sectors. In the year 2000, ICRISAT’s Hybrid Parents Research Consortium collaborated with private Sector seed companies in India and abroad to deliver improved hybrids and varieties to underprivileged farmers. They improved hybrid parents for sweet stalk traits for biofuel and single cut forages and identified high green biomass breeding lines, germplasm and cultivars. A total of 60–70% of pearl millet hybrids grown in India are based on ICRISAT-bred A-lines or on proprietary A-lines developed from improved lines bred at ICRISAT (Rao et al. 2018). Farmers in both India and the US prefer high-quality seeds for fodder cultivation to obtain quality fodder and high biomass. However, in African nations, farmers struggle to afford improved seeds due to their high cost and the lack of an efficient seed supply chain. The role of government is crucial in formulating seed policies in the tropics to ensure farmers receive high standard, pure seed (Prasanna et al. 2020). The development of improved cultivars for single and multi-cut fodder can be achieved by selecting lines from diverse heterotic pools for hybrid development through crossing and by employing CMS system. Additionally, population improvement of promising inbred lines can be achieved using various recurrent selection methods to develop open-pollinated varieties (Fig. 2).

Breeding interspecific hybrids

Wild relatives of cultivated species serve as reservoirs for desirable genes such as disease resistance, yield increase and various forage-related traits (Hanna et al. 1987). The genetic diversity within the genus *Pennisetum* is classified into three groups viz., primary, secondary and tertiary gene pools, based on Harlan and De Wet (1971). At ICRISAT,

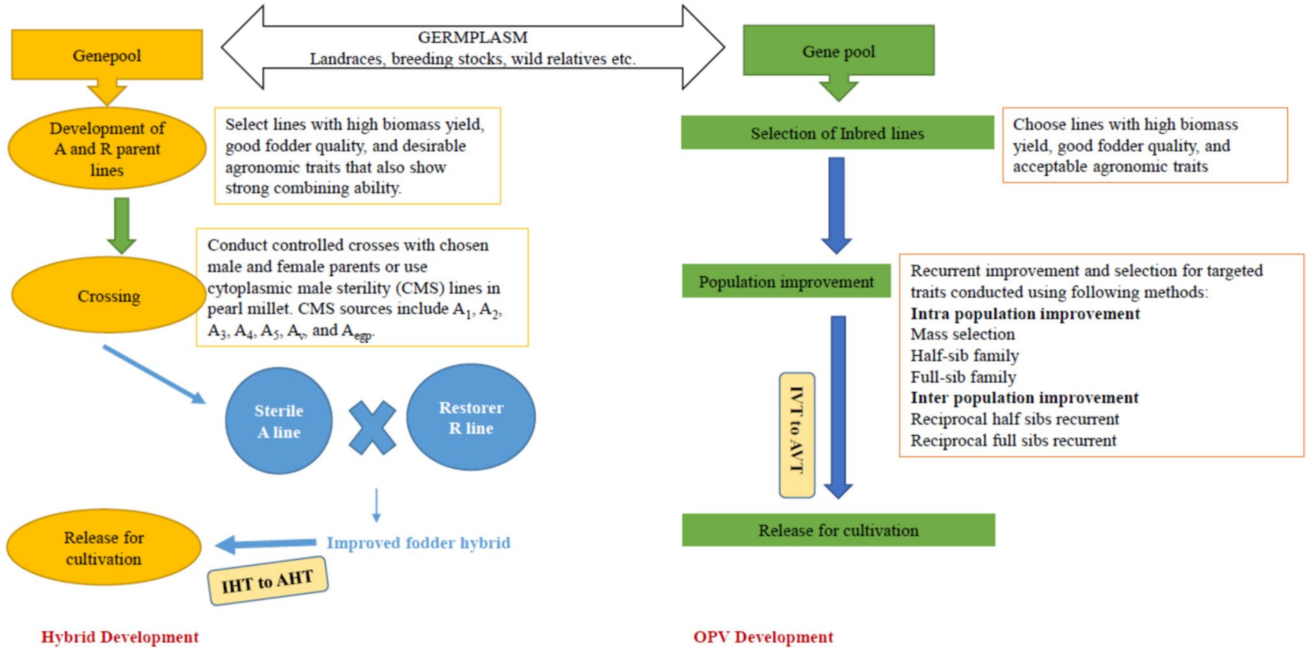

Fig. 2 Hybrid and open-pollinated variety (OPV) development approaches for pearl millet. IVT- Initial varietal trial: AVT- Advanced varietal trials: IHT- Initial hybrid trials: AHT- Advanced varietal trials

140 species of the genus *Pennisetum* are conserved, contributing to crop improvement by transferring desirable traits from wild relatives to elite lines (Andrews and Kumar 1996; Serba et al. 2017). Cross-compatibility and homeologous pairing of haploid chromosomes after fertilization, categorize species into three gene pools. The primary gene pool includes cultivated, weedy and wild diploids with chromosome number ($2n = 2x = 14$). The secondary gene pool comprises tetraploid species with ($2n = 4x = 28$) such as *P. purpureum Schum*. The tertiary gene pool encompasses wild species with different ploidy levels (Dujardin and Hanna 1989). It is difficult to make a cross and transfer genes from tertiary to primary species due to limited homology. Bridge species with intermediate ploidy levels are required to overcome pre fertilization barriers between non-crossable species (Hanna et al. 2010).

The wild species *P. glaucum subsp. monodii* from the primary gene pool is a source of A_4 cytoplasm, which is resistant to many diseases. It is now widely used as a source for hybrid seed production (Hanna et al. 1989) and also leads the way to cytoplasmic diversity from A_1 based hybrids. The species belonging to the secondary gene pool are reservoirs of fodder-related traits that might provide valuable genes for fodder quality and biomass production. One of the most famous fodder interspecific hybrids between cultivated *Pennisetum glaucum* ($2n = 2x = 14$) X *P. purpureum Schum* (also known as Napier grass) ($2n = 4x = 28$) known as Napier bajra hybrid is cultivated widely. The F_1 produced after crossing both species is always sterile due to triploidy. After development, it is easily propagated using stem cuttings, making it suitable for perennial fodder cultivation (Jauhar et al. 1998). The resultant fodder hybrid combines the forage quality of cultivated pearl millet with dry matter and biomass production of Napier grass. Napier hybrid has good regenerative ability, green fodder yield, leaf-to-stem ratio and high forage quality with no anti-nutritional components. It can be grown in various soil types and cultivation systems, including mixed, relay and intercropping. The Napier hybrid also provides biological pest management strategy against stem borer (*Coniesta ignefusalis*) in maize and pearl millet cultivation through the pull–push strategy, attracting moths toward themselves and away from other crops (Khan et al. 2007).

In the tertiary gene pool, several species having multi-disease resistance, forage quality and apomixes genes are present. *P. pedicellutum trin* (Deenanath grass) and *P. polystachianh. schult* (Mission grass) species have downy mildew resistance genes along with fodder quality and biomass traits. Species, *P. orientale* and *P. ciliare*, are reservoirs of drought tolerance, fodder and apomixes traits (Hanna et al. 1982). *P. squamulatum* has winter hardiness genes. These desirable traits can be incorporated into elite pearl millet lines using bridge species or various biotechnological approaches, such as tissue culture, to overcome pre and post-fertilization barriers. A combination of conventional and marker-assisted breeding could aid in overcoming the challenges posed by distinct gene pools with no or less homology.

Cytoplasmic male sterility systems

Cytoplasmic male sterility (CMS) is maternally governed and is characterized by the failure of anthers to produce viable or functional pollen, whereas the development of stigma is normal. This is based on an interaction between nuclear and cytoplasmic genes, in which nuclear Rf genes act as fertility restoration of the sterile parent after crossing and maintenance is done by isonucleic male fertile line. In pearl millet, the first A_1 CMS-based line was widely used for hybrid seed production. Therefore, efforts were made to discover alternative CMS sources and that process led to the identification of two alternative CMS sources A_2 and A_3 from genetic stocks and their derivatives (Athwal 1961, 1965a). Additional CMS sources A_v and A_4 were discovered from wild species in the primary gene pool of *P. glaucum sbsp. monodii* (Marchais et al. 1985; Hanna 1989). Two more CMS sources Aegp and A_5 from gene pools were also identified from cultivated species (Sujata et al. 1994; Rai et al. 1995).

CMS sources A_1, A_4, A_v, A_5 and A_{egp} were crossed with common fertility restorers and resulting hybrids derived from these crosses showed the differential male fertility restoration pattern, providing their distinctness as different CMS sources. These CMS sources were further categorized based on their commercial viability by comparing them based on stability, character association and frequency of maintainers, and these all factors are responsible for their breeding efficacy as a seed parent (Rai et al. 1995; Rai et al. 1996, 2009; Yadav 1996; Yadav et al. 2012). Inheritance of fertility restoration in A_4 CMS system was studied by Gupta et al. (2012) reporting dominant monogenic inheritance of the Rf gene. Similar results were reported in an advanced study on gene mapping of Rf. Maintainer loci of A_4 CMS system using an F_2 population 138 plants showed the same monogenic segregation pattern of 3:1 (Pucher et al. 2016).

A_m (m = *P. glaucum subsp. monodii*) = A_4 CMS system produces the highest frequency of hybrids and is good for hybrid seed production. A_4 and A_5 both are very good sources of CMS due to their stability. As pollen shedding in A_5 CMS is very low compared to all other CMS sources and maintenance frequency is high, due to the problem of fertility restorers, it could not be used at large scale for grain hybrid production. Nevertheless, it can be used for forage hybrid production due to its easy maintenance with high frequency (Rai 1995). A_4 CMS is now widely used for hybrid seed production for both grain and fodder in the African tropics and India due to the availability of good amount of fertility restorers.

Generation of genetic and genomic resources for forage improvement

Genetic resources

The availability of genomic resources is crucial for advancing crop improvement in response to changing climates. The foundation of crop development relies on the accessibility and generation of genetic resources, that are essential for identifying regions that control desirable agronomic and economic traits. The availability of variability for targeted traits is a prerequisite for the development of genomic resources. Fortunately, pearl millet, with its cross pollination nature and adaptation to adverse conditions, possesses a significant amount of genetic diversity for various traits (Upadhaya et al. 2007).

In the case of pearl millet, several National and International Institutes have been involved for many years, resulting in 66,682 accessions globally available accessions. ICRISAT hold a major share with ~ 21,594 accessions from 51 countries (Singh and Upadhaya 2016). ICRISAT's Core and mini core collections are utilized for allele mining studies, identifying loci governing various agronomic traits, biotic and abiotic stress resistance for the improvement of cultivars (Srivastava et al. 2020). Other gene banks, such as the Institute of Research and Development (IRD, France), Canadian Genetic Resources (Saskatoon, Canada) and US Germplasm Resource Information Network (GRIN), also house substantial genetic resources (Yadav 2007).

Upadhaya et al. (2018) had conducted an investigation which illustrates the pearl millet gene pool's variability for fodder traits and its stability in various agroecologies. They evaluated 326 inbred lines of pearl millet and reported a significant genotype x environment interaction. In longer rainy season days, late maturity, tall plant height and thick stems having long and broad leaves were observed; however, in post rainy season, antagonistic results were reported. Yadav et al. (2018) characterized pearl millet germplasm for grain and fodder. They found that landraces from lower-latitude regions (below 20 degrees north and south) mature later, grow taller and have high tillering, making them more suitable for fodder production. Hybrid parents evaluated by Govintharaj et al. (2017) showed significant differences in forage traits such as plant height, green forage yield, dry forage yield and crude protein, indicating notable genetic variation. The greater genetic diversity was observed in pollinator parents by Ponnaiah et al. (2019), suggesting the potential for breeding high-quality, high-yielding hybrids for improved forage traits. Gupta et al. (2022) reported a significant differences for total green and dry forage yields, as well as key forage quality traits across cuts. Three-way top cross hybrids outperformed other cultivars, offering superior yields and quality traits, making them preferable for smallholder farmers and seed companies. In summary, these studies highlight the genetic diversity and potential for breeding high-quality pearl millet hybrids for improved grain and fodder production.

At ICRISAT, the Pearl Millet Inbred Germplasm Association Panel (PMiGAP) was developed, representing global diversity, comprises 346 lines, represents diverse cultivars, landraces and mapping population parents from 27 countries and re-sequenced using the whole genome resequencing (WGRS) approach. It has a repository of circa 29 million genome-wide single nucleotide polymorphisms (SNPs). From this panel, 45 diverse lines were used to develop the RIL mapping populations, and these RILs have been used for mapping different traits viz., drought tolerance, grain Fe and Zn content, nitrogen use efficiency, components of endosperm starch, grain yield, etc. (Srivastava et al. 2020). These genetic resources could also be valuable for developing genomic resources for fodder quality and biomass-related traits in pearl millet.

Genomic resources

The genome sequencing of pearl millet (Varshney et al. 2017) has opened a way to tap on its broad genetic diversity to breed varieties and hybrids for future needs. This enables the characterization of germplasm and mapping of functionally important genes associated with diverse traits for numerous individuals simultaneously (Mogga et al. 2018). The multiplexing approach, genotyping by sequencing (GBS), has emerged as a promising method for molecular marker discovery and genetic diversity analysis. It is considered as a cost-effective tool for QTL discovery, high resolution mapping, genomic selection and genome-wide association mapping for complex traits in crop improvement (Elshire et al. 2011; Sânchez-Sevilla et al. 2015). The advent of these genomic techniques has reduced genotyping costs, leading to a substantial allocation of project budgets to phenotyping, precise phenotyping of a large number of individuals is crucial for dissecting complex traits (Hall et al. 2010).

By combination of conventional methods and bioinformatics tools facilitates the use of sequencing data for deciphering the mechanism behind the targeted traits and their functional studies. In pearl millet, various omics tools are widely applied for morphological, quality, biotic and abiotic stress improvement. However, the utilization of these tools for fodder traits is rare, with only a few reported cases. This indicates a significant opportunity for applying these tools to generate resources for fodder improvement. In plant sciences, various techniques are available for uncovering genomic regions responsible for traits, each tools varies in its capacity of resolution; however, each has its pros and cons which are discussed as under:

QTL mapping (traditional mapping using biparental population)

Compared to other cereal crops, there are limited reports on the development and application of molecular markers in pearl millet. The first linkage map for pearl millet was developed in 1994 by Liu et al. (1994), utilizing a bi-parental mapping population consisting of 132 F_2 plants. They employed restriction fragment length polymorphic (RFLP) markers and successfully placed 181 markers on seven linkage groups, covering a map length of 303 cM. Before this, Smith et al. (1993) had developed RFLP and random amplified polymorphic DNA (RAPD) genetic markers to characterize the pearl millet genome. Their linkage analyses revealed 64 markers linked to QTLs associated with various plant traits. These QTL-linked markers laid the foundation for genetic study on important biomass/forage productivity and quality traits.

The traditional QTL mapping technique is extensively employed in various cereal fodder crops (Table 2). In pearl millet, QTLs related to various traits were mapped using biparental mapping populations; however, no investigation to date has been reported for the mapping of green fodder quality- and biomass-related traits. Several RIL mapping populations in pearl millet, developed by selecting contrasting parents for different traits, have been utilized for mapping. For instance, Yadav et al. (2002) used a segregating population from a cross between two early maturing pearl millet inbred lines to construct linkage map. They identified QTLs related to grain and stover yield under terminal drought stress conditions, reporting significant variation. The resulting linkage map consisted of 50 markers covering seven linkage groups (LGs) with a genetic map length of 352 cM. Subsequent investigations by Yadav et al. (2003) utilized the same genetic linkage map to map and characterize QTL × environment (E) interactions for traits determining grain and stover yield. They detected three classes of QTLs viz., QTLs associated with genotypic effects for grain and biomass yield on linkage group 4, the second class associated with G × E interaction mapped on LG 5 for flowering time and harvest index on LG 2 and 4. The third type covered the majority of traits, and many QTLs were mapped for this category which are associated with G and G × E effects. Nepolean et al. (2006) used a set of F_2 derived self-bulk progenies of pearl millet to map drought tolerant and stover quality QTLs, identified three QTLs distributed across LG 3, 4 and 5, also introgression was carried for four parental lines of existing hybrids.

This pattern of limited investigations on QTL mapping for different fodder-related traits is observed in other major

Table 2 Details of mapping studies for forage quality and biomass-related traits in various fodder crops

Crop	Traits	PVE (%)	No. of QTL/ SNP	References
Pearl millet	Flowering time, stover yield, biomass yield, harvest index	11.4–38.1	12	Yadav et al. 2002
	Flowering time, stover yield, biomass yield, harvest index		13	Yadav et al. 2003
	Flowering time, plant height	22.9–39.8	19	Kumar et al. 2017
	IVOMD, ME, dry stover yield, nitrogen dry matter	8.5–26	14	Nepolean et al. 2006
	IVOMD, CP		11	Govintharaj et al. 2021
Alfalfa	Biomass production		41	Robins et al. 2007a
	Fodder yield, plant height and forage regrowth	11–44	86	Robins et al. 2007b
	Fodder quality and stem histology		86	Espinoza and Julier 2013
	Fodder yield, lodging resistance, spring vigour	9.4–27.9	6	McCord et al. 2014
	Forage biomass productivity under drought	2.8–8.1		Ray et al. 2015
	Biomass yield, acid detergent fibre, acid detergent lignin, neutral detergent fibre and stem composition	2–6	17	Li et al. 2011
	Lignin biosynthesis genes, acid detergent fibre, Neutral detergent fibre, acid detergent lignin, plant height and biomass yield		7	Sakiroglu et al. 2012
	Spring yield and cumulative summer biomass		23	Adhikari et al. 2019
	Biomass yield under drought (greenhouse)		19	Zhang et al. 2015
	Neutral detergent fibre, acid detergent fibre, neutral detergent fibre digestibility and leaf/stem ratio	10–20.2	83	Biazzi et al. 2017
	Forage quality traits	2.48–9.66	124	Wang et al. 2016a
	Crude protein, mineral concentration	2.1–4.09	2–8	Jia et al. 2017
	Biomass yield (drought in field conditions)		7–32	Yu 2017
	Biomass	8–38	42	Liu and Yu 2017
	Forage yield, nutritive value		65	Sakiroglu and Brummer 2017
Soybean	Shoot fresh weight, shoot dry weight and shoot fresh weight/ shoot dry weight	12–34	10	Brensha et al. 2012
	Shoot fresh weight	6.6–21.3	3	Asekova et al. 2016b
	Crude protein neutral detergent fibre and acid detergent fibre	6.6–21.3	16	Asekova et al. 2016a
Maize	Crude protein and in vitro organic matter digestibility		30 In exp 1 26 in exp 2	Lubberstedt et al. 1997
	Neutral detergent fibre, acid detergent fibre and in vitro organic matter digestibility	4.2–6.2	56	Wang et al. 2016a, b
	Crude protein	7.5–13.6	4	Barrière et al. 2001
	Cell wall and digestibility		34	Barrière et al. 2007
	Digestibility	3–18	6	Bohn et al. 2000
	Neutral detergent fibre, acid detergent fibre and acid detergent lignin	45–66	26	Cardinal et al. 2003
	Cell wall and digestibility		10	Fontaine and Briand et al. 2003
	Cell wall		17	Krakowsky et al. 2003
	Cell wall	71	13	Krakowsky et al. 2005
	Neutral detergent fibre and acid detergent fibre	25–58	24	Krakowsky et al. 2006
	Neutral detergent fibre, acid detergent lignin and in vitro organic matter digestibility	7.6–13.5	13	Méchin et al. 2001
	digestibility		3	Papst et al. 2001
	Neutral detergent fibre, acid detergent lignin	7.7–26.7	6	Riboulet et al. 2008
	Cell wall and digestibility	6.7–27.7	37	Roussel et al. 2002
	Cell wall	25–47.4	47	Li et al. 2017
	Neutral detergent fibre, acid detergent fibre	10–41	20	Wang et al. 2020

Table 2 (continued)

Crop	Traits	PVE (%)	No. of QTL/ SNP	References
Wheat	Neutral detergent fibre, acid detergent lignin, in vitro organic matter digestibility, metabolizable energy ash and acid detergent lignin		1–17	Joshi et al. 2019
Sorghum	Neutral detergent fibre, acid detergent lignin, in vitro organic matter digestibility, metabolizable energy ash and acid detergent lignin	5.15–15.34	296 in different environments	Somegowda et al. 2022
	Neutral detergent fibre, acid detergent lignin, hemicellulose, crude lignin and crude protein	0.28–10.58	43	Li et al. 2018

PVE phenotypic variation, *QTL* quantitative trait loci, *SNP* single nucleotide polymorphism

fodder crops as well. In *Medicago truncatula*, Lagunes et al. (2013) utilized four connected mapping populations for QTL mapping of fodder quality and identified 86 QTLs across the years. In sorghum, Somegowda et al. (2022) investigated mapping QTLs related to fodder quality in terminal drought stress environment. These studies collectively highlight the efficacy of mapping populations in QTL mapping studies for various traits. While various biparental populations are available for mapping, however, RILs carried a broad spectrum of variability arising from recombination events that occur in F_2, providing an opportunity for multilocation phenotypic analysis essential for precise mapping of quantitative traits influenced by the environment. Therefore, the utilization of such an immortal population coupled with precise phenotyping and high-quality genotyping holds the potential for fruitful outcomes.

Genome-wide association mapping

Genome-wide association studies (GWASs) are an approach for studying associations between a genome-wide set of markers and desired phenotypic traits. This quantitative evaluation relies on the non-random association of alleles at different loci (Flint-Garcia et al. 2003; Uffelmann et al. 2021). The genotyping process involves utilizing densely distributed markers across the entire genome to analyse a panel collected in a manner that encompasses all alleles within the gene pool, contributing to the observed traits. Phenotypic data, along with various covariates, are incorporated for statistical analysis, aiming to identify associations between markers and traits.

Several studies have been conducted in pearl millet to map various traits using genome-wide association mapping approach. These traits include grain iron, zinc and protein content, flowering, starch contributing to low glycaemic index and metabolite diversity related to nutritional traits and drought tolerance (Anuradha et al. 2017; Pujar et al. 2020; Diack et al. 2020; Yadav et al. 2021a,b; Sehgal et al. 2015; Varshney et al. 2017; Debieu et al. 2018). Recently, Govintharaj et al. (2021) conducted GWAS for fodder quality and biomass using three different sets of populations: set-I (80 single cross hybrids), set-II (50 top cross hybrids) and set-III (105 forage type hybrid parents) and evaluated at multiple locations for total dry fodder yield, IVOMD and CP. Their findings revealed a stable SNP on LG4 and nine SNPs for IVOMD distributed across all linkage groups except LG2. Additionally, they identified one gene each for crude protein at the first and second cuts, along with six candidate genes at the first cut and three at the second cut for digestibility. To date, this is the sole investigation in pearl millet conducted for fodder-related traits. These findings still require further validation for the utilization in breeding programmes for improvement of fodder quality and quantity.

Overall, research on fodder-related traits is significantly behind other traits. This gap requires urgent attention, particularly with the continuous increase in livestock. Other crops have seen a few reports utilizing GWAS and the development of gene-based functional markers for crop improvement of traits. Such as, in sorghum, Xia et al. (2018) conducted a GWAS analysis across 694 diverse sorghum inbreds, revealing an association between zinc finger homeodomain (ZF-HD) and midrib colour variation. Another study genotyped 245 sorghum accessions with 85,585 SNPs and identified 42 SNPs associated with five forage quality traits, including a concurrent association of CP, ADF and NDF (Li et al. 2018). Similarly, in Bermunda, grass (Gitau et al. 2017), maize (Vinayan et al. 2013; Wang et al. 2016a, b) and alfalfa (Li et al. 2011) studies have been conducted. Biazzi et al. (2017) observed differential genetic control in the leaf and stem of alfalfa. All these studies aimed at dissecting the genetic architecture of fodder quality and biomass-related traits, contributing to the development of genomic resources for enhancing targeted traits. Therefore, adopting modern genomic approaches with proper knowledge and expertise can overcome the limitations of conventional approaches ultimately increasing the genetic gains.

Genomic selection (GS)

The availability of cost-effective, high throughput molecular markers and robust SNP genotyping platforms has paved the way for genomic selection, even in orphan crops where research always lags (Bhat et al. 2016). Initially, the genomic selection approach aimed to predict complex traits in animals and plants (Meuwissen et al. 2001). Recently adopted in breeding, several investigations have reported better genetic gain per year compared to conventional breeding approaches. Marker-assisted selection (MAS) and GS are marker-assisted breeding approaches used for crop improvement; however, MAS is often considered an inferior method due to the utilization of molecular markers developed from linkage QTL mapping and GWAS, which may be biased toward minor QTLs. Only QTLs which explain a significant percentage of phenotypic variance are deemed useful for selection (Zhao et al. 2014). GS is an approach that overcomes these obstacles, enabling efficient and rapid crop improvement. The potential of GS has been demonstrated in various studies (Das et al. 2020; Shikha et al. 2017; Das et al. 2020; Heffner et al. 2009; Zhong et al. 2009; Crossa et al. 2010; Ornella et al. 2012; Poland et al. 2012; Spindel et al. 2015; Muleta et al. 2019).

In pearl millet, GS has been adopted to predict grain yield for test crosses in various environments. Varshney et al. (2017) utilized WGRS data for GS and achieved high prediction accuracies of 0.6 in all environments. Furthermore, the GS strategy was employed to analyse grain yield data with 3,02,110 SNPs to predict hybrid performance. Out of the 170 promising hybrid combinations detected, 11 were already reported to be used for hybrid production. However, in pearl millet, GS has not been applied for fodder improvement due to resource constraints. Nevertheless, reports exist in other crop species. For instance, in alfalfa, Biazzi et al. (2017) used 154 genotypes from a broadly based reference population, genotyped them using a GBS approach, and employed 11,450 polymorphic SNP markers for GS with three prediction models. All three models have provided similar selection accuracies ranging from 0.3 to 0.4. Notably, compared to morphological traits, accuracy was reported to be higher for the quality-related traits. The findings from these experiments collectively demonstrate the efficiency of GS in comparison with other selection techniques in improving fodder-related traits within a short duration. According to simulations and empirical studies, genomic selection proves to be more effective than traditional phenotypic selection, resulting in larger gains per unit of time. The incorporation of genomic selection into current pearl millet breeding programmes will undoubtedly enhance selection efficiency and yield greater genetic gains (Kapoor et al. 2022).

Transcriptomics

In the era of omics, transcriptomics has become the mainstream approach for expression profiling in crop plants. Using RNA-Seq analysis, differentially expressed genes at various stages in different tissues can be identified. In pearl millet, numerous studies have been conducted using this approach to decipher the mechanism behind various traits and genes involved in their expression, such as drought tolerance (Jaiswal et al. 2018; Dudhate et al. 2018; Sun et al. 2020; Shivhare et al. 2020; Ji et al. 2021; Ndiaye et al. 2022; Reddy et al. 2022), heat stress (Sun et al. 2021; Yan et al. 2023), salt stress (Shinde et al. 2018; Khan et al. 2023), downy mildew (Kulkarni et al. 2016) and iron and zinc (Mahendrakar et al. 2020; Satyavathi et al. 2022).

In pearl millet, and even in other major fodder crops, no report is available where the identification of candidate genes for fodder quality through gene expression analysis or transcriptomics has been conducted. However, there is wide scope for this approach to be used in the future for identifying fodder-related traits in pearl millet. In the current era of information technology, which provides vast amounts of data at different omics levels such as genome, transcriptomics and proteomics may be harnessed using various bioinformatics tools to develop genomic resources. Additionally, the homology existing between different species can be exploited to transfer information generated in one species to another. Therefore, the integrated approach of breeding, biotechnology and bioinformatics will assist in efficiently and precisely generating genetic and genomic resources for crop improvement. In conclusion, the potential of using gene expression analysis and bioinformatics tools in identifying candidate genes for fodder quality in pearl millet and other fodder crops is considerable, marking a promising avenue for future research and crop enhancement.

Other traits for forage quality improvement

The brown midrib (Bmr)

The brown midrib (bmr) mutants, occurring naturally in certain plant species, improve the digestibility of fodder and quality traits, except crude protein. They are considered to be one approach for favourably changing the quantity and quality of lignin (Cherney et al. 1991). The bmr mutants have lower lignin content in leaves and stems and can be distinguished easily from wild types due to their tan to reddish- brown midrib versus white or green midrib of leaves.

In maize and sorghum, the bmr trait is controlled by one recessive gene (Barnes et al. 1971; Cherney et al. 1988; Lechtenberg et al. 1972; Muller et al. 1971, 1972). Silage made from bmr mutants in maize outperforms that made from normal fodder in terms of animal performance, as measured by average daily gain, feed efficiency and dry matter intake (Colenbrander et al. 1973; Frenchick et al. 1976; Lechtenberg et al. 1974). In maize, brown pigmentation was initially observed in the midrib, tassel, cob and roots as early as 1924 (Jorgenson 1931). There are six known bmr mutations (bmr 1–6) and four non-allelic brown midrib genes found in maize (Kuc and Nelson 1964). However, the trait causes weak stems, leading to lodging and resulting in greater losses in corn compared to sorghum and pearl millet (Eastridge 1999). In pearl millet, Bmr mutants have been reported to produce 77% more fodder than typical F_3 lines and 5% higher digestibility than non-bmr lines in a comparative study. Additionally, bmr mutant plants were reported to show 11% more digestibility in the stem portion than non-bmr plants (Sattler et al. 2014). The bmr trait was reported to have outstanding potential for improving the forage quality of fodder and grazed millets (Table 3) (Cherney et al. in 1988). SDML89107, a bmr genotype, exhibits a 16.2% higher stem IVDMD at 50% flowering than that of its normal counterpart, with the entire plant IVDMD being 10.7% higher (Gupta 1995). Overall, the bmr trait was found to elevate the forage quality of pearl millet at par with conventional corn. In pearl millet, efforts have been made to develop high-quality fodder varieties by introgressing the bmr trait (Yadav and Weltzein 1998; Blummel et al. 2003). Recently, at ICRISAT, inbred lines with stable expression of the bmr gene and high biomass potential have been identified, which can be further utilized for fodder improvement (Gupta et al. 2023).

In summary, the bmr trait influences both the biomass and quality of pearl millet fodder, positively impacting one aspect while negatively affecting the other. Both factors play a crucial role in maintaining the sustainability of the dairy industry, with an emphasis on higher-quality fodder over high yields. This preference is justified by the resulting net gain in animal productivity. Consequently, lines featuring the bmr trait emerge as promising candidates for developing high-quality climate-resilient fodder cultivars.

Table 3 Comparison of different nutrient components of normal and bmr mutants in pearl millet (Cherney et al. 1988)

Component	Normal	bmr
Leaf: Stem (ratio)	2.2	2.2
IVDMD (g/kg dry matter)	659	726
NDF (g/kg dry matter)	656	635
Cellulose (g/kg dry matter)	305	293
Hemicellulose (g/kg dry matter)	303	298
Lignin (g/kg dry matter)	50	40

IVDMD in vitro dry matter digestibility; *NDF* neutral detergent fibre

Lignin pathway and genetic alterations

Lignin is a secondary metabolite synthesized through the phenylalanine and tyrosine pathway in plants. Phenylalanine plays a key role in producing lignin subunits (Feduraev et al 2020). In plants, phenylalanine constitutes approximately 30% of the carbon flow (Pascual et al 2016). Lignin biosynthesis involves the production and transfer of lignin monolignols from the cytoplasm to the apoplast, where they undergo polymerization with the help of enzymes such as peroxidase (POD) and laccase (LAC) (Alejandro et al. 2012; Miao et al. 2010; Liu et al. 2011).

Targeting the lignin pathway using genome modification tools helps understand cell wall-related components and their genetic control. Genes involved in initial steps, such as *PAL* (phenylalanine ammonia-lyase), *4CL* (4-coumarate) and *C3H* (p-coumarate 3-hydroxylase), have been reported to negatively affect plant growth, leading to sterility. However, downregulating genes later in the pathway namely, *F5H* (ferulate 5-hydroxylase), *CCoAOMT* (caffeoyl-CoA O-methyltransferase), *CCR* (cinnamoyl-CoA reductase), *COMT* (caffeic acid O-methyltransferase) and *CAD* (cinnamyl alcohol dehydrogenase) has shown no adverse impact on the plant growth (Fig. 3). Lignin plays a crucial role in plant development, providing pests and pathogen resistance (Ithal et al. 2007) contributing to plant lodging resistance, and responding to various environmental stresses (Tripathi et al. 2003; Shadle et al. 2007). Genes involved in lignin biosynthesis have been targeted for modification in crops such as alfalfa (Inoue et al. 1998; Guo et al. 200; Barros et al. 2019; Baucher et al 1999) and tall fescue (Chen et al. 2003) to improve forage quality.

Genes involved in the lignin biosynthesis were targeted to improve fodder digestibility and identified potential genes with low lignin content with increased digestibility having no impact on plant growth. Giordano et al. (2014) reported the increased digestibility in *Paspalumdilatatum* after the down regulation of *CCR* gene and suggested it as a potential candidate for the production of low lignin plants in C_4. Another investigation involving *CCR1* and *COMT1* genes reported significantly reduced lignin content and composition and increased digestibility without any negative impact on the fitness of plant and biomass yield in ryegrass (Tu et al. 2010).

Other investigations involving lignin engineering in plants reported 20–40% reduction in lignin content along with the other changes in plants such as dwarfism (Gui et al. 2011; Wagner et al. 2009), reduced resistance to diseases and pests (Huang et al. 2010; Duan et al. 2014; Jannoey et al.2017; Wang et al. 2017; Fujimoto et al. 2015; Tianpei et al. 2015), sutructural deformities (Wang et al. 2008) and increased sterility (Thevenin et al. 2011; Schilmiller et al. 2009), seed propagation and germination (Derikvand et al.

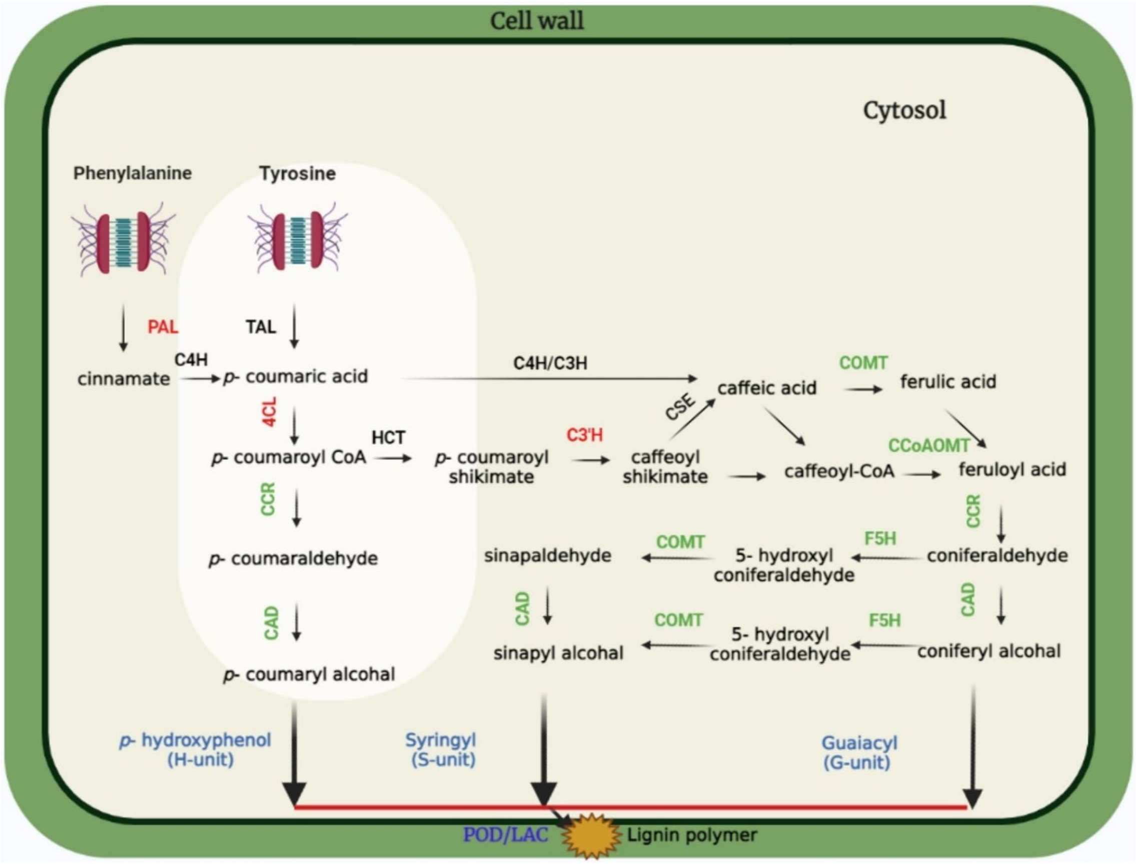

Fig. 3 Lignin biosynthesis pathway. Genes in red colour reported to be negatively impact plant growth and green colour genes represent the positive targets for lignin alteration in plants. PAL, phenylalanine ammonia-lyase; TAL, tyrosine ammonia-lyase; C4H, cinnamate 4-hydroxylase; 4CL, 4-coumarate: CoA ligase; CCR, cinnamoyl-CoA reductase; HCT, hydroxycinnamoyl-CoA shikimate/Quinatehydroxycinnamoyltransferase; C3H, p-coumarate 3-hydroxylase; CCoAOMT, caffeoyl-CoA O-methyltransferase; F5H, ferulate 5-hydroxylase; CSE, caffeoyl shikimate esterase; COMT, caffeic acid O-methyltransferase; CAD, cinnamyl alcohol dehydrogenase; LAC, laccase; POD, peroxidase

2008; Liljegren et al. 2000; Liang et al. 2006) and lodging (Peng et al. 2014; Zheng et al. 2017; Hu et al. 2017).

Biochemical pathways involved in fodder quality

Carbohydrate metabolism involves the breakdown and use of carbohydrates such as cellulose, hemicellulose and pectin—key components of plant cell walls that affect the digestibility of plant matter. In crops like maize, genes associated with carbohydrate metabolism, including those examined by Li et al. (2016), play a crucial role in boosting plant productivity and quality. Nitrogen metabolism is vital for plant health because nitrogen is essential for protein and amino acid synthesis, facilitated by key enzymes such as glutamine synthetase (GS) and asparagine synthetase (ASN). Chlorophyll synthesis is fundamental to photosynthesis and thus to plant growth and development, with genes such as magnesium chelatase (CHLH) and chlorophyll b reductase (NYC1) being crucial for chlorophyll production and potential targets for increasing the nutritional value of plant material.

Therefore, by focusing on the genes involved in the lignin pathway and creating mutants with the bmr phenotype using novel functional techniques, there exists significant potential for improving the digestibility of fodder and ultimately elevating animal production in the future. While these mutants prove advantageous as grazing dwarf plant types, the development of standard fodder cultivars necessitates a robust stalk to confer structural stability and resistance to lodging. Addressing the detrimental impact of these mutants on biomass is of paramount importance. It is crucial to identify genes that counteract these effects in plants with altered lignin concentration, thereby mitigating this issue. Further, combination of high throughput and cost-effective techniques will enable the mapping of QTLs and the identification of candidate genes for numerous forage quality and biomass-related traits, resulting in the development of useful gene-based markers. By specifically targeting genes involved in lignin biosynthesis, carbohydrate metabolism, nitrogen metabolism and chlorophyll synthesis, crop scientists can engineer crops with superior forage quality. This, in turn, contributes to the advancement of animal health and productivity.

Special attributes

Climate resilience

Pearl millet is suitable food choice for patients with celiac disease because it is gluten-free and classified as a nutricereal (Saini et al. 2021). In addition to its health benefits for humans, it also serves as a quality fodder and feed crop for livestock and poultry (Cisse et al. 2017; Hall et al. 2004). Pearl millet can flower in temperatures above 40 °C without compromising yield and quality, making it a climate change future-ready crop that requires improvement only in terms of yield and quality rather than its ability to withstand increasing temperatures and climate changes (Satyavathi et al. 2021). However, its genomics potential remains underutilized due to limited funding and its status as being a poor man's crop. But now, there is a need to harness the available genetic variability in the gene pool of this crop species employing a holistic and integrated approach to alleviate the complex problems of agriculture. With the efforts of the Indian Government, the United Nations declared 2023 as the 'International Year of Millets', which is a blessing for this crop and may help in understanding the different aspects of this nutri-cereal grown in adversity and further development of desirable cultivars in synchronization with the requirement. This can benefit many dairy farmers and may help in sustaining milk production in developing African and Asian nations and other countries.

Silage potential

Pearl millet is a versatile and valuable forage crop with the potential to yield high-quality forage, especially during growing seasons with favourable moisture. It stands out as a significant source of silage with good nutritive value, contributing to the availability of quality fodder during the lean periods, such as November–December and May–June (Tripathi et al. 1995). Non-legume fodders like maize, sorghum and pearl millet are rich in sugars and carbohydrates, making them ideal candidates for silage production. To optimize silage quality, it is crucial to harvest pearl millet at the peak nutrient stage typically before reaching 50% flowering, with a recommended dry matter content of 30–35% (Bogdan et al. 2019). The dry matter content can be assessed by forming a ball from chaffed fodder. If the hands do not moist, the fodder has the desired dry matter and is fit for silage-making.

The pearl millet silage has comparable potential to corn silage and has lower lignin, high crude protein and greater digestibility than sorghum despite consuming very less resources (Table 1) (Hassanat 2007). Dunavin (1970) conducted a study comparing pearl millet (Gahi 1) and sorghum-Sudangrass hybrids (Lindsey 77F and Sudax) on beef cattle. The results indicated higher live weight gain per hectare per day and increased carrying capacity for Gahi 1 compared to Lindsey 77F and Sudax. Additionally, Amer and Mustafa (2010) found that pearl millet silage had comparable potential to corn silage, exhibiting lower lignin, higher crude protein and greater digestibility than sorghum, making it an attractive option for forage and reported that complete replacement of corn silage with pearl millet silage had no detrimental effects on dairy cow feed intake or milk yield. However, regular millet relative to corn silage reduced milk yield, energy-connected milk, and solid corrected milk as reported by Brunette et al. (2014). Morales et al. (2011) investigated the productivity and nutritive value of pearl millet at different maturity stages for silage and hay conservation methods. The results indicated that the stage of maturity did not significantly affect silage quality, and regrowth was stronger when forage was cut at the booting stage. Hill et al. (1999) explored the potential of pearl millet silage for growing beef cattle and reported that wilting did not enhance fermentation compared to corn silage. However, the addition of silage inoculants and fermentable carbohydrate sources enhanced fermentation characteristics and increased dry matter content in later experiments. Despite these improvements, steer gains were still lower on millet silage diets than on corn silage diets, possibly due to the inherent difference in energy content.

In conclusion, pearl millet emerges as a promising forage crop, providing high-quality silage with favourable attributes for livestock nutrition. While it may not completely replace corn silage in all scenarios, its unique nutritional composition and adaptability make it a valuable addition to forage options, particularly in regions where temperate conditions prevail. Continued research and evaluation will contribute to refining the optimal utilization of pearl millet for silage production in diverse agricultural settings. (Pattanashetti et al. 2015).

Conclusion

Pearl millet is a warm-season climate change-ready crop that is widely cultivated in Africa and Asia. In addition to being a staple food crop, pearl millet is also a promising fodder crop that can provide high-quality forage for livestock. The millet forage has a high nutritional value, with higher crude protein and digestibility and a good balance of essential amino acids, making it a valuable protein source for livestock. Forage quality improvement relies heavily on the development of genetic and genomic resources in pearl millet for forage quality-related traits. With the availability of chromosome-level reference genome assemblies and other cutting-edge genetic and genomic resources, there is an enormous opportunity to deploy modern genomic tools in pearl millet improvement. The trait-based markers and candidate genes may help in breeding programmes for improving fodder and biomass-related traits by using different approaches like genomic selection and marker-assisted forward breeding and gene-editing.

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Conflict of interest The authors declare no conflict of interest.

Consent to participate Not applicable.

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