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ENHANCING FODDER COWPEA THROUGH BREEDING AND OMIC INNOVATIONS: A REVIEW

Mukund Kumar Thakur¹, Ezhilarasi Thailappan^{2*}, Pushpam Ramamoorthy², S. Kavitha³
and S.R. Shrirangasami²

¹Department of Genetics and Plant Breeding, Tamil Nadu Agricultural University, Coimbatore - 641 003 Tamilnadu, India.

²Department of Forage Crops, Centre for Plant Breeding and Genetics, T.N.A.U., Coimbatore - 641 003 Tamilnadu, India.

³Department of Seed Science & Technology, Tamil Nadu Agricultural University, Coimbatore - 641 003, Tamilnadu, India.

*Corresponding author E-mail : tezhilarasitnau@gmail.com

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ABSTRACT

This comprehensive review paper examines the advancements in breeding techniques and omic innovations for fodder cowpea [*Vigna unguiculata* L. (Walp)], a key crop in semi-arid regions for both human and animal nutrition. It highlights the effective combination of traditional breeding methods, which leverage natural genetic variation and controlled mating, with advanced omic technologies such as genomics, transcriptomics, proteomics and metabolomics. These approaches have facilitated the development of cowpea varieties with improved yields, early maturity and enhanced resistance to environmental stresses.

Key words : Cowpea, Fodder, Quality, Forage yield, Omic technologies.

Introduction

Cowpea [*Vigna unguiculata* (L.) Walp.; $2n = 2x = 22$] is an important crop in Africa, America and Asia. It is not only a food staple but also an important part of fodder systems because it grows quickly and is called the hungry-season crop because it can provide a reliable feed source during critical lean periods, which increases livestock productivity (Gómez, 2004). The crop's versatility is showcased through its multifaceted use-seeds, pods, leaves and haulms with the latter being particularly critical in Sub-Saharan Africa's fodder regime, emphasizing its indispensability in maintaining livestock sustenance during arid seasons (Oluokun, 2005; Savadogo *et al.*, 2000a). Globally, cowpea covered about 12 million hectares in 1996, with over 80% of its production situated in Africa, alongside significant outputs in Asia, Brazil and the United States, marking its utilization in various forms including seeds, pods, leaves and haulms, with the latter being especially crucial in Sub-Saharan Africa (Anele *et al.*, 2012; Oluokun, 2005; Quinn and Myers, 1999; Savadogo *et al.*, 2000b; Singh and Tarawali,

1997; Singh *et al.*, 2010). The adaptability of cowpeas to temperatures ranging from 25°C to 35°C and annual rainfall between 750 mm and 1100 mm showcases their resilience in well-drained soils and tolerance to shading and waterlogging, contributing to their widespread cultivation (FAO, 2015; Madamba *et al.*, 2006; Tarawali *et al.*, 2003). The dry matter (DM) forage yields of cowpea vary from 0.5 to over 4 t/ha on dry land, with the potential to reach up to 8 t/ha under irrigation. It is characterized by a high protein content in both grain (20–25% dry weight) and fodder (up to 18.6 g per 100 g of dry weight), making it a valuable feed (Mullen and Watson, 1999; Singh *et al.*, 2003). In pasture and cut-and-carry systems, particularly those developed in Asia and Australia, cowpea forage supports regrowth after grazing or cutting, facilitating sustainable fodder production. It's essential to manage grazing to minimize plant damage, employing sequential grazing by different livestock types to optimize fodder utilization (Oushy, 2012; Singh and Tarawali, 1997). The timing of cowpea harvest is critical and varies by region for hay production, with a general

emphasis on harvesting at optimal maturity stages to ensure quality preservation (Cameron, 2003a; Illo *et al.*, 2018). Cowpea haulms, a by-product of seed harvest are valued as hay, particularly in Africa, contributing to the availability of quality fodder (Cook *et al.*, 2005; Göhl, 1982; Hedayetullah and Zaman, 2022; FAO, 2015). Additionally, cowpea pairs well with cereals like maize for silage production, enhancing their utility in fodder systems (Cook *et al.*, 2005; Göhl, 1982; Hedayetullah and Zaman, 2022). As a nitrogen-fixing legume, cowpea improves soil fertility by adding 20 to 140 kg of residual nitrogen per hectare, making it a valuable green manure in crop rotations, particularly when added at the peak of flowering (Cameron, 2003b; Creamer, 1999; Mullen and Watson, 1999). Fodder cowpea production is facing significant challenges from global population growth, climate change, shrinking arable land and evolving pest and disease patterns (Guzzetti *et al.*, 2019; Melo *et al.*, 2022; Wamalwa *et al.*, 2016). In response, the evolution of breeding techniques and the advent of omic technologies, including genomics, transcriptomics, proteomics and metabolomics, offer promising avenues for enhancing cowpea varieties with improved yield, protein content and environmental stress resilience (Groen *et al.*, 2020; Li *et al.*, 2020). This review aims to explore the advancements in fodder cowpea improvement through conventional breeding and omic innovations, highlighting the latest developments, current challenges and future directions in cowpea breeding to enhance fodder production efficiency and quality.

Conventional breeding methods and their impact on Fodder cowpea improvement

Conventional breeding, a traditional method for developing new varieties without introducing new genes or foreign genes, involves using natural processes to transfer desirable traits from existing plants within the same species or closely related species (Jain and Kharkwal, 2012; Jakowitsch *et al.*, 1999). Conventional breeding of cowpeas was led by the International Institute of Tropical Agriculture (IITA). There were three main stages: (1) breeding plants based on natural genetic variation; (2) breeding plants with more genetic variation through controlled mating and (3) breeding plants with new genetic variation, such as through mutagenesis (Singh *et al.*, 2002). Important morphological traits, such as leaf shape and size, the number of primary branches per plant and the leaf-to-stem ratio, have been crucial in the selection of better fodder cowpea varieties (Wu *et al.*, 2022). These traits are vital as they directly influence the rate of photosynthesis in cowpeas, a key factor in biomass yield (Digrado *et al.*, 2022). Because of these studies,

many improved pure-line and hybrid fodder cowpea cultivars have been created. These are known for having high biomass yield, early maturity, higher nutrient content, and resistance to pests and diseases (Boukar *et al.*, 2019).

Breeding plants based on natural genetic variation

The first stage of conventional breeding relies on selecting naturally occurring variations within wild populations. Humans have been using this method for centuries to improve livestock and crops. As agriculture developed, this practice continued in fields where farmers would save seeds from the best plants each year to plant the next season. This allowed them to gradually select desirable traits, such as higher yields, disease resistance and better taste.

Domestication

The first step in the origin of cowpea crops was domestication, *i.e.*, bringing wild species under human management, which began before 2500 BC and spread by 400 BC across sub-Saharan Africa, the Mediterranean Basin, India and Southeast Asia (Herniter *et al.*, 2020). While a diverse array of *Vigna* species exist globally, only three have undergone domestication: *Vigna unguiculata*, *Vigna subterranea* and *Vigna vexillata* (Panzeri *et al.*, 2022). However, this process did not come without a cost. Domestication narrowed the genetic diversity of cultivated cowpea plants through the founder effect. This led to the unfortunate loss of numerous genes vital for pest resistance and nutritional quality, leaving them absent from the cultivated gene pool (Xiong *et al.*, 2016). Despite narrowing genetic diversity, the domestication of cowpeas led to increased yields and improved adaptability to specific environments. This paved the way for stage 1 of conventional breeding for fodder cowpea, where breeders utilized the remaining genetic variation to further develop the crop. However, while domestication offered benefits, it also reduced genetic diversity through the founder effect. Fortunately, valuable diversity was preserved in landraces.

Landraces: A Crucial Genetic Reservoir

As crucial reservoirs of genetic diversity, landraces are traditional cultivars developed by both natural selection and farmer practices. They are adapted to the local soil type, climatic conditions, and resistance to diseases and pests. Preserving these valuable genetic resources is important for future breeding programs because of the unintentional loss of landrace diversity caused by the widespread adoption of modern cowpea cultivars. Recent research highlights the significant gains achievable in fodder yield through the long-term direct selection of landraces under real field conditions (Omirou *et al.*, 2019).

Their study, focusing on a traditional cowpea landrace in Cyprus, demonstrated a substantial increase in biomass production, providing valuable insights into the potential of landraces for improving fodder quality and quantity. Additionally, Gulseven and Okcu (2023) conducted a study in Erzurum, Turkey, to look into the potential of five cowpea genotypes (four cultivars and one landrace) as feed crops at various sowing times. Interestingly, the red cowpea landrace exhibited particularly strong performance as a feed source, demonstrating comparable or even superior results to the tested cultivars. This finding underscores the potential of landraces to offer competitive yields and desirable traits for specific purposes, like fodder production.

Germplasm

Crop genetic resources, particularly cowpea germplasm, are invaluable for agrobiodiversity and sustainable agricultural advancements (Huynh *et al.*, 2013). Leading this effort, the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria, maintains the world's most extensive collection of cowpea germplasm, with over 17,000 accessions from 90 countries meticulously stored in its gene bank (Genebank Platform, 2020). In addition to IITA, the USDA-ARS in Griffin, Georgia, USA and the University of California, Riverside, also maintain significant collections, holding approximately 7,737 and 6,000 accessions, respectively (Fatokun *et al.*, 2018; Muñoz Amatriaín *et al.*, 2021). IITA has created a core collection of 2062 cultivated cowpea accessions using geographical, agronomic and botanical descriptors (Mahalakshmi *et al.*, 2007).

Progeny selection and Pure Line selection (The Origin of Cultivars)

Louis de Vilmorin proposed the idea of the progeny selection method in 1856 based on his research. Beetroot (*Beta vulgaris*) involves selecting superior individual plants (progeny) within a population based on desired traits, such as high yield, disease resistance and nutritional value. The underlying presumption is that the progeny of these selected plants will inherit the genes responsible for these desirable traits, leading to the evolution of improved fodder cultivars over time.

Fodder cowpea, a self-pollinating species, landraces serve as reservoirs of genetic diversity. These landraces can be thought of as mixtures of pure lines and individuals with heterozygous characteristics arising from occasional cross-pollination, chromosomal aberrations and spontaneous mutations. Pure line selection, introduced by Johannsen in 1903, involves selecting and harvesting individual plants from a landrace population. Each selected

plant is then self-pollinated, and its progeny are evaluated for desired traits. The best lines are then released as pure-line varieties. This method ensures genetic uniformity, which is advantageous for farmers and breeders.

Additive genetic variation is common in cowpeas, according to studies by Ezin *et al.* (2023) and Ayo-Vaughan *et al.* (2013). This means that these traits can be used in traditional breeding methods, such as pure line selection. This approach has proven successful in developing improved lines for various traits, including nodulation ability in pigeon peas (Saxena, 2008). While progeny selection and pure line selection have played significant roles in fodder cowpea improvement, it is important to recognize their limitations. Progeny selection is time-consuming and susceptible to biased selection. Pure lines may lack the adaptability and resilience needed to thrive in diverse environmental conditions.

Controlled mating in plant breeding

Due to selective breeding for specific traits, landrace populations and traditional crop varieties, which farmers have cultivated over many generations are at risk of rapidly narrowing their natural genetic diversity. To address this, breeders make different crosses using different pure lines to introduce new genetic diversity, an essential step for adaptation to environmental changes and emerging threats such as pests and diseases. However, evaluating a large number of plants resulting from these crosses can be both time-consuming and costly. In response, researchers are developing high-throughput methods for handling seeds, crossing, planting, evaluating and harvesting. Now, we will discuss the principal methods that have been developed for controlled mating in plant breeding, aimed at optimizing the available resource and ensuring the effective creation and evaluation of new genetic diversity in landrace and traditional pure line varieties.

Pedigree Breeding

Love introduced the pedigree breeding method in 1927 and it is important for creating cultivars of self-pollinated crops. This method carefully tracks individual plants selected from segregating generations (*e.g.*, F_2F_3 , etc.). Each selected plant is grown separately and a detailed record of all parent-offspring relationships is maintained. This process of individual plant selection continues for several generations until the progenies exhibit no further segregation for the desired traits. Typically, the selection of the best progeny depends on factors such as high yield, biomass production, protein and fiber content, digestibility, and disease resistance (Annicchiarico

et al., 2011). Pedigree breeding offers the advantage of allowing breeders to track desirable traits and develop pure breeding lines with specific characteristics. Metwally *et al.* (2021) and other studies have shown that pedigree selection can help improve fodder cowpea. Their research identified Line 6 was found to be the best genotype because it matures early (73.5–73.9 days), produces a large number of seeds (573–647 g/m²) and has a high crude protein content (22.7–24.3%). Furthermore, Fernandes Santos *et al.* (2012) observe that pedigree selection could enhance cowpea total protein, which is beneficial for self-pollinated crop species. Similarly, Ayo-Vaughan *et al.* (2013) used this method to study pod and seed traits, showcasing its versatility in breeding.

However, it is important to acknowledge the limitations of pedigree breeding. The key challenges include the delayed evaluation of yield and the necessity of maintaining detailed pedigree records. This means breeders can only accurately assess the yield potential of lines at the final stages of the process after the line has attained complete homozygosity. As noted by Sarutayophat *et al.* (2008), this can lead to inefficient use of resources, with time and effort potentially being invested in low-yielding lines that are ultimately discarded.

Bulk population breeding

Unlike pedigree breeding, the bulk population method utilizes natural selection by harvesting F₂ and subsequent generations in bulk to maintain initial genetic variability (Briggs *et al.*, 1968). This method offers greater chances of isolating transgressive segregants than pedigree breeding due to the large population sizes employed (Kuczyńska *et al.*, 2007). After several generations (F₆ or later), individual plants are then selected based on desired traits, such as high biomass yield, disease resistance, or specific physical characteristics (Bakhsh *et al.*, 2005). Horn *et al.* (2016) successfully implemented this method in their cowpea breeding program in Namibia by selecting mutant genotypes. One problem with this method is that it might cause less competitive agronomic traits to be lost through natural selection in the early generations (Acquaah, 2015). Additionally, undesirable dominant traits, if present, may persist in later generations by masking desirable recessive traits, potentially hindering breeding efforts.

Single-seed descent selection method

The single-seed descent (SSD) selection method aims to rapidly advance F₂ plant generations toward homozygosity while delaying selection (Allard, 1999). This repeated process involves collecting single seeds from each F₂ plant, bulking them to grow the F₃ generation,

and repeating the process until homozygosity has been attained, typically around F₅ or F₆ generations. Parmar *et al.* (2021), combining SSD with low-cost rapid generation advancement further improves this strategy. At the F₆ stage, individual plants from selected lines are grown separately to evaluate their performance and identify promising ones (Tigchelaar and Casali, 1976). Delaying selection until this stage allows for a more comprehensive assessment of a wider genetic pool. The best-performing lines from the F₇ and F₈ generations are then chosen for further testing.

Backcross breeding

Backcrossing is a technique used to transfer certain genes from a donor parent to a cultivar that has already been adopted. This increases homozygosity and the selection of desirable genotypes from homozygous or desirable genetic backgrounds (Acquaah, 2015). Schrauf *et al.* (2003) conducted backcrosses to transfer disease and pest-resistance genes and introduce genetic variability in crop plants. Another study by Hall (1990) used backcrosses to improve cowpea heat tolerance.

Heterosis in hybrid breeding

Heterosis, or hybrid vigor, is a fundamental concept in the breeding of cowpea, a crucial legume crop. Hybrid varieties exhibit superiority over their parent plants in terms of high biomass yield, grain yield, and other agronomic traits (Shull, 1948). Studies by Agble (1971), Bhaskaraiah, Shivashankar and Virupakshappa (1981), and Bhushana *et al.* (2000) have highlighted the significant benefits of heterosis in cowpea, such as increased seed size, higher grain yield, and improved pod characteristics. Additionally, Mak and Yap (1977) reported notable increases in protein content in Yardlong beans. Recent advancements in cowpea breeding have been notable, as demonstrated by Owusu *et al.* (2018), who identified superior cross combinations such as IT86D-610 × PADI-TUYA, SONGOTRA × PADI-TUYA, and IT86D-610 × SARC 57–2. These combinations exhibit high *per se* performance and significant positive specific combining ability effects, along with remarkable heterosis over the better parent, impacting traits like seed yield, number of branches, days to flowering and canopy width measurement, thus aligning with earlier findings by Dias *et al.* (2016), Ayo-Vaughan *et al.* (2013), Pandey and Singh (2010) and Patij and Navale (2006).

However, harnessing the full potential of heterosis in cowpea breeding is met with several challenges. One of the primary obstacles is cross-incompatibility, particularly with wild relatives outside the section *Catiang*, which complicates the introduction of desirable traits from these

varieties into cultivated cowpea. For compatible crossings, such as with *Vigna unguiculata* ssp. *pubescens*, advanced techniques like embryo rescue are often required to overcome fertility barriers, but these efforts generally result in only partially fertile F₁ hybrids (Fatokun and Singh, 1987). Even more challenging is the attempt to hybridize cowpea with *V. vexillata*, known for its pest-resistant genes. In these cases, issues like disrupted pollen tube growth in the stigmatic tissues lead to low fertilization rates (Barone and Ng, 1990; Fatokun, 2002), hindering the successful exploitation of heterosis.

The development of hybrid cowpea cultivars, therefore, is still limited by the crop's high self-pollination rate and the lack of cytoplasmic male sterility, which has been identified only genetically so far (Ladeinde *et al.*, 1980). Overcoming these limitations requires a focused approach in research to understand the genetic and physiological factors that affect hybrid breeding in cowpea. The introduction of cytoplasmic male sterility could be a significant breakthrough in cowpea hybrid breeding, leading to the creation of high biomass yield, nutritionally superior, and more pest-resistant varieties. This progress is crucial not only for enhancing the crop's agricultural performance but also for improving food security and sustainable agriculture in regions heavily reliant on cowpea.

Creating Novel Genetic variation

Mutation breeding has emerged as a significant approach for introducing new genetic variations in fodder cowpeas. Techniques like gamma irradiation, X-rays and chemical mutagenesis are employed to induce mutations in cowpea germplasm, leading to a broader genetic diversity. Supported by the International Atomic Energy Agency (IAEA) and the Food and Agriculture Organization (FAO), these methods have been instrumental in developing cowpea varieties better adapted to climate change with enhanced nutritional value and increased resistance to diseases and pests. The FAO/IAEA Mutant Varieties Database indicates that by the end of 2000, there were 2,252 officially released mutant varieties, nearly half of which were released in the preceding 15 years (Maluszynski, 2001). The Bhabha Atomic Research Centre in Trombay, from 1981 to 2007, successfully utilized mutation breeding to develop seven novel cowpea cultivars, each offering unique advantages (Punniyamoorthy *et al.*, 2007). Subsequent advancements in mutation breeding have improved various traits in cowpeas, such as plant height, maturity, resistance to seed shattering, disease resistance and the quality of oil and starch content (Goyal and Khan, 2010;

Singh *et al.*, 2013). This groundbreaking work has significantly contributed to enhancing fodder cowpea cultivation globally.

Ideotype breeding

In 1968, Donald introduced the ideotype approach as a method for crop improvement, focusing on selectively modifying specific plant traits to enhance overall performance, such as yield. He defined a crop ideotype as an ideal plant model possessing characteristics optimal for photosynthesis, growth, and high biomass production, informed by an understanding of plant physiology and morphology. This method has numerous benefits, including efficient gains, scientific value, and profound insights into plant growth and development processes. However, it faces challenges like negative trait correlations, limited germplasm availability and genetic incompatibility. To address these, techniques like backcrossing and pre-breeding are employed (Kumar *et al.*, 2003). Backcrossing allows for the gradual incorporation of desired genes into elite cultivars while maintaining their advantageous genetic background. Pre-breeding, on the other hand, involves developing vector lines with isolated desired traits for easy incorporation into high-quality germplasm. Despite these obstacles, ideotype breeding is a potent, strategic tool for crop improvement, capable of revealing and precisely manipulating plant genetics. Recent research in forage pea breeding, for instance, identified key traits for maximizing yield and nutritional value (Mihailoviæ and Mikiæ, 2014). Traits like optimal growth, moderate stem length to reduce leaf withering, and a leaf proportion above 50% of the aboveground biomass increase both forage quantity and quality. Early-maturing varieties improve flexibility in cropping systems. High forage dry matter content (over 25%) and crude protein levels (more than 2 tons per hectare) significantly boost yield and nutritional value. Lowering dietary fiber and lignin content improves digestibility in animals, enhancing their performance and feed efficiency. Moreover, innovative semi-leafless cultivars offer excellent forage quality, standability and increased seed production. By combining these traits, it's possible to develop cultivars surpassing 10 tons per hectare in dry matter and 2 tons per hectare in crude protein, contributing to sustainable livestock production and food security.

In Table 1, the details of varieties of fodder cowpea released in India through conventional breeding methods has been mentioned.

Role of Omic technologies in Cowpea enhancement

The rapid advancements in omic technologies bring

Table 1 : Details of fodder cowpea varieties released in India through conventional breeding.

Name of Cultivar	Method of Breeding/Selection	Potential Yield
1. Bundel Lobia-1	Single plant selection from indigenous material (IL-515)	GFY: 370.0 q/ha DMY: 65.0 q/ha
2. Bundel Lobia-2	Single plant selection from indigenous material (IL-978)	GFY:350.0q/ha DMY: 56.0 q/ha
3. Charodi	Pure line selection from the mixture of the old variety Charodi	GFY:328.0q/ha DMY: 57.0 q/ha
4. CL74	Pedigree (FAS 68 x Strain No. 102)	GFY:3000q/ha Seed yield: 13.5 q/ha
5. CL-367	Hybridization followed by bulking of the selected lines in F6 generation	GFY: 350.0 q/ha DMY: 57.0 q/ha Seed yield: 12.0 q/ha
6. CO (FC)-8	Pedigree method (Derivative of the cross CO-5 x N 331)	GFY (Irrigated): 215.0 q/ha GFY (Rainfed): 175.0 q/ha Seed Yield: 9.5 q/ha
7. CO-5	Selection irradiated mutant of variety CO-1 treated with Gamma rays (30 kR)	GFY: 445.0 q/ha DMY: 85.0 q/ha
8. Cowpea-88	Irradiation of F1 seeds followed by Pedigree method (Cowpea-74 x Strain No. H-2)	GFY: 315.0 q/ha DMY: 56.0 q/ha
9. EC-4216	Selection from exotic material	GFY: 300.0 q/ha DMY: 55.0 q/ha
10. Gujarat Forage Cowpea-1 (GFC-1)	Pure line selection	GFY: 310.0 q/ha, DMY: 48.0 q/ha
11. Gujarat Forage Cowpea-2 (GFC-2)	Pure line selection	GFY: 273.0 q/ha, DMY: 39.0 q/ha
12. Gujarat Forage Cowpea-3 (GFC-3)	Pure line selection	GFY: 276.0 q/ha, DMY: 51.0 q/ha, CPY: 5.7 q/ha
13. Gujarat Forage Cowpea-4 (GFC-4)	Pure line selection	GFY: 200 q/ha, DMY: 30-35 q/ha, CPY: 5 q/ha
14. Hara Lobia (HFC-42-1)	Pedigree method	GFY: 310.0 q/ha, DMY: 54.0 q/ha
15. Haryana Lobia-88 (HC-88)	Pedigree method	GFY: 345.0 q/ha, DMY: 62.0 q/ha, CPY: 9.5 q/ha, Seed yield: 7.5 q/ha
16. HCP-46	Selection	Grain Yield: 12.3 q/ha
17. IL 1177	Single plant selection	-
18. KBC-2	Mutant Breeding	GFY: 337.04 q/ha, DMY: 21.3 q/ha, Seed Yield: 5.0-5.5 q/ha
19. Kohinoor (S-450)	Single plant selection	GFY: 360.0 q/ha, DMY: 60.0 q/ha
20. Konka Fodder Cowpea-1 (DFC-1)	Single plan selection	GFY: 250 q/ha (<i>Kharif</i>), 220.0 q/ha (<i>Rabi</i>), DMY: 50.0 q/ha, Seed Yield: 7.5 q/ha

Table 1 continued...

Table 1 continued...

21. MFC-08-14	Pedigree	GFY: 350 q/ha
22. Konka Fodder Cowpea-1 (DFC-1)	Single plant selection	GFY: 250 q/ha (<i>Kharif</i>), 220.0 q/ha (<i>Rabi</i>)
23. MFC-08-14	Pedigree Breeding	350 q/ha
24. MFC-09-1	Pedigree Breeding	321.7 q/ha
25. Shweta (No. 988)	Selection from the germplasm	GFY: 318.0 q/ha
26. Type-2	Single plant selection from indigenous material	GFY: 330.0 q/ha
27. UPC-287	Pure line selection	GFY: 350.0 q/ha
28. UPC-4200	Single plant selection from germplasm line No.4200	GFY: 325.0 q/ha
29. UPC-5286	Single plant selection from the germplasm line No. 5286	GFY: 328.0 q/ha, DMY: 52.0 q/ha
30. UPC-5287	Single plant selection from the line CK 74-5287	GFY: 360.0 q/ha, DMY: 63.0 q/ha
31. UPC-607	Developed through hybridization followed by the Pedigree method of selection	GFY: 420.0 q/ha, DMY: 63.0 q/ha
32. UPC-618	Hybridization followed by Pedigree method	GFY: 390.0 q/ha, DMY: 65.0 q/ha
33. UPC 621	Pedigree Breeding	350 – 450 q/ha green fodder, 50 – 55 q/ha dry fodder in 85 – 90 days
34. UPC-622	Developed through hybridization followed by the Pedigree method	GFY: 396.0 q/ha, DMY: 64.0 q/ha, Seed yield: 11.5 q/ha
35. UPC-625	Developed through hybridization followed by the Pedigree method of selection	GFY: 420.0 q/ha, DMY: 63.0 q/ha
36. UPC 628	Pedigree Breeding	340-360 q/ha
37. UPC-8705	Hybridization followed by the Pedigree method of breeding	GFY: 385.0 q/ha (at 85 to 90 days), DMY: 60.5 q/ha CPY: 6.8 q/ha
38. UPC-9202	Hybridization followed by Pedigree method	GFY: 400.0 q/ha, DMY: 60.0 q/ha, Seed Yield: 11.0 q/ha
39. TNFC-0926	Pedigree method	GFY: 252.9 q/ha, DMY: 49.4 q/ha
40. CO9 (TNFC 0924)	Hybridization and selection	GFY: 228.2 q/ha
41. Aiswarya	Hybridisation and selection	27.10 t/ha
42. Vijaya	Mass selection	Mean GFY- 300 q/ha, Mean DFY -42 q/ha, Seed yield potential - 8.0 q/ha

GFY - Green Fodder Yield, DMY - Dry Matter Yield, CPY - Crude Protein Yield, and the yields are given as q/ha (quintals per hectare) or t/ha (tons per hectare). Source: All India Coordinated Research Project on Forage Crops & Utilization (Indian Council of Agricultural Research) ICAR-IGFRI, Jhansi <https://aicrponforagecrops.icar.gov.in/pdfs/Database-of-Forage-Crop-Varieties-2020.pdf>

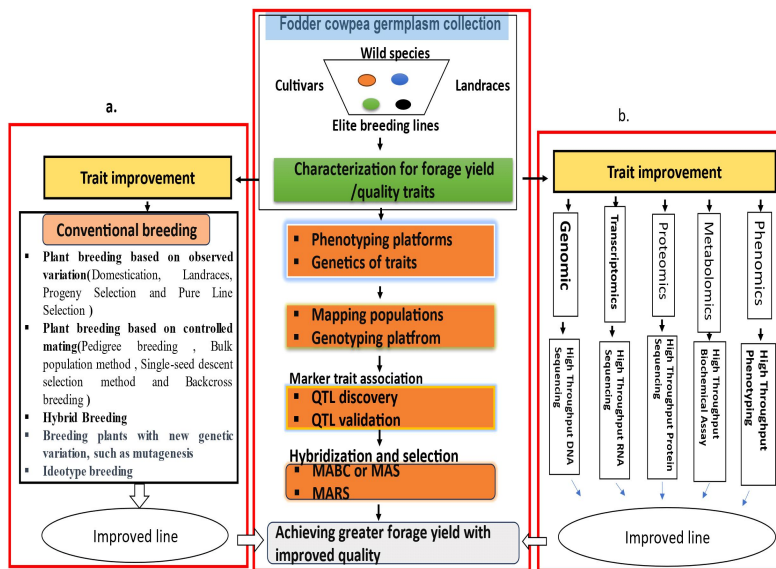


Fig. 1 : Schematic diagram showing improved fodder cowpea line through conventional breeding and omics innovation.

exciting new opportunities to agriculture, helping to address its many challenges (Chaudhary *et al.*, 2021). It is now possible to use genomics, transcriptomics, proteomics, metabolomics and phenomics together to find important genes, physiological processes, and pathways of key metabolites that improve important morphological traits (Groen *et al.*, 2020; H. Li *et al.*, 2020). Comparative omic analysis across different environmental conditions aids in identifying genes essential for adaptation (Li *et al.*, 2020). These identified genes can be manipulated or transferred to develop new hybrids or varieties with desirable characteristics (Razzaq *et al.*, 2019; Somegowda *et al.*, 2021). Furthermore, the integration of multi-omics has been successfully implemented for yield increment and developing tolerance and resistance to biotic and abiotic stresses in crops. In the context of cowpeas, a comprehensive approach that includes both conventional and omic technologies is vital (*e.g.*, as shown in Fig. 1). Genomics, transcriptomics, proteomics and metabolomics all help us to understand how plants respond to different stresses by showing us how their many complex interactions and control pathways work. This gives us a deeper understanding of the need to improve crop yield and quality.

This figure illustrates the process of trait improvement in fodder cowpea, depicting two primary pathways. The highlights (a) Conventional Breeding which includes methods such as plant breeding based on observed variation, controlled mating, backcross breeding, hybrid breeding and idiotypic breeding, leading to improved lines. The (b) emphasizes modern Trait Improvement strategies integrating Omics technologies, such as genomics,

transcriptomics, proteomics, metabolomics and phenomics, to advance breeding programs further. Both sections converge on the goal of achieving greater forage yield with improved quality, showcasing the blend of traditional and contemporary techniques in crop improvement programs.

Molecular breeding

Conventional breeding methods, characterized by multi-generational selection and laborious trials with limited insight into trait inheritance, often prove slow and inefficient (Beaver and Osorno, 2009). In contrast, molecular marker-assisted selection (MAS) offers a more targeted and rapid alternative, linking DNA markers to desired traits. MAS facilitates the early selection of plants, streamlining the breeding process by eliminating unnecessary trials and focusing on key genes controlling essential traits. This approach accelerates breeding cycles, reduces the need for extensive generations of selection, and enhances genetic gain rates in plant breeding programs (Ehlers *et al.*, 2012). MAS is particularly useful in resistance gene pyramiding against diseases caused by diverse pathogens. It addresses complex gene interactions, known as epistatic effects, which significantly impact trait expression. Unlike traditional breeding, MAS simplifies the combination of marker-tagged resistance genes without extensive phenotypic screening. This proves beneficial in preventive breeding for resistance to pathogens not yet present in a region where phenotypic screening is impractical. Optimized sets of molecular markers in MAS, often combined for high-throughput genotyping, improve breeding programs. Key steps in MAS include high-throughput genotyping, high-density genetic maps, phenotyping, marker-trait associations, and molecular breeding deployment (Boukar *et al.*, 2019). This integrated approach not only overcomes the limitations of traditional breeding methods but also establishes a more efficient paradigm in plant breeding.

Molecular markers, such as SSRs and SNPs, play a pivotal role in molecular breeding. Due to their abundance and compatibility with high-throughput genotyping techniques, SNPs have surpassed SSRs in popularity. The introduction of the 1536 Illumina Golden Gate SNP genotyping platform in 2009 revolutionized cowpea breeding by providing unprecedented capabilities for genetic variation analysis (Muchero, Diop *et al.*, 2009). To enhance access, K Biosciences adapted approximately

Table 2 : Mapping of some cowpea traits.

Trait	Population	Type	No. of Markers/QTLs	Locations	PV %	References
Cowpea golden mosaic virus	IT97 K-499-35 × Canapu T16	F2	3(AFLP)	Same linkage group	-	Rodrigues <i>et al.</i> (2012)
Striga resistance	TVx3236 × IT82D-849	F2	3(AFLP)	LG1	-	Ouédraogo <i>et al.</i> (2001)
Drought-induced senescence	IT93K503-1×CB46	RIL	10(AFLP)	LG1, LG2, LG3, LG5, LG6, LG7, LG9, LG10	5-24	Muchero <i>et al.</i> (2010)
Foliar thrips	CB46×IT93 K-503-1 and CB27 × IT82E-18	RILs	3(AFLP)	LG5 and 7	9-32	Muchero <i>et al.</i> (2010)
Charcoal rot resistance	IT93 K-503-1 × CB46	RIL	9(AFLP)	LG2, LG3, LG5, LG6, LG11	8-40	Muchero <i>et al.</i> (2011)
Seed size	524B × 219-01	RIL	6(SSR)	LG1, LG10	9-19	Andargie <i>et al.</i> (2011)
Pod fiber layer thickness	524B × 219-01	RIL	4(SSR)	LG1, LG10	6-17	Andargie <i>et al.</i> (2011)
Pod length	(JP81610 × TVu457) × JP81610	BC1F1	9(SSR) LG4, LG5, LG7, LG8, LG9, LG11	LG1, LG2, LG3,	31	Kongjaimun <i>et al.</i> (2012a)
Seed weight	524B × 219-01	RIL	6(SSR)	LG1, LG2, LG3, LG10	8-19	Andargie <i>et al.</i> (2011)
Time of flower opening	524 B × 219-01	RIL	5(SSR)	LG1	9-30	Andargie <i>et al.</i> (2013)
Days to flower	524 B × 219-01	RIL	3(SSR)	LG1	6-19	Andargie <i>et al.</i> (2013)
Pod number per plant	ZN016 × ZJ282	RIL	3(SSR)	LG3, LG2, LG4	11-20	Xu <i>et al.</i> (2013)
Leaf senescence	ZN016 × ZJ282	RIL	2(SSR)	LG11, LG3, LG7	11-29	Xu <i>et al.</i> (2013)
Floral scent compounds	524 B × 219-01	RIL	63(SSR)	LG1, LG2, LG4	60	Andargie <i>et al.</i> (2014)
Pod tenderness	(JP81610 × JP89083) × JP81610	BC1F1	3(SSR)	LG 7, LG8, LG11	6-50	Kongjaimun <i>et al.</i> (2013)
Cowpea bacterial blight resistance	Danilla × TW7778	RIL	3(SSR)	LG3, LG5, LG9	10-22	Agbicodo <i>et al.</i> (2010)
Hastate leaf shape	Sanzi × Vita 7	RIL	1(SSR)	LG 15	74.7	Pottorff <i>et al.</i> (2012a)
Foliar thrips resistance	CB46 × 1793 K-503-1 and CB27 × IT82E-18	RILs	3(SNP)	LG2, LG4 and LG10	9-32	Lucas <i>et al.</i> (2012)
Flower and seed coat color	ZN016 × Zhijang 28-2	RIL	1 each (SNP)	LG8	-	Xu <i>et al.</i> (2011)
Days to first flowering	ZN016 × ZJ282	RIL	3(SNP)	LG11, LG10, LG3	10-32	Xu <i>et al.</i> , 2013
Nodies to first flower	ZN016 × ZJ282	RIL	4(SNP)	LG11, LG4, LG2, LG6	11-22	Xu <i>et al.</i> (2013)

Table 2 continued...

Table 2 continued...

Leaf senescence	ZN016×ZJ282	RIL	2(SNP)	LG11, LG3, LG7	11-29	Xu <i>et al.</i> (2013)
Heat tolerance	CB27×IT82E-18	RIL	5(SNP)	LG2, LG7, LG8, LG10, LG3	12-18	Lucas <i>et al.</i> (2013)
Seed size	Eight different populations	RIL	10(SNP)	LG5, LG7, LG2, LG6, LG8, LG10	47	Lucas <i>et al.</i> (2013b)
Fusarium wilt resistance (Fot race 3)	CB27×24-1258-1	RIL	1(SNP)	LG6	28	Pottorff <i>et al.</i> (2012b)
Fusarium wilt resistance (Fot race 4)	IT93K-603-1×CB46, CB27×24-1258-1, CB27×IT82E-18	RIL	1(SNP)	LG8, LG9, LG3	19-47, 32-40, 18-27	Pottorff <i>et al.</i> (2014)

PV% represents ranges of phenotypic variation of the given QTLs. Adapted and updated from Abhishek *et al.* (2014).

Source : Boukar *et al.* (2016)

1,000 mapped SNPs from the Illumina platform onto their KASP marker system, making advanced genetic analysis accessible globally (Muchero, Diop, *et al.*, 2009). The Illumina Cowpea iSelect Consortium Array, a genotyping assay for 51,128 SNPs derived from an IITA-developed line (IT97K-499-35) and 36 different accessions, represents a significant advancement, expanding tools available for cowpea breeders and offering enhanced resolution for mapping and selection (Muñoz Amatriaín *et al.*, 2017).

Genetic linkage maps play a pivotal role in understanding the complex genetic makeup of plants' quantitative traits. For cowpeas, creating these maps has involved a variety of mapping populations and molecular markers (Boukar *et al.*, 2019). Fatokun *et al.* (1993) initiated this endeavor with 58 F₂ plants from a cross between two cowpea varieties, resulting in a map featuring 89 loci across 10 linkage groups covering 680 cM. Building upon this, Menéndez, Hall and Gepts (1997) developed another linkage map using 94 F₈ RILs from a different cowpea cross, which contained 181 loci spanning 972 cM. Ouédraogo *et al.* (2002) expanded this map further by adding 242 AFLP markers, thereby extending it to 2670 cM across 11 linkage groups. Ewa, Hodeba and George (2000) contributed a third map of 80 loci over 669.8 cM. Muchero, Ehlers *et al.* (2009) then introduced an Illumina GoldenGate Assay and an SNP consensus map with 928 SNP markers across 11 linkage groups covering 680 cM. He improved this consensus genetic map even more by genotyping more populations. They found 856 bins with 37,372 SNP loci, which led to a higher average density of 1 bin per 0.26 cm (Xu *et al.*, 2017).

The use of Genomic Tools in Breeding Programs

Phenotyping and marker-trait association play critical

roles in transforming cowpea breeding programs. Modern strategies heavily rely on high-throughput phenotyping platforms for rapid and accurate data collection regarding growth, yield and stress resistance. Precise phenotypic and genotypic data are essential, necessitating refined screening protocols for both biotic and abiotic stresses. Tools like the Breeding Management System (BMS) and electronic field books on handheld devices (Boukar *et al.*, 2019) have streamlined data capture and can reduce errors (<https://integratedbreeding.net/>). Additionally, barcoding technology enhances data accuracy, facilitating integration with advanced molecular marker technologies. Analyzing this combined data enables breeders to identify markers linked to target traits, thus directing breeding efforts towards desirable characteristics such as disease resistance or high yield. This data-driven approach significantly accelerates the development of improved cowpea varieties.

A recent review by Boukar *et al.* (2016) offers a comprehensive analysis of the relationships between genetic markers and traits in cowpea, with a focus on stress tolerance and agronomic characteristics. Utilizing Amplified Fragment Length Polymorphism (AFLP), Simple Sequence Repeat (SSR), Restriction Fragment Length Polymorphism (RFLP) and Single Nucleotide Polymorphism (SNP) markers, the research identifies quantitative trait loci (QTLs) essential for resistance to various stresses and diseases affecting fodder cowpea. Significant advancements are evident in the identification of QTLs influencing critical traits such as maturity (Muchero, Ehlers *et al.*, 2009; Muchero *et al.*, 2011), flowering time Andargie *et al.* (2013) and pod-length variation (Lo *et al.*, 2018), which are vital for the yield and quality of fodder cowpeas. The development and application of SNP-based linkage maps in trait mapping

have been particularly effective in uncovering QTLs associated with drought tolerance and other key traits crucial for fodder cowpea cultivation. This analytical approach is key in pinpointing genomic regions affecting forage quality and yield in cowpeas. As sequencing becomes more affordable and genotyping methods advance, there is an expectation of a rise in linkage analysis and association mapping. These studies are crucial for understanding the genetic traits of fodder cowpeas, leading to the development of resilient, high-yield cultivars suited to various climates.

Molecular Breeding deployment

In molecular breeding deployment, diverse global projects illustrate the effectiveness of these techniques in cowpea. The Tropical Legumes I project, for instance, has implemented strategies like marker-assisted backcrossing (MABC) at the International Institute of Tropical Agriculture (IITA) in Nigeria and other institutions across Africa, focusing on traits such as Striga resistance, drought tolerance, and nematode resistance. Marker-assisted selection (MAS) has also been utilized for developing new lines by combining favorable traits, as seen in the works of ISRA and INERA. Further, marker-assisted recurrent selection (MARS) has been applied to enhance grain yield, using elite-by-elite crosses guided by selection indices based on grain yield and associated QTLs. More research, like that by Batierno *et al.* (2016) which used MABC to create drought-tolerant varieties, broadens the use of molecular breeding in cowpea. Collectively, these efforts showcase a comprehensive approach to cowpea breeding, leveraging molecular tools for trait introgression, cultivar development and addressing various agricultural challenges.

Transcriptomics

Transcriptomics, the study of the complete set of RNA transcripts produced by the genome of an organism under specific conditions has become increasingly crucial in understanding cellular processes, identifying new genes, and deciphering gene functions (Guo *et al.*, 2021; Lowe *et al.*, 2017). Despite its importance, cowpea transcriptomics has been underutilized for fodder purposes. Recent studies have explored cowpea growth, development, and stress-related genes, with a particular focus on understanding how transcriptomics influences seed and pod development (Yao *et al.*, 2016). Chen *et al.* (2017) used Illumina paired-end sequencing to look into cowpea transcriptomics. They got 54 million cDNA sequence reads and found 47,899 unigenes. Notably, 75.8% of these unigenes showed similarity to known proteins. The study also discovered 5560 potential genic

molecular markers (SSRs), with 54 polymorphic markers validated. These findings contribute to understanding agronomic traits and facilitate genetic studies and breeding in cowpeas and related *Vigna* species. In the study of Ferreira-Neto *et al.* (2021) delved into cowpea kinases (VuPKs) using transcriptomic data. This detailed analysis provided new insights into genomic features, evolutionary processes, and expression changes in response to stress. The study found out more about the structure of 1,293 VuPKs, where they are found in the genome, and how they stay the same across *Viridiplantae* species. Additionally, it was found that some VuPK families were turned on more when different stresses happened, providing useful information for future research on how cowpea kinases evolved and what their molecular functions are. In a subsequent study, MacWilliams *et al.* (2023) infested with aphids two cowpea lines and examined their transcriptomes to identify susceptibility and resistance genes. Key changes induced by aphids in cowpea development and signaling were instrumental in determining plant susceptibility. Genes associated with aphid resistance were identified enabling differentiation between susceptible and resistant cowpea lines. The global remodeling of the cowpea aphid transcriptome was found to be influenced by feeding duration and host-plant resistance.

Metabolomics

Metabolomics serves as a precise scientific tool for the comprehensive analysis of intricate cellular metabolites, offering detailed insights into cell functionality (Wishart, 2019). Its primary objective is to identify and quantify small molecules, such as sugars, amino acids, organic acids, lipids, and secondary metabolites, essential for crucial aspects of plant life, including growth, development, organismal interactions, and responses to the environment (Razzaq *et al.*, 2019; Sousa Silva *et al.*, 2023). In plant metabolomics, high-throughput analysis is a fast way to separate, describe and measure different mixtures of metabolites in plant extracts. Quantitative analysis commonly involves nuclear magnetic resonance (NMR) and mass spectrometry (MS), with Fourier transform infrared spectroscopy (FTIR) gaining popularity due to technological advancements (Jockoviæ *et al.*, 2021). Using metabolomics data to help us understand basic plant traits and the role of genes in metabolic pathways has been very helpful. It has helped us figure out how complicated metabolic networks are.

Metabolomics plays a vital role in understanding the physiological reactions of cowpeas to stress and in enhancing crop development. Goufo *et al.* (2017)

examined the osmotic adjustment and protective mechanisms in cowpea plants under drought conditions. The study found that during drought conditions, roots showed a higher distribution of amino acids, sugars and proanthocyanidins, suggesting their crucial involvement in both growth and the initial perception of stress. This is important because some metabolites, like proline, galactinol and a form of quercetin, responded more strongly to drought, showing that they were using a smart way to adapt. This inquiry shows potential for advancements in strategies to improve crops and enhance food security. Fühns *et al.* (2009) investigated the effects of manganese toxicity in cowpea and suggested that silicon could potentially mitigate these effects. The study focused on how apoplastic peroxidases and phenols affect NADH peroxidase activity and how they play a part in manganese toxicity. Moreover, the research revealed notable changes in photosynthesis, primary carbohydrate, and nitrogen metabolism, specifically in cultivars that are sensitive to manganese. Gomes *et al.* (2020) conducted a parallel study where they used a comprehensive approach, combining physiological and biochemical analyses, to investigate how cowpea plants respond to drought. We were able to tell the difference between cowpea genotypes based on how well they could handle drought by looking at leaf gas exchanges, chlorophyll fluorescence, photoprotective pigments, RuBisCO activity and primary metabolite profiling. The A116 genotype exhibited the highest level of drought tolerance and a significant number of responsive metabolites, indicating their potential use as indicators of drought tolerance. Yeo *et al.* (2018) conducted a specific study to examine the metabolic alterations in *Vigna unguiculata* sprouts when exposed to various light-emitting diodes (LEDs). The research employed various analytical methods to identify and measure hydrophilic compounds, phenylpropanoids, and carotenoids. The findings indicated that blue LED light had the greatest impact on elevating the levels of total carotenoids and phenylpropanoids in *V. unguiculata* sprouts. This provided researchers with crucial insights to enhance the manufacturing of these chemicals in agricultural environments. Ramalingam *et al.* (2015) provided a comprehensive analysis emphasizing the importance of proteomics and metabolomics in enhancing legume development. The review stressed how important it is to understand how molecules react to different stressors and how transcriptomics, proteomics and metabolomics can be used together to figure out complicated pathways in legumes. The use of this comprehensive approach is considered crucial for precise biomarker discovery in intelligent breeding initiatives for

leguminous plants. The objective is to collaboratively investigate these regions in order to cultivate fodder cowpea varieties that are resistant to stress, have higher yields, and can adapt to a wider range of conditions. This will ultimately help improve food security and promote sustainable agriculture.

Dual-purpose cowpea

Recent studies have underscored the effectiveness of cowpea (*Vigna unguiculata*) as a dual-purpose crop, where breeding efforts have successfully increased both grain and fodder yields without compromising either (Kamara *et al.*, 2018; Okike *et al.*, 2002). Despite the development of several dual-purpose lines through a collaborative program between IITA and ILRI since the 1980s, farmers often show a preference for multiple cowpea varieties, indicating that dual-purpose varieties may not entirely fulfill all farmer needs (Okike *et al.*, 2002; Tarawali *et al.*, 2003). The integration of molecular markers in breeding has accelerated the selection of varieties with favorable traits, and tools like Near-Infrared Reflectance Spectroscopy (NIRS) have facilitated rapid, cost-effective assessment of forage nutritional quality (Blümmel *et al.*, 2007; Melchinger *et al.*, 1986). A study evaluating 157 genetically diverse cowpea accessions in Minjibir, Kano, Nigeria, revealed a positive correlation between seed and fodder yield, suggesting that selecting for forage yield does not negatively impact grain yield (Kumar *et al.*, 2003; Okike *et al.*, 2002). This research also indicated a wide range in haulm nitrogen content and metabolizable energy and found correlations between fodder yield and days to pod maturity, which is crucial for drought avoidance (Singh *et al.*, 2003). Furthermore, analysis based on growth habits from the IITA gene bank database showed that dual-purpose varieties need not be limited to semi-prostrate or prostrate types. This gene bank reference collection offers significant variation within cowpea germplasm, providing a rich resource for advancing the development of dual-purpose varieties and enhancing marker-assisted selection for traits pertinent to both food and feed uses.

Conclusion

Cowpea is a key crop in Africa, America and Asia, known for its crucial role during the hungry season due to its early harvest and use as both food and livestock fodder. Flourishing in tropical, semi-arid regions and adaptable to poor soils, cowpea is significant for its various forms—seeds, pods, leaves and haulms—particularly in Sub-Saharan Africa. Its large genome indicates genetic complexity, and as a nitrogen-fixing legume, it enhances soil fertility, making it beneficial for crop rotations. The

International Institute of Tropical Agriculture in Nigeria conserves the world's largest cowpea germplasm collection, which is crucial for agricultural diversity and advancements. Breeding efforts focus on enhancing biomass yield, protein content and resistance to pests and diseases using methods ranging from conventional breeding, like natural variation selection and controlled mating, to molecular techniques such as marker-assisted selection. Omic technologies, including genomics, transcriptomics and metabolomics, have furthered these efforts by providing deeper molecular insights and aiding in the development of resilient varieties for improved crop yield and quality. Overall, the comprehensive approach to cowpea breeding, combining traditional and modern methods, is essential for meeting global food and fodder demands, promoting sustainable agriculture and enhancing food security.

Future perspectives

Cowpea (*Vigna unguiculata*) cultivation is set for significant advancements, focusing on integrating genome editing techniques like CRISPR/Cas9 for precise trait improvements, developing climate-resilient varieties to withstand environmental stresses and enhancing pest management strategies. Nutritional quality and forage efficiency will remain a priority, with efforts to increase biomass and improve digestibility. Conservation of a diverse genetic pool will be crucial, alongside involving farmers in the breeding process to ensure the development of locally adapted varieties. The integration of technologies such as Near-Infrared Reflectance Spectroscopy (NIRS) and remote sensing will streamline breeding and cultivation, while global collaboration in research and germplasm exchange will play a key role in addressing the challenges of food security and sustainable agriculture in semi-arid regions.

Author contributions

E.T. and M.K.T., Conceptualization, M.K.T., contributed to writing and original draft preparation and E.T., P.R., K.S. and S.R., edited the manuscript and contributed to supervision and project administration.

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Conflict of interest

The study holds no conflict of interest.

Ethics approval

As it is review-based data, no ethical community is involved.

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