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REVIEW PAPER

Genetic and genomic resources for accelerating marker-assisted ideotype breeding in pigeonpea (*Cajanus cajan* L. Millsp.)

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Abstract

Pigeonpea (*Cajanus cajan* L. Millsp.) is a grain legume crop that is crucial for food and nutrition security in the subtropical regions of Asia and Africa. However, its production is constrained by undesirable varietal features and susceptibility to biotic and abiotic stresses. There is an urgent need to develop pigeonpea varieties with ideotype combining traits needed by the stakeholders. Landraces and wild relatives of pigeonpea are rich source of genes for genetic advance towards the desired ideotype. Pigeonpea genome and extensive transcriptome data required for gene discovery are available. Simple sequence repeat and single nucleotide polymorphism marker assays have been designed and used in mapping of genes and quantitative trait loci for key traits, but these need to be validated and utilized in breeding. Pigeonpea genetically modified for pod borer resistance is awaiting regulatory approval, and the power of genome editing is poised to be harnessed. Marker-assisted selection is still not a practical reality in pigeonpea, but mapping studies position the crop for future breakthroughs. Marker-assisted selection is expected to play a greater role in accelerating pigeonpea ideotype breeding. This review provides a comprehensive account of stakeholder preferences of varietal traits and genetic and genomic resources to help devise molecular breeding strategies for pigeonpea.

Keywords: Genes and quantitative trait loci, genomic resources, germplasm, ideotype breeding, marker-assisted selection, pigeonpea.

Abbreviations: AFLP, amplified fragment length polymorphism; CMS, cytoplasmic male sterility; CWR, crop wild relative; DArT, diversity arrays technology DEG, differentially expressed gene; EST, expressed sequence tag; FW, Fusarium wilt; GBS, genotyping by sequencing; GEd, genome editing; HI, harvest index; MAS, marker-assisted selection; PSB, Phytophthora stem blight; RAPD, random amplified polymorphic DNA; RFLP, restriction fragment length polymorphism; SMD, sterility mosaic disease; SSR, simple sequence repeat; T2T, telomere-to-telomere; TSA, transcriptome shotgun assembly.

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Introduction

Pigeonpea (*Cajanus cajan* L. Millsp.) is the sixth most important grain legume crop of the world. It serves as an important source of dietary protein and is a rich source of carbohydrates, crude fibre, micronutrients, and water-soluble vitamins such as thiamine, riboflavin, and niacin (K. B. Saxena *et al.*, 2010; Susmitha *et al.*, 2022). Leaves, seed husk and pod peel of pigeonpea are nutritious cattle feed, and its root and fallen leaves add vital organic matter and other essential nutrients to the soil, which is enriched further by symbiotic nitrogen fixation of up to 235 kg N ha^{-1} (Odeny, 2007; Orwa *et al.*, 2009). Pigeonpea is cultivated in many parts of Asia, sub-Saharan Africa and Central America, but is an underutilized crop despite its high nutritional and medicinal properties (Gargi *et al.*, 2022; Henderson, 2023). It is a potential crop for enhanced adoption in Africa because of its drought tolerance, climate resilience, and high nutritive value for human and livestock (Odeny, 2007; Abebe, 2022). It is consumed on a daily basis as *dal* and *sambhar* (stews made of de-husked split dried seeds) in India, which is by far the largest consumer and producer of pigeonpea and where productivity has remained low and static over the last six decades despite steady rise in production due to area expansion (Fig. 1A, B). There is a significant gap between demand and supply of pigeonpea in India leading to regular imports and price rises (V. Jadhav *et al.*, 2018). Pigeonpea has ample variation for traits such as number of seeds per pod, seed size, seed coat colour, plant height, and crop duration (Fig. 1C–G). However, most of the cultivars belong to medium (160–180 d) or long (>200 d) duration groups, and only a low proportion belong to the desired short duration (130–145 d) group. The undesired features of pigeonpea varieties include long duration and tall bushy plant type with low harvest index (HI) (K. B. Saxena, 2008; R. K. Srivastava and Saxena, 2019). Major biotic stresses limiting pigeonpea productivity are insect pests such as gram pod borer (*Helicoverpa armigera*), pod fly (*Melanagromyza obtusa*), Maruca pod borer (*Maruca vitrata*), and the diseases like Fusarium wilt (FW), Phytophthora stem blight (PSB), and sterility mosaic disease (SMD) (Jones *et al.*, 2004). The abiotic stresses affecting pigeonpea yield include waterlogging at seedling or early growth stage and flower drop due to cold at reproductive stage. Although the closed flower favors self-pollination, it is often cross-pollinated by insects, in the range of 25–30%, resulting in contamination of pure line varieties (K. B. Saxena *et al.*, 1992b, 2021a). Landraces and traditional varieties of pigeonpea with useful traits have been identified, and its wild relatives are rich source of genes for stress tolerance. However, these have not been utilized adequately in varietal improvement. Advances in genomics have enhanced our understanding of the molecular basis of agronomic traits, which may be utilized in pigeonpea breeding. Here we present a comprehensive review of the varietal trait preferences among the stakeholders, desired plant ideotype, available germplasm resources, genomic insights, marker development, and how these could be utilized for accelerating ideotype breeding in pigeonpea.

Stakeholder preferences of pigeonpea varietal traits

Understanding the varietal trait preferences of stakeholders in the entire value chain from production to consumption is crucial for pigeonpea breeders to effectively address their specific needs. India is the largest producer and consumer of pigeonpea with average annual production of 4 138 038 tons (FAOSTAT, 2023), and a survey was carried out in the pigeonpea-growing states of Maharashtra and Telangana to understand the varietal trait preferences of the stakeholders under the Indo-Swiss Collaboration in Biotechnology (ISCB) pigeonpea project (A. Singh *et al.*, 2020, Preprint). Farmers prioritized earliness, pod borer resistance, drought tolerance, and yield stability as the key traits, with plant height being the least important, perhaps due to lack of choice for dwarf varieties. They preferred short-duration varieties because these avoid losses due to flower drops during cold winter and fetch higher prices due to early arrival in the market. The millers prefer uniform grain size, light red seeds, and easy seed coat removal. The seed coat trait is crucial because it significantly affects the processing time and cost. A moderately soft and thin seed coat facilitates easy splitting during milling, resulting in dal with sharp edges that fetches a premium price. Medium-sized grains (12–14 g per 100 seeds) are preferred over very large or small grains by the millers, while dal consumers like clean uniform dal grains with a short cooking time of 5–7 min (Table 1).

Malawi is the second largest producer of pigeonpea with average annual production of 436 703 tons. Here a survey of farmers and focused group discussion with individual farmers revealed susceptibility to diseases and insect pests and long crop duration as the biggest constraints (Yohane *et al.*, 2021). The trait preferences in Malawi are early maturity, high yield, long shelf-life, disease and pest resistance, cream seed coat colour, large seed size, short cooking time and palatability. There are no structured studies on pigeonpea stakeholder preferences in Myanmar, but plant breeders have identified the need for developing short duration high-yielding varieties with adaptability to drought (Kyu *et al.*, 2016). Myanmar exports 80–90% of its pigeonpea to India, and therefore the millers and consumers preferences of India are also applicable there (Thu *et al.*, 2022). In Tanzania, a structured survey and focused group discussion showed maize–pigeonpea intercropping to be the most preferred production system (Kimaro *et al.*, 2017). The major issues for the farmers are susceptibility to diseases and insects, drought sensitivity, long crop duration, and limited access to seeds of improved cultivars (Majili *et al.*, 2020). Kenya is the fifth largest producer of pigeonpea. Here it is grown in the dryland regions for domestic consumption. The preferred varietal traits are light seed coat colour, high yield, short to medium duration, drought tolerance,

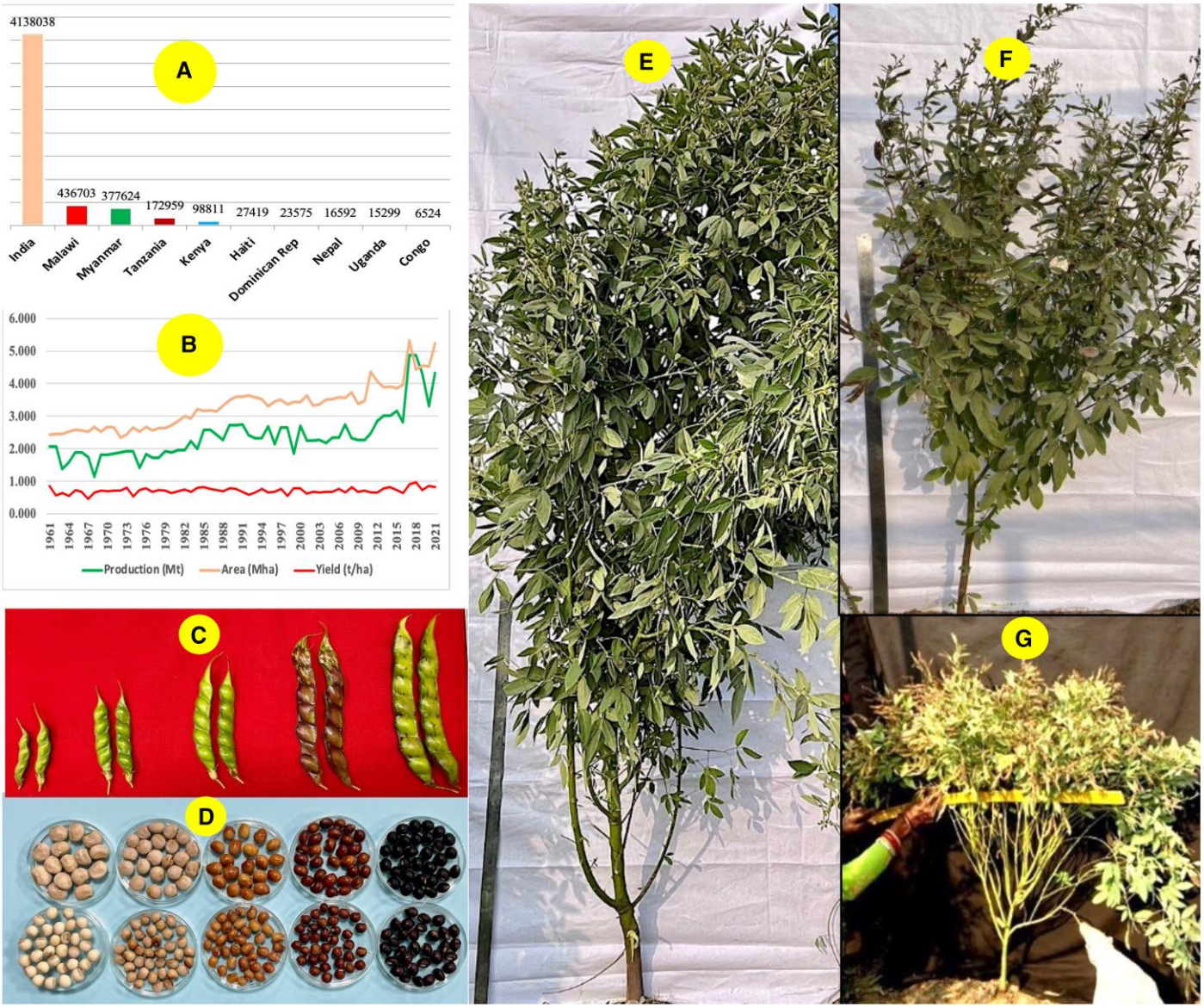

Fig. 1. Pigeonpea production statistics (FAO database 2021) and trait variability in cultivars. (A) Global share of top 10 producers in metric tons based on 5 year average of 2017–2021. (B) Area, production and productivity trends in India during 1961–2021. (C) Variation in number of seeds per pod: three seeded (MC99), four seeded (M50), five seeded (MC 89), six seeded (UP74), seven seeded (ICPL85063). (D) Variation in seed type. Upper panel (large-seeded): white (ICP13633), cream (ICP13884), light red (ICP11833), red (ICP14638), black (ICPL11811). Lower panel (small-seeded): white (ICP7507), cream (ICP1071), light red (ICP5142), red (ICP8266), black (ICP7223). (E) Long duration indeterminate bushy tall (Pusa Arhar 24-1, height 260 cm). (F) Short duration indeterminate semi-dwarf (Pusa 2018-2, height 160 cm). (G) Short duration determinate dwarf (Pusa Dwarf/HDM04-1 line, height 95 cm).

resistance to FW, leaf spot, pod borer and pod fly, palatability, and short cooking time (Oteino *et al.*, 2011). Earliness, high yield potential and greater number of large green seeds are preferred for vegetable purpose (Ojwang *et al.*, 2016). A survey in Republic of Benin showed lack of improved varieties and good quality seeds as the major constraints, whereas early maturity, high yield, and resistance to pod borer were the most preferred traits (Ayenan *et al.*, 2017). In Uganda, pigeonpea is grown in preference to other crops because of its nitrogen fixing ability, high biomass, multiple end usage including fodder and firewood, and ease of harvesting. Farmers perceived aphids, pod borer, leaf miner, and FW as major production constraints (Namuyiga *et al.*, 2022). Continued surveys of the stakeholders are important for revisiting the objectives and priorities of the pigeonpea breeding programme.

Ideotype of pigeonpea varieties

Breeders need to tailor pigeonpea varieties in such a way as to meet the needs and requirements of the stakeholders (Table 1).

Table 1. Pigeonpea ideotype traits based on stakeholder preferences across the value chain that need to be addressed by the breeders

Stakeholder	Ideotype traits	Requirement
Farmers	Crop duration	Early maturity (120–140 d) for pure crop, medium maturity (160–180 d) for intercrop with uniform maturity
	Grain yield	High yield (>4 tons ha^{-1}), high harvest index (>50%)
	Plant type	Dwarf (height ~100 cm) semi-erect (branching angle ~30°, canopy width ~75 cm) plants for easy mechanical operations and light penetration, short sturdy primary stem (~15 cm), short internodes (<5 cm), determinate growth habit (axial and terminal flowers) with long pod bearing length (30–50 cm), large number of primary (10–15) and secondary (5–8 per primary branch) branches, greater than 1000 pods per plant, 6–8 seeds per pod, deep tap root >50 cm with profuse lateral branching radiating up to 40 cm for subsurface nutrient foraging and symbiotic N-fixation
	Abiotic stress tolerance	Tolerance to waterlogging at early stage, drought and cold at reproductive stage, soil salinity/sodicity and Al toxicity
	Disease and pest resistance	Fusarium wilt, PPSMV (SMD), PSB, YMV, leaf blight, pod borers (*Helicoverpa*, *Maruca*), pod fly, leaf mites, nematodes
Millers and traders	Seed coat colour	Light red/brown or white for dal, and green for vegetable
	Seed coat thickness	Soft thin easy to remove during milling
	Seed size	Medium (12–14 g per 100 seeds)
	Grain uniformity	Uniform color and size, no green shriveled seeds
	Grain storage	Log shelf life, pulse beetle (bruchid) resistance
Consumers	Appearance	Light yellow cotyledons for dal, large green seeds for vegetable, should not turn dark (reddish brown or blackish) upon cooking
	Cooking time	Short cooking time of 5–7 min for full disintegration of dal
Seed industry	Cleistogamy	For maintaining purity of varieties and hybrid parental lines
	Hybrid seed production	Full CMS/TGMS sterility and fertility restoration
	Heterosis	High heterosis and combining ability for harnessing hybrid vigor

CMS, cytoplasmic male sterility; PPSMV, pigeon pea sterility mosaic virus; PSB, Phytophthora stem blight; SMD, sterility mosaic disease; TGMS, thermo-sensitive genic male sterile; YMV, yellow mosaic virus.

This brings to the fore the importance of ideotype breeding in pigeonpea. The concept of the ideotype was first introduced in wheat, where it was defined as an ideal plant type, combining morphological and physiological traits, with potential to maximize the yield and quality in a defined environment (Donald, 1968). These included features such as a short strong stem, few small and erect leaves, large erect ears, presence of awns, and single culm. These features were updated to include physiological traits including high photosynthetic productivity, improved grain filling, and partitioning of photosynthate into grains (Parry *et al.*, 2011; Richards *et al.*, 2019). The ideotype concept in rice has driven breeding of productive new plant type varieties with upright leaves, strong culm, and large panicles (Khush, 1995; Peng *et al.*, 2008). The maize ideotype constitutes stiff vertically orientated leaves, short interval between pollen shedding and silk emergence, small tassel, longer grain filling period, slow senescence, and high grain number (Mock and Pearce, 1975; Xiao *et al.*, 2020). In oilseed *Brassica*, the ideotype constitutes optimized flowering time, apetalous flowers, long upright pods, and greater numbers of pods, seeds per pod and seed weight (Thurling, 1991; Siles *et al.*, 2020, Preprint). The pigeonpea ideotype has not been described and therefore we have tried to define it based on the needs and requirements of the stakeholders (Table 1; Fig. 2).

The pigeonpea ideotype should have the desired traits for plant type, physiological efficiency, processing, and nutritional quality as well as resistance to different environmental stresses. The plant type and physiological traits include: (i) semi-dwarf plant height of about 100 cm, (ii) canopy width of about 75 cm, (iii) sturdy primary stem length of about 15 cm, (iv) short internode lengths of less than 5 cm, (v) 10–15 primary branches and 5–8 secondary branches per primary branch, (vi) branching angle of about 30° for a semi-erect canopy, (vii) uncluttered long pod-bearing length of 30–40 cm, (viii) 6–8 well-filled grains per pod, (ix) small, thick, erect leaves for good light penetration and stress tolerance, (x) determinate growth habit for uniform height and maturity, (xi) thick deep tap root of >50 cm with profuse lateral branching radiating up to 40 cm, (xii) high photosynthetic efficiency, (xiii) efficient partitioning of photosynthate into grains, (xiv) HI of more than 50%, and (xv) high symbiotic nitrogen fixing ability in root nodules. The post-harvest processing and nutritional quality traits include: (i) light red or cream seed coat colour, (ii) uniform round, medium-size seeds of 12–14 g per 100 seeds, (iii) soft thin husk for easy milling, (iv) short cooking time of 5–7 min without browning, (v) palatable taste and pleasant mild flavor, without bitterness or off-beany flavor, and (vi) high seed protein (28–30%) and micronutrient contents, and low anti-nutritional factors such as trypsin inhibitor and phytic acid. For yield stability the pigeonpea ideotype needs to have: (i) resistance against the prevailing diseases and pests, (ii) tolerance to soil salinity, sodicity, and acidity, waterlogging

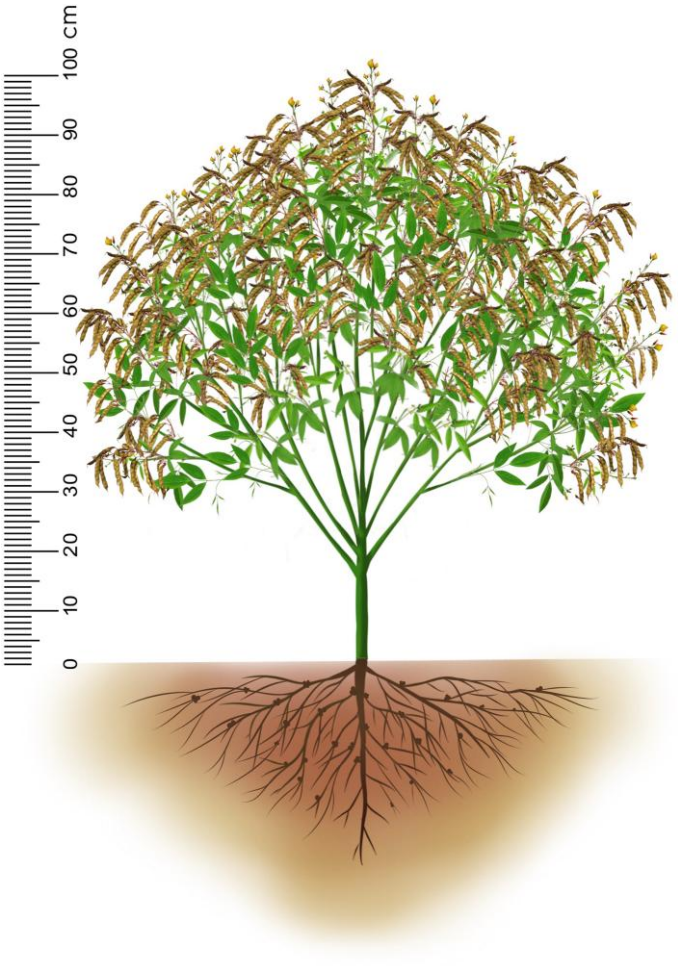

Fig. 2. Schematic diagram of pigeonpea plant ideotype with dwarf stature (height ~100 cm), semi-erect (branching angle ~30°, canopy width ~75 cm) plants for easy mechanical operations and light penetration, short sturdy primary stem (~15 cm), short internodes (<5 cm), determinate growth habit, long pod bearing length (30–50 cm), 10–15 primary branches, 5–8 secondary branches/primary branch, 6–8 seeds per pod, >1000 pods per plant with uniform maturity, deep tap root >50 cm with profuse lateral branching radiating up to 40 cm for subsurface nutrient foraging and symbiotic N-fixation.

at early stage, and drought and cold at reproductive stage; and (iii) uniform maturity to prevent shriveled green seeds at harvesting. Short duration determinate dwarf varieties are needed for smooth mechanical operations. The HI of pigeonpea is inversely correlated with the crop duration. Extra early varieties have HI of above 40%, early varieties about 35%, and medium duration varieties 21–24% (Kalaimagal, 2022). Long duration varieties have HI of less than 20% because they accumulate a large proportion of the biomass in woody stem and leaves. Short duration (130–145 d) varieties are needed for sole cropping under pigeonpea–wheat/mustard/potato systems, whereas medium duration varieties (160–185 d) are needed for intercropping with soybean, cotton, sorghum, or maize. Intercropping varieties may have indeterminate growth habit, semi-spreading primary branches, greater number of secondary and tertiary branches, and longer pod bearing length (K. B. Saxena *et al.*, 2018a). Extra early varieties (125–135 d) are needed for rainfed areas with no assured irrigation (Wanjari *et al.*, 2016). Effective communication and collaboration between breeders, researchers, and stakeholders is essential to ensure that breeding efforts align with societal needs.

Pigeonpea improvement through conventional breeding

Breeding efforts in pigeonpea have been reviewed periodically, and the key milestones are shown in Fig. 3 (Wanjari *et al.*, 2016; K. B. Saxena *et al.*, 2021a). Early focus was on evaluation of local landraces and selection of uniform flowering, light seed colour, non-shattering, disease resistant high-yielding pure lines (Pal, 1934). India started systematic research on pulses in 1966 under the All India Coordinated Pulses Improvement Project (AICPIP) at ICAR-Indian Agricultural Research Institute (IARI), New Delhi, which was later shifted to Kanpur and became ICAR-Indian Institute of Pulses Research in 1983. Pigeonpea breeding received a significant boost by establishment of International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in 1972. I. P. Singh *et al.* (2016) gave the details of 86 pigeonpea cultivars released in India. Here we present an updated list of 201 cultivars, comprising 70 short duration, 103 medium duration, and 28 long duration cultivars, including 13 hybrids (Supplementary Tables S1–S3). Initial varieties were developed by pure line selection, of which C11, T17, and UPAS 120 occupied large areas (Wanjari *et al.*, 2016), and some are still under cultivation, such as Bahar, BDN 1, TTB 7, and Maruti. Later, hybridization followed by pedigree selection became the norm and landmark varieties were released, such as Manak, Pragati, Pusa 991, Asha, BDN 716, and Mal 13. Naik *et al.* (2020) analysed 150 varieties released till 2018 and found that most of them were developed using a limited number of founder lines. The ISCB pigeonpea project started focusing on plant type in 2015 leading to release of dwarf varieties. Pusa Arhar 16 was the first determinate semi-dwarf (160 cm) released in 2018, and Pusa Jawahar Dwarf 22-1 the first determinate dwarf (100 cm) released in 2024 (Supplementary Table S1).

The countries of sub-Saharan Africa and Myanmar have relied largely on local varieties and landraces. Malawi farmers grow pigeonpea as an intercrop with maize or sorghum, and 'Mthawajuni' is the most popular traditional variety (Yohane *et al.*, 2021). The other popular varieties 'Namanjo' and 'Rozikhuthula' are also local landraces preferred for their pod borer resistance, short cooking time, and taste. ICRISAT introduced improved varieties to Malawi, but these were not adopted despite higher yields because they did not meet local needs (Yohane *et al.*, 2021). Tanzanian farmers

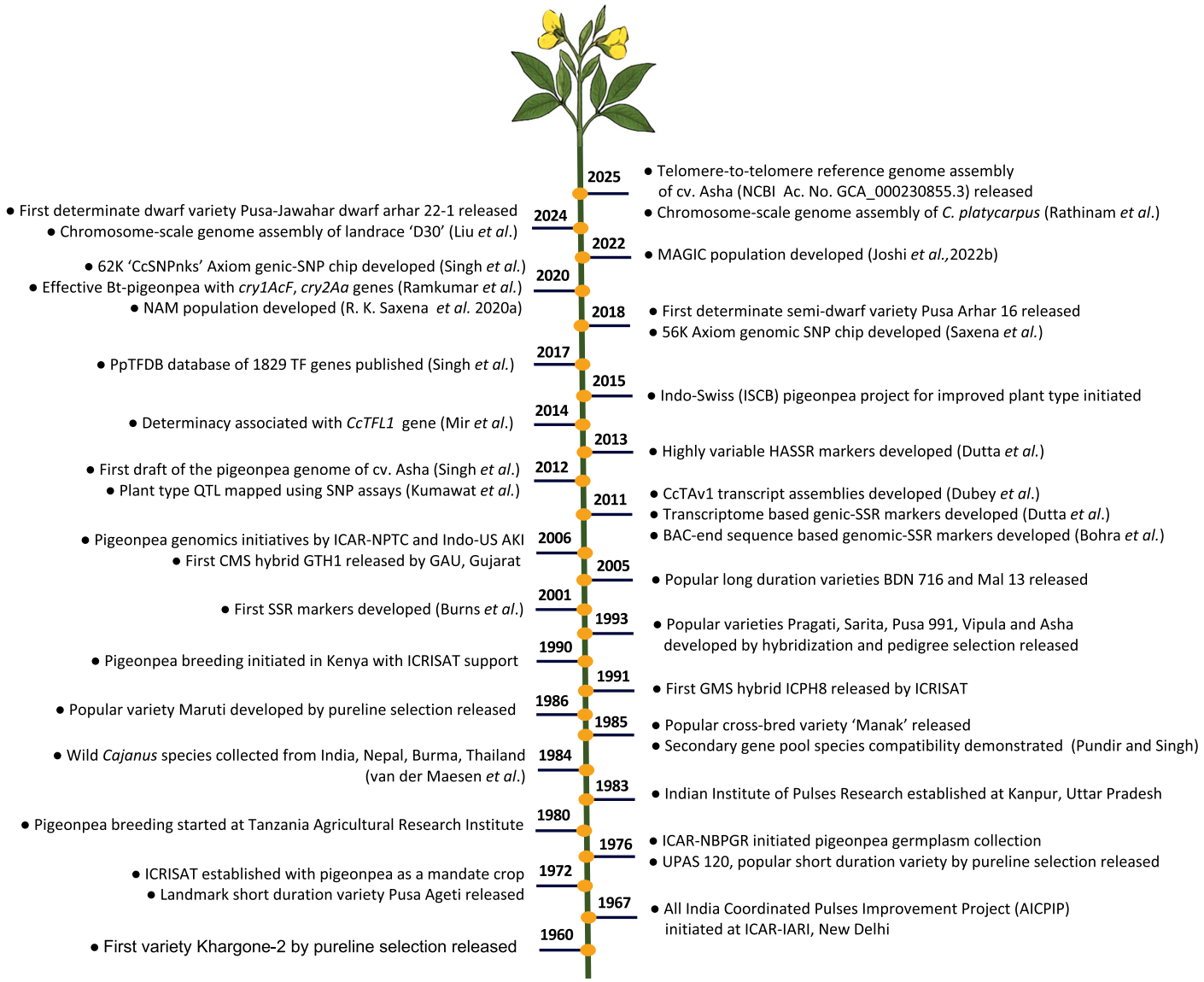

Fig. 3. Major landmarks in institutional setup, genetic resource conservation, breeding, and development of genomic resources in pigeonpea.

cultivate mostly local varieties and landraces (Manyasa *et al.*, 2008; Kimaro *et al.*, 2017). Pigeonpea breeding started at the Tanzania Agricultural Research Institute in 1980, and the first set of improved varieties were released through an ICRISAT collaboration, namely short duration Komboa, medium duration Mali, and long duration Tumia (Shiferaw *et al.*, 2007; Gangarao *et al.*, 2016; Kimaro *et al.*, 2020). Pigeonpea breeding in Kenya was initiated in the 1990s, and five improved varieties were released, viz. KAT 60/8, ICPL 89091, ICEAP 68, NPP 670, and ICP 6927 (Oteino *et al.*, 2011). Ojwang *et al.* (2016) recommended six varieties each for the rain-fed and irrigated regions of Kenya. Ten more improved varieties, namely KARI Mbaazi 1, KARI Mbaazi 2, KAT 60/8, Kajani, Mituki, Egerton Mbaazi M1, Egerton Mbaazi 3, Egerton Mbaazi M4, Peacock, and Karai were developed by the Kenya Agricultural and Livestock Research Organization (Wasike *et al.*, 2022). Farmers in Benin cultivate 84 different landraces of pigeonpea for food, soil conservation, and cash crops, which are often named according to their visible traits or geographical origin (Zavinon *et al.*, 2019; Kinhoégbè *et al.*, 2020). Pigeonpea was introduced in Mozambique in the 19th century by Indian immigrants, where local varieties and landraces are cultivated by small farmers (Pedro *et al.*, 2022). High-yielding varieties were introduced and two of these, viz. ICEAP 20 and ICEAP 40, are popular (Kaoneka *et al.*, 2016). In Myanmar, ICRISAT introduced six improved varieties that are grown as Yezin-1 to Yezin 6 (Kyu *et al.*, 2016). Local varieties are cultivated for food in Puerto Rico

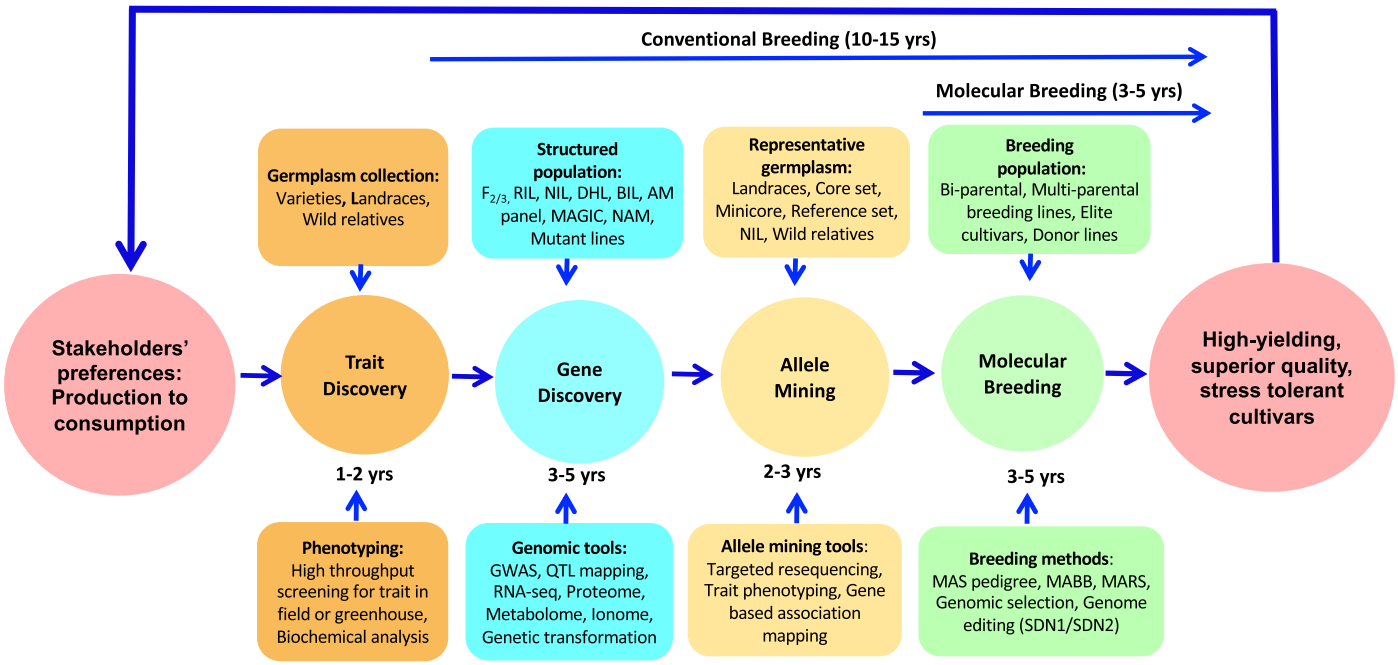

Fig. 4. Gene discovery and utilization process flow and timeline for plant varietal development. Trait and gene discoveries are driven by circular feedback from stakeholders so that the varieties meet their needs and expectations. Varieties should also have the traits required to meet the strategic objectives of climate-resilience and alleviation of hidden hunger. Conventional breeding begins with hybridization of lines with desired traits followed by phenotypic selection, whereas molecular breeding leverages precise knowledge of genes/markers for the traits, defined breeding population/elite cultivar and DNA marker-assisted indirect selection. AM, association mapping; BIL, backcross inbred lines; DHL, doubled haploid lines; GWAS, genome wide association studies; MABB, marker-assisted backcross breeding; MAGIC, multiparent advance generation intercross; MARS, marker-assisted recurrent selection; MAS, marker-assisted selection; NAM, nested association mapping; NIL, near-isogenic lines; QTL, quantitative trat locus; RIL, recombinant inbred lines; RNA-seq, RNA sequencing; SDN, site-directed nuclease.

and Dominican Republic. The medium duration variety Lazaro has been popular in Puerto Rico, but recently a new short duration semi-dwarf variety, 'Isabela', has been released with yield potential of 3409 kg ha^{-1} (Viteri and Linares-Ramírez, 2023).

Hybrids in pigeonpea have received continued attention starting with a genetic male sterility (GMS) system (B. V. S. Reddy *et al.*, 1978; K. B. Saxena *et al.*, 2018c; I. P. Singh *et al.*, 2024). ICRISAT released the first GMS hybrid, ICPH 8 with 35% yield advantage over the check variety, but the system was abandoned due to difficulties in maintaining purity of parental lines (R. K. Saxena *et al.*, 2018a; K. B. Saxena *et al.*, 2018c). It was replaced by a cytoplasmic male sterility (CMS) system allowing easier maintenance of lines. The first CMS hybrid, GTH 1, was developed by GAU using A2 cytoplasm of *C. scarabioedes* and released for cultivation in 2008 (Tikka *et al.*, 1997; K. B. Saxena and Kumar, 2003; I. P. Singh *et al.*, 2024). Subsequently, ICPH 2671 was developed by ICRISAT using A4 cytoplasm of *C. cajanifolius* and released in 2010 (Mallikarjuna and Saxena, 2005; K. B. Saxena *et al.*, 2005, 2013). Two more A4 hybrids (ICPH 3762, ICPH 2740) and three more A2 hybrids (IPH 15-03, IPH 09-5, PAH 5) were released up to 2023 (K. B. Saxena *et al.*, 2018c, 2021b; Supplementary Tables S1, S2). Despite yield superiority the adoption of pigeonpea hybrids is limited to about 150 000 ha in India, which is less than 5% of the total sown area and there are no reports of pigeonpea hybrids outside India. The future of hybrids in pigeonpea will depend on the level of heterosis over the best pure line cultivars and on cost-effective hybrid seed production.

Pigeonpea genetic resources

Genetic improvement of crop plants depends on effective exploration, conservation, evaluation, and utilization of the genetic resources including traditional varieties, landraces, and crop wild relatives (CWR). Integration of marker-assisted selection (MAS) has enhanced the pace and precision of breeding in crops with rich genomic resources such as, rice, maize, soybean, and tomato. A gene discovery and utilization process flow and timeline for plant varietal development through molecular breeding is shown in Fig. 4. Genetic advances in pigeonpea were hindered by scarce genomic resources and limited variability in the primary gene pool (Bohra *et al.*, 2020). ICAR–National Bureau of Plant Genetic Resources (NBPGR), New Delhi, State Agricultural Universities (SAUs) in India, and ICRISAT maintain large collections of pigeonpea germplasm. In total 11 221 accessions are conserved at ICAR-NBPGR and 13 771 accessions at ICRISAT,

including 555 accessions of 66 wild related species from 74 countries. A further 4116 accessions are conserved at USDA, 1288 accessions at National Genebank of Kenya, and 433 at National Plant Genetic Resources Laboratory, Philippines (Remanandan, 1981; Gowda *et al.*, 2013; N. Singh *et al.*, 2013; Pazhamala *et al.*, 2015; Upadhyaya *et al.*, 2016; Semwal *et al.*, 2017). A core set of 1290 genotypes and a mini-core set of 146 genotypes were developed based on 34 morpho-agronomic traits (L. J. Reddy *et al.*, 2005; Upadhyaya *et al.*, 2006). Genotyping-based core sets have also been developed (Gowda *et al.*, 2013; Pazhamala *et al.*, 2015). There is a need to utilize the above genetic resources in pigeonpea breeding for introgression of desired ideotype traits and to broaden the genetic base of cultivars. The popular pigeonpea cultivars in India, such as Asha, Bahar, BDN-1, Maruti, and Mal 13, were developed decades ago, indicating slow progress in varietal improvement (Bantilan and Joshi, 1996; K. B. Saxena *et al.*, 2021a).

Pigeonpea varieties and landraces have been evaluated for yield parameters, quality traits, and tolerance to environmental stresses, and donor lines have been identified (Supplementary Table S4). However, there has been limited validation and utilization of the identified lines in breeding (M. Singh *et al.*, 2014; K. B. Saxena *et al.*, 2021a). Donor lines have been identified for earliness, dwarfness, seed size, number of branches per plant, pods per plant, and seeds per pod (K. B. Saxena and Sharma, 1995; Ram Dhari and Waldia, 2005; Upadhyaya *et al.*, 2010; Arumugam *et al.*, 2018). Accession ICP 13828 has the highest number of 10 seeds per pod (Sastry *et al.*, 2006). Donors for high seed protein and micronutrient contents have been identified (L. J. Reddy *et al.*, 1997; K. B. Saxena *et al.*, 2008; Upadhyaya *et al.*, 2010). Waterlogging at early vegetative stage seriously impairs crop establishment, and genotypes have been found with waterlogging tolerance (Chauhan *et al.*, 1997; Sarode *et al.*, 2007; L. Krishnamurthy *et al.*, 2011; Sultana *et al.*, 2013; Hingane *et al.*, 2015). Pigeonpea cultivars are relatively drought tolerant but suffer from water deficit at flowering stage, and drought tolerant genotypes have been identified (P. J. Reddy, 2001; D. V. Deshmukh *et al.*, 2009; Suresh *et al.*, 2016; Sangeetha *et al.*, 2020). Cold tolerant lines have also been identified that retain 60–80% of the flowers/pods under cold stress, while sensitive varieties show <10% retention (B. B. Singh *et al.*, 1997; M. N. Singh and Singh, 2010; Tiwari *et al.*, 2022). Soil salinity and aluminum tolerant genotypes have also been identified (Subbarao *et al.*, 1991; N. Srivastava *et al.*, 2006; Choudhary *et al.*, 2011; Joshi *et al.*, 2022a). Among the biotic stresses, SMD, FW, PSB, legume pod borer, Maruca pod borer, pod fly, and nematode (*Rotylenchulus reniformis*) are serious threats for which resistant accessions have been identified (Supplementary Table S4), for example SMD resistance (M. Sharma *et al.*, 2012; M. Singh *et al.*, 2014), FW resistance (Gwata *et al.*, 2006; M. Sharma *et al.*, 2012; M. Singh *et al.*, 2014; Murali-Baskaran *et al.*, 2022), and PSB resistance (Kannaiyan *et al.*, 1981; M. Singh *et al.*, 2014). No variety has complete resistance to pod borer but moderately resistant lines have been identified (Upadhyaya *et al.*, 2013b; M. Singh *et al.*, 2014). Similarly, genotypes have been identified with pod fly and reniform nematode resistance (S. B. Sharma *et al.*, 2000; M. Singh *et al.*, 2014). There is a need to map the genes/quantitative trait loci (QTL) for desired traits in these donor lines and to utilize them in pigeonpea breeding.

Interspecific hybridization has great scope in pigeonpea varietal improvement as done successfully in rice, wheat, tomato, and other crops (Brar and Khush, 1997; Atwell *et al.*, 2014; S. Mishra *et al.*, 2016; Pour-Aboughadareh *et al.*, 2021; Khazaei and Madduri, 2022). ICRISAT started collecting pigeonpea CWRs from the areas of prevalence in India, Nepal, Burma, and Thailand (van der Maesen *et al.*, 1984). They recorded the patterns of occurrence of *Cajanus* spp. and related genera and observed that the habitats of several species have shrunk significantly. *Cajanus elongatus* and *C. villosus* in North-East India, *C. grandiflorus* in the North and North-East India, and *C. sericeus* in the Eastern Ghats of India were on the brink of extinction. They found 34 species of subtribe *Cajaninae* in Australia, where genus *Cajanus* was represented by 17 species most of them endemic to Australia. *Dunbaria* has two species, *Eriosema* one species, and *Flemingia* eight species endemic to Australia. Genus *Rhynchosia* has six species with several variants in Australia. Four new species were also described, viz. *C. hirtopilosus* Maesen, *C. geminatus* Pedley ex Maesen, *R. bungarensis* Maesen, and *R. filiformis* Maesen (van der Maesen, 2003). Genus *Cajanus* has 32 species of which *Cajanus cajan* is the only cultivated one (van der Maesen, 1990). Pigeonpea germplasm is categorized into four gene pools according to the systematic classification of Harlan and de Wet (1971). The 32 *Cajanus* species belong to primary, secondary, and tertiary gene pools based on morphology and cross-compatibility with the cultivars (Fig. 5). The landraces, traditional varieties, and improved cultivars make up the primary gene pool of *Cajanus cajan*. The remaining 31 *Cajanus* species constituting the secondary and tertiary gene pools are indigenous to Asia and Australia, with maximum concentration in South Asia, South-East Asia, and Northern Australia (Fig. 5). Ten related genera constituting the quaternary gene pool are distributed throughout the world, except that South and Central America have only *Rhyncosia* spp. The cultivated pigeonpea has its origin in India based on the concept of the 'centre of diversity' for crops and wild species (Vavilov, 1951; van der Maesen, 1990). Archeological evidence also indicates domestication of pigeonpea in the Eastern Peninsular region of India 5000–4500 years ago (Fuller *et al.*, 2019).

Wild *Cajanus* species are a deep reservoir of genes for enriching variability in the cultivars (Supplementary Table S5; Remanandan, 1981; S. B. Sharma *et al.*, 1993; Kameswara Rao *et al.*, 2003; S. Sharma and Upadhyaya, 2016; S. Sharma *et al.*, 2019). Use of CWRs in pigeonpea breeding is limited

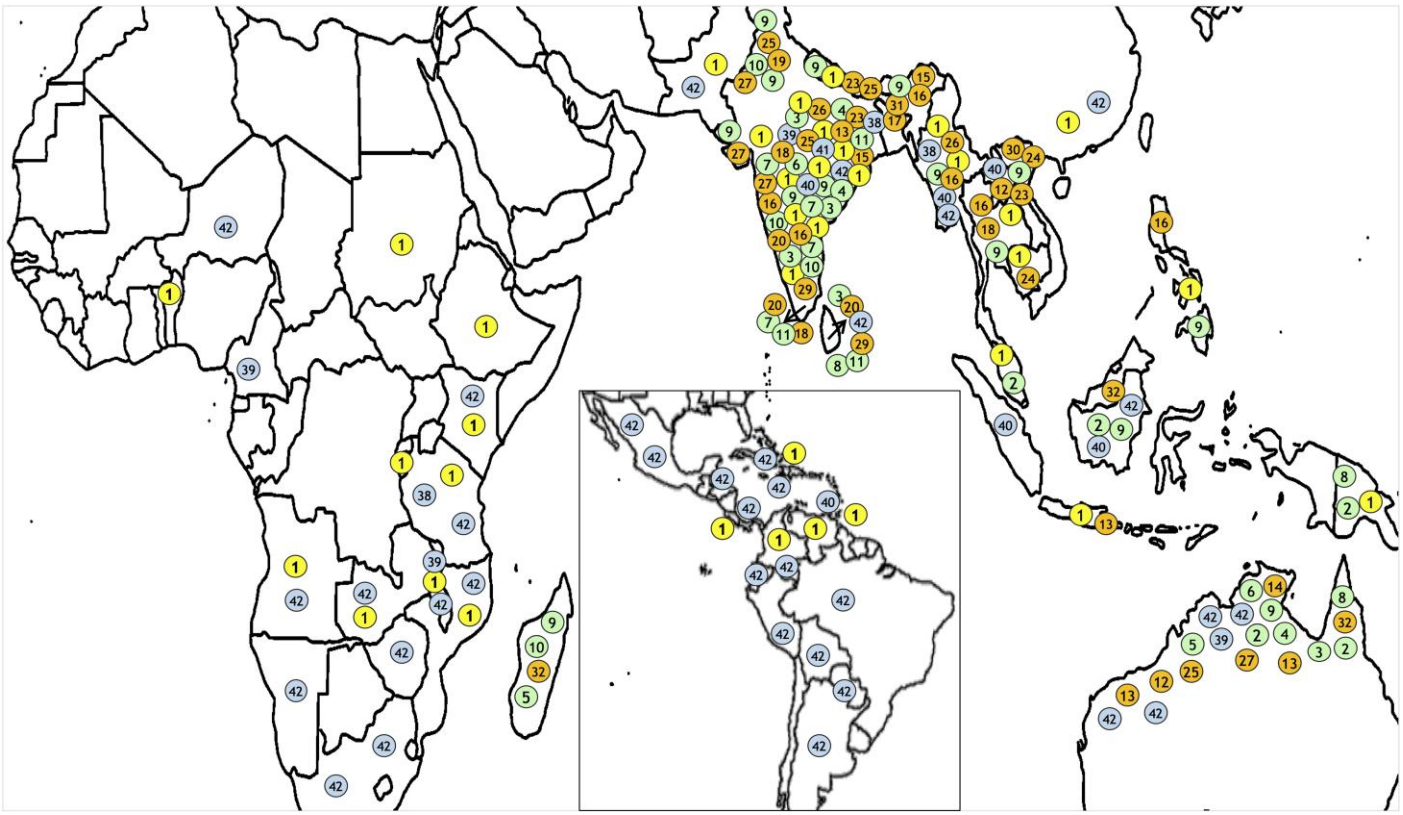

Fig. 5. Geographical distribution of the pigeonpea varieties making up the primary gene pool (yellow circles), related wild *Cajanus* species comprising the secondary (green circles) and tertiary (orange circles) gene pools, and related genera comprising the quaternary (blue circles) gene pool. The numbers within the circle represent different taxa: 1, *Cajanus cajan*; 2, *C. acutifolius*; 3, *C. albicans*; 4, *C. cajanifolius*; 5, *C. lanceolatus*; 6, *C. latisepalus*; 7, *C. lineatus*; 8, *C. reticulatus*; 9, *C. scarabaeoides*; 10, *C. sericeus*; 11, *C. trinervius*; 12, *C. aromaticus*; 13, *C. cinereus*; 14, *C. convertiflorus*; 15, *C. crassicaulis*; 16, *C. crassus*; 17, *C. elongatus*; 18, *C. goensis*; 19, *C. grandiflorus*; 20, *C. heynei*; 21, *C. kerstingii*; 22, *C. lanuginosus*; 23, *C. mareebensis*; 24, *C. marmoratus*; 25, *C. mollis*; 26, *C. niveus*; 27, *C. platycarpus*; 28, *C. pubescens*; 29, *C. rugosus*; 30, *C. vicsidus*; 31, *C. villosus*; 32, *C. volubilis*; 33, *Adenodolichos*; 34, *Baukea*; 35, *Bolusafra*; 36, *Carissoa*; 37, *Chrysoscias*; 38, *Dunbaria*; 39, *Erisema*; 40, *Flemingia*; 41, *Paracalyx*; 42, *Rhynchosia*.

by cross-incompatibility between species. However, species of the secondary gene pool do not require specialized techniques for hybridization with *C. cajan* (Pundir and Singh, 1985; N. Mallikarjuna et al., 2011a, b). Successful examples include development of lines with cleistogamy, high seed protein content, PSB resistance, nematode resistance, pod borer tolerance, earliness, and dwarfness (Supplementary Table S5). Advance generation lines from crosses with *C. acutifolius* have shown resistance to pod borer, pod fly, bruchid beetle, and waterlogging tolerance (H. C. Sharma *et al.*, 2003; Mallikarjuna *et al.*, 2007; Sujana *et al.*, 2008; H. C. Sharma *et al.*, 2009; D. R. Jadhav *et al.*, 2012a, b; Hingane *et al.*, 2015). Introgression lines with yield traits from *C. acutifolius* and *C. cajanifolius* into cv. Asha have been evaluated in diverse environments (Mallikarjuna and Saxena, 2002; D. R. Jadhav *et al.*, 2012b; S. Sharma *et al.*, 2019). High seed protein lines have been obtained from crosses with *C. albicans*, *C. scarabaeoides*, and *C. sericeus* (K. B. Saxena *et al.*, 2023). Crosses with *C. lanceolatus* produced lines with resistance to bruchids and pod borer due to higher proteinase inhibitor activity (Srikanth *et al.*, 2015 , 2017). Crosses with *Atylosia lineata* (*C. lineatus*) resulted in lines with cleistogamy, useful for maintaining pure lines by ensured self-pollination (K. B. Saxena *et al.*, 1992a, b). Crosses with *C. scarabaeoides* resulted in SMD and insect resistance (Kulkarni *et al.*, 2003; Ngugi-Dawit *et al.*, 2020), and photoperiod-insensitive lines were developed from crosses with *C. sericeus* (Kameswara Rao *et al.*, 2003; Hussain *et al.*, 2022). Nine different CMS systems (A1–A9) have been developed by crosses with wild *Cajanus* species [Supplementary Table S5; Ariyanayagam *et al.*, 1995 (A1); Tikka *et al.*, 1997 (A2); Wanjari *et al.*, 1999 (A3); K. B. Saxena *et al.*, 2005 (A4); Mallikarjuna and Saxena, 2005 (A5); K. B. Saxena and Kumar, 2010 (A6); N. Mallikarjuna *et al.*, 2011b (A7); K. B. Saxena, 2013 (A8); Srikanth *et al.*, 2015 (A9)]. Surprisingly, in A5 and A9 the source of sterile cytoplasm was *Cajanus cajan*.

There are 21 *Cajanus* species in the tertiary gene pool, which are difficult to hybridize due to crossability and post-zygotic barriers (Pundir and Singh, 1985, 1987; Mallikarjuna and Moss, 1995); nevertheless some of these have been crossed successfully and useful traits transferred to cultivars (Supplementary

Table S5). *Cajanus cinereus* contributed to high seed protein content, and *C. mollis* to cold, pod borer, and PSB resistance (Remanandan, 1981; Upadhyaya *et al.*, 2013a; Khoury *et al.*, 2015). *Cajanus platycarpus* has several useful traits including earliness and photoperiod insensitivity (Ariyanayagam and Spence, 1978; K. B. Saxena *et al.*, 1996; Mallikarjuna *et al.*, 2006; S. Sharma *et al.*, 2020), FW and PSB resistance (Pundir and Singh, 1987; Mallikarjuna *et al.*, 2005; N. Mallikarjuna *et al.*, 2011b), salinity tolerance (Subbarao, 1988; Subbarao *et al.*, 1990, 1991; N. Srivastava *et al.*, 2006), nematode resistance (S. B. Sharma, 1995), and pod borer and SMD resistance (P. L. Kumar *et al.*, 2005; Sujana *et al.*, 2008). *Cajanus platycarpus* was hybridized with *C. cajan* using embryo rescue, and backcross progenies showed variation for days to flowering, growth habit, seed number, size and color, and resistance to pod borer, pod fly, bruchids, FW, and SMD (Mallikarjuna and Moss, 1995; Mallikarjuna *et al.*, 2006; N. Mallikarjuna et al., 2011a, b; S. B. Sharma *et al.*, 2020). Photoperiod insensitive lines were also derived from *C. platycarpus* (Ariyanayagam and Spence, 1978; Hussain *et al.*, 2022). *Cajanus volubilis* was crossed with pigeonpea cultivars to obtain short duration lines (Mallikarjuna, 2014). There are 10 related genera in the quaternary gene pool under subtribe *Cajaninae*, viz. *Adenodolichos*, *Baukea*, *Bolusafra*, *Carissoa*, *Chrysoscias Dunbaria*, *Erisema*, *Flemingia*, *Paracalyx*, and *Rhynchosia* (Fig. 5). *Rhyncosia* spp. possess nutritional and therapeutic properties (Bakshu and Venkatraju, 2001; Drabu *et al.*, 2011), and have been crossed with pigeonpea by hormone-aided pollination to obtain self and backcross progenies (Mallikarjuna, 2014). These CWR derivatives have been utilized in pigeonpea improvement to a limited degree.

Pigeonpea genome sequencing

A high-quality reference genome is essential for systematic discovery of useful genes and allele mining by targeted re-sequencing of diverse varieties (Fig. 4). Advances in omics technologies are poised to accelerate the development of nutrient-rich, stress-tolerant, high-yielding pigeonpea varieties (A. Singh and Singh, 2022). The mitochondrial and chloroplast genomes of pigeonpea are published, which are useful in exploring genes for CMS and photosynthetic efficiency (Tuteja *et al.*, 2013; Kaila *et al.*, 2016). The first draft of the nuclear genome of pigeonpea cv. Asha was published by N. K. Singh *et al.* (2012) through the Pigeonpea Genomics Initiative (PGI) of the Indian Council of Agricultural Research (ICAR) under the Indo-US Agricultural Knowledge Initiative (AKI) and Network Project on Transgenics in Crops (NPTC), led by ICAR-National Institute for Plant Biotechnology (NIPB), New Delhi. The NIPB-draft genome was assembled using next generation sequencing (NGS) reads from the 454 GS FLX platform with a mean read length of 550 bp and >10-fold genome coverage. The 192 089 sequence contigs constituted a genome assembly of 510.8 Mbp, with 97.9% of the bases having Phred quality scores of ≥40. *Ab initio* gene prediction identified 47 004 protein-coding genes, of which 1213 were disease resistance-like or defense response genes, and 152 were abiotic stress tolerance genes. The genome coverage of NIPB-draft was enhanced to 648.2 Mbp and 56 888 protein-coding genes by integrating Illumina sequencing (Mahato *et al.*, 2018). It was used to develop a pigeonpea transcription factor database (PpTFDB) of 1829 genes belonging to different families (A. Singh *et al.*, 2017), and genome wide distribution and expression pattern of chitinase gene families (Mahato *et al.*, 2019).

In a parallel effort another draft genome of cv. Asha was assembled in 173 708 contigs by ICRISAT (ICRISAT-draft) using Illumina short reads with total scaffold size of 605.7 Mbp, including 34 Mbp (5.69%) of sequence gaps, with 40 071 protein-coding genes (Varshney *et al.*, 2012). Marla *et al.* (2020) integrated the NIPB and ICRISAT drafts (Acc no. GCA_000340665.1 and GCA_000230855.2) with 75.6% and 70.6% genome coverage, respectively, to generate a genome assembly with enhanced contiguity. The integrated assembly showed genome coverage of 82.4% and longer scaffolds as compared with the two original drafts. A pangenome of pigeonpea was assembled by re-sequencing of 89 diverse pigeonpea varieties from India and The Philippines using ICRISAT-draft as reference, adding 35 445 scaffolds with 35 Mbp sequence data to the reference leading to a pangenome size of 622.8 Mbp and 55 512 protein-coding genes (J. Zhao *et al.*, 2020). Subsequently, the ICRISAT group used HiC sequencing to improve chromosome-level scaffolding (C-assembly) of the ICRISAT-draft (D-assembly) (Garg *et al.*, 2022). They identified 4573 errors in the 'D-assembly' including several mis-joins, non-joins and inversions and produced an improved chromosome-level assembly of 594 Mbp with 29 482 protein-coding genes in 850 scaffolds, 93.1% of which were anchored to the 11 chromosomes. Integration of HiC data resulted in a higher level of scaffolding and chromosome anchoring, but low genome coverage and high percentage of sequence gaps still does not qualify it as a high-quality reference genome. Recently, a chromosome-scale reference quality genome of Chinese pigeonpea landrace D30 was published, but D30 has a divergence time of 25 million years from *C. cajan* cv. Asha, and it groups closer to wild *Cajanus* species than *C. cajan* cultivars (Liu *et al.*, 2024). Rathinam et al (2025) developed a 482.2 Mbp chromosome-scale genome assembly of *C. platycarpus*, offering novel insights into its superior ability to resist the pod borer *Helicoverpa armigera*. Initially, the genome size of *C. cajan* was reported as 880 Mbp (1 C=0.9 pg) by Bennett and Smith (1976). Subsequently, a genome size of 834 Mbp and 807 Mbp was estimated based on Feulgen stain densitometry and propidium iodide (PI) flow cytometry, respectively (Greilhuber and Obermayer, 1998). Considering the estimated genome size of over 800 Mbp, a full-coverage reference genome of pigeonpea was long awaited, but the gap has been filled now by public release of a 750 Mbp telomere to telomere (T2T) reference

genome assembly of *C. cajan* cv. Asha by ICAR-NIPB (NCBI GenBank Ac. No. GCA_000230855.3).

Expressed sequence tags and transcriptome studies in pigeonpea

The literature on developmental and stress-related gene expression studies useful for gene discovery in pigeonpea is compiled in Supplementary Table S6. The earliest gene expression profiling in pigeonpea used Sanger expressed sequence tag (EST) sequencing, hybridization of RNA extracts to microarray probes, and RT-PCR. The first set of 85 ESTs from drought stressed leaves and roots of pigeonpea were made public through NCBI dbEST database in 2006 (Priyanka *et al.*, 2010). The Indo-US AKI gave a boost to pigeonpea genomics during 2006–2009, through which a large number of ESTs were deposited to NCBI (Varshney *et al.*, 2010). ICAR-NIPB contributed the largest number of 13 690 ESTs from 16 cDNA libraries of different tissues of pigeonpea cv. Asha, UPAS 120, and *C. scarabaeoides* grown under control and stress conditions (NCBI BioSample ID SAMN00169055–SAMN169070). ICRISAT deposited 9888 ESTs from 16 cDNA libraries of four pigeonpea genotypes with contrasting response to FW and SMD (Raju *et al.*, 2010). R. R. Kumar *et al.* (2015) identified drought responsive genes by EST sequencing of a suppression subtractive hybridization library of drought stressed roots. Northern blotting showed up-regulation of ornithine aminotransferase, cyclophilin, dehydration responsive element binding protein (DREB), and peroxidase genes. Presently, there are a total of 24 953 pigeonpea ESTs in the NCBI dbEST database.

NGS-based RNA sequencing (RNA-seq) replaced Sanger EST sequencing, thus facilitating genomewide analysis of differentially expressed genes (DEGs). RNA-seq studies have focused on changes in gene expression during development and differentiation, cytoplasmic male sterility, response to abiotic stresses such as aluminum toxicity, drought, heat, phosphorus deficiency, soil salinity, and waterlogging, and biotic stresses such as SMD, FW, and pod borer infestation. Pooled cDNA libraries of root, shoot, leaves, and immature seeds of cv. Asha and UPAS 120 were sequenced using the 454 GS FLX platform (Dutta *et al.*, 2011). In another study, 454 GS FLX sequence reads from 31 different tissues of cv. Pusa Ageti were combined with 10 817 Sanger ESTs to generate *C. cajan* transcript assemblies (CcTAv1) comprising 127 754 unique sequences (A. N. Dubey *et al.*, 2011). Kudapa *et al.* (2012) did transcriptome assembly of Illumina, 454 GS FLX, and Sanger ESTs to develop the CcTAv2 database comprising 21 434 transcript contigs. Pazhamala *et al.* (2016, 2017) studied temporal and spatial regulation of gene expression during seed development from zero to 30 d after anthesis, and prepared a gene expression atlas (CcGEA) of cv. Asha representing 30 different tissues and developmental stages, revealing a compendium 28 793 genes with constitutive, spatiotemporal, and differential expression patterns.

To identify genes for male sterility, Pazhamala *et al.* (2020) analysed DEGs in thermosensitive male sterile line EnvsSel107, and its fertile counterpart using multi-omics approaches. They showed that the male fertility to sterility transition was due to perturbation of auxin homeostasis. S. Saxena *et al.* (2020) identified 3167 DEGs between A2-CMS line AKCMS11 and its fertility restorer AKPR303. Bohra *et al.* (2021a) and Bohra *et al.* (2021b) identified 10 and 582 DEGs, respectively, between A4-CMS line ICPA2043A and its maintainer line ICPB2043B at two stages of flower bud development, and 505 DEGs between A2-CMS line ICPL88039A and its maintainer ICPL88039B. Gene annotation and network analyses revealed association of CMS with four major pathways namely, glucose and lipid metabolism, ATP production, pollen development and pollen tube growth, and reactive oxygen species scavenging.

Transcriptome analysis to identify pathways for drought stress tolerance revealed the role of flavonoid biosynthesis regulated by abscisic acid and methyl jasmonate (Du *et al.*, 2021; W. Yang *et al.*, 2021; J. Yang *et al.*, 2022). Pahal *et al.* (2024) analysed drought stress response using RNA-seq and identified novel genes and transcription factors for drought susceptibility. Awana *et al.* (2020) analysed root and shoot transcriptome of contrasting pigeonpea genotypes to unravel salinity-induced gene expression pathways. Song *et al.* (2022) combined transcriptome and metabolome analyses to show melatonin-induced flavonoid enrichment for tolerance to multiple abiotic stresses. M. Wang *et al.* (2023) used RNA-seq to elucidate molecular mechanisms of naringenin-regulated flavonoid biosynthesis for salt tolerance. Ramakrishna *et al.* (2021) analysed heat stress-induced DEGs between a sensitive pigeonpea cultivar and tolerant wild relatives and found that oxidoreductase activities, transcription factors, oxygen-evolving complex, photosystem II, and phenylpropanoid and flavonoid biosynthetic pathways were highly affected. Tyagi *et al.* (2023) used RNA-seq to identify DEGs between waterlogging tolerant and sensitive pigeonpea genotypes. Niu *et al.* (2021) investigated role of ABCG transporters in the adaptation of pigeonpea to drought, salinity, and cold. Analysis of 51 *CcABCG* genes by qRT-PCR showed differential expression under cold stress. *CcABCG28* was up-regulated at low temperature, whereas *CcABCG7* was up-regulated under drought and aluminum stress. Liu *et al.* (2022) investigated physiological and molecular response of pigeonpea roots to phosphate (Pi) starvation by integrating multi-omics analyses. A number of genes involved in the Pi-starvation response were up-regulated in Pi-deficient roots. Among these, four gene families have expanded by tandem duplication, viz. phosphate transporter 1, phosphoethanolamine/phosphocholine phosphatase, fasciclin-like arabinogalactan protein, and glutamate decarboxylase. These are likely involved in Pi uptake, phospholipid recycling, and regulation of organic acid exudation. Gao *et al.* (2020) did a time series RNA-seq analysis of pigeonpea roots under Al stress and found that genes of flavonoid and phenolic pathways were down-regulated under Al

stress. Dong *et al.* (2024) elucidated the role of citrate transporter CcMATE35 and transcription factor CcNFYB3 regulating Al-stress tolerance, and identified a long ncRNA regulating expression of the citrate synthase gene (*CcLTCS*) in roots for Al tolerance. Mandlik *et al.* (2022) analysed role of aquaporins in silicon uptake and tolerance to arsenic, antimony, and germanium in pigeonpea.

Towards gene discovery for biotic stress resistance, Purohit *et al.* (2021) analysed FW-induced genes in susceptible and resistant cultivars at the invasion stage of pathogenesis by cDNA-amplified fragment length polymorphism (AFLP). Soren *et al.* (2021) analysed metabolic pathways affected by FW infection in susceptible and resistant cultivars at different time intervals and identified candidate genes including defensin and disease resistance-like genes. Nigam *et al.* (2017) did transcriptome profiling of bud and leaf tissues of *C. scarabaeoides* and described 81 799 unigenes with annotation. Rathinam *et al.* (2019a, b) analysed susceptible cultivar and tolerant *C. platycarpus* against *H. armigera* herbivory at different time points and showed expression of insect resistance genes in *C. platycarpus*. Njaci *et al.* (2021) analysed *H. armigera* resistance in *C. scarabaeoides* against a susceptible cultivar and found higher expression of flavonoids, terpenes, and glucosinolate pathway genes in *C. scarabaeoides*. V. R. Patil *et al.* (2021) analysed expression of 10 defence genes in resistant and susceptible genotypes at different time points after *Fusarium udum* inoculation and found *LOX* gene played a role in susceptibility to FW.

The limitation of transcriptome profiling is that alone it provides too many DEGs, making it difficult to narrow down the causal gene(s) behind trait variation. Most of the studies in pigeonpea did not combine the power of transcriptome profiling with genetic approach of QTL mapping and fine mapping to identify the causal genes, as done in other crops, for example rice, sorghum, corn, and apricot (R. Deshmukh *et al.*, 2010; Pandit *et al.*, 2010; Gelli *et al.*, 2017; T. Wang *et al.*, 2023; Jiang *et al.*, 2025). Discovery and validation of trait-specific genes and functional markers is needed for use in molecular breeding (Fig. 4).

Proteome and metabolome profiling of pigeonpea

Proteome profiling provides information for understanding the structural, functional, and protein dynamics of the plant tissues (Ramalingam *et al.*, 2015). Protein identification by 2D electrophoresis integrated with mass spectrometry (MS) provides high accuracy and resolution, whereas matrix-assisted laser desorption/ionization time of flight (MALDI-TOF) MS and electrospray ionization (ESI) MS with tandem mass spectrometry (MS/MS) provide higher speed and sensitivity (Griffin and Aebersold, 2001; Griffin *et al.*, 2001; van Wijk, 2001; Subramanian and Smith, 2013). Jan *et al.* (2023) has reviewed usefulness of proteomics in identifying abiotic stress-responsive proteins in legumes. Proteome profiling studies in pigeonpea are compiled in Supplementary Table S7. Protein extraction protocols from young leaves, flowers, and seeds of pigeonpea were optimized for 2-D gel electrophoresis (N. Singh *et al.*, 2015). Krishnan *et al.* (2017) analysed seed proteins of pigeonpea using 2-D electrophoresis followed by MALDI-TOF-TOF and identified 373 different seed proteins. A number of stress-responsive proteins associated with adaptation to drought stress were identified and a seed proteome map was developed. H. Dubey *et al.* (2018) identified 14 differentially expressed proteins from acid-tolerant and acid-sensitive *Rhizobium* isolates of pigeonpea roots using peptide mass fingerprinting. These proteins were implicated in the modulation of the chemo-taxis system, including enzymes catalysing redox transformations, biosynthesis, detoxification, export/import of substrates, receptors for osmotic solutes, methylation, protein transport, and cellular metabolism. B. Yadav *et al.* (2020) analysed genetic relationship of pigeonpea genotypes by SDS-PAGE protein profiling of leaf and seed tissues. Proteome analysis was used to identify proteins for *H. armigera* tolerance in *C. scarabaeoides* accession IBS-3471, suggesting that it is a suitable donor for pigeonpea improvement via host plant resistance (Ngugi-Dawit *et al.*, 2021). Rathinam *et al.* (2020) performed comparative proteome analysis of *H. armigera* resistance in *C. platycarpus*, revealing association with up-regulation of proteins in the phenylpropanoid and polyamine synthesis pathways, which restricted the herbivore growth. Pazhamala *et al.* (2020) used multi-omics approach for unraveling the fertility transition in a two-line thermo-sensitive genic male sterile hybrid system. Male sterile and fertile anthers from five developmental stages were analysed by integrated transcriptomics, proteomics, and metabolomics approaches to identify 17 differentially expressed proteins. Awana *et al.* (2020) used an integrated proteomics–transcriptomics approach for analysing root and shoot tissues of contrasting salt-sensitive (ICP 1071) and salt-tolerant (ICP 7) pigeonpea varieties to unravel the genes and pathways for salinity tolerance. Jain *et al.* (2021) did proteome analysis of control and salt-stressed pigeonpea plants, showing a varied response of amino acids serine, aspartate, and phenylalanine, DoF transcription factors, and glycine betaine biosynthesis. They identified a role of choline precursors in serine and glycine betaine biosynthetic pathways in salinity tolerance. Protein interaction network analysis highlighted a potential role of cytochrome *c* oxidases in sensing and signaling cascades governing salt stress response. Meng *et al.* (2021) identified CcCIPK14–CcCBL1 modulation of drought tolerance in pigeonpea through enhanced flavonoid biosynthesis. These proteomic insights will help identify causal genes for stress tolerance and nutritional quality traits (N. Singh *et al.*, 2020).

DNA markers, genetic diversity, and QTL mapping in pigeonpea

The earliest DNA markers for pigeonpea included restriction fragment length polymorphism (RFLP), random amplified

polymorphic DNA (RAPD), AFLP and inter-simple sequence repeats (ISSR). Nadimpalli *et al.* (1993) performed a phylogenetic analysis of 24 accessions representing 12 species by RFLP and showed that pigeonpea cultivars were most closely related to *C. cajanifolius*. RFLP analysis of mitochondrial and chloroplast DNA was used to study species relationships in pigeonpea (Sivaramakrishnan *et al.*, 1997, 2002; Lakshmi *et al.*, 2000). RAPD and AFLP markers were used for diversity analysis and species relationships among pigeonpea cultivars and wild taxa (Ratnaparkhe *et al.*, 1995; Lohithaswa *et al.*, 2003; Panguluri *et al.*, 2006; Aruna *et al.*, 2009; Malviya and Yadav, 2010; Wasike *et al.*, 2020). Genetic diversity was also analysed using ISSR markers among 34 genotypes of 12 *Cajanus* species (Sahu *et al.*, 2016). Burns *et al.* (2001) were the first to develop simple sequence repeat (SSR) markers for pigeonpea by sequencing of SSR-containing genomic clones and used 10 SSR markers to study polymorphism among cultivars. Genomic survey sequence was used to develop 20 SSR markers for analysing pigeonpea cultivars and wild species (Odeny *et al.*, 2007). Another set of 16 SSR markers were developed from SSR-enriched genomic libraries, and used for fingerprinting of 32 cultivars and eight wild species (R. K. Saxena *et al.*, 2010). These SSR markers were also used for diversity analysis by other researchers (S. Singh *et al.*, 2008; Songok *et al.*, 2010; Upadhyaya *et al.*, 2011). Diversity arrays technology (DArT) was used in genotyping of thousands of polymorphic loci for diversity analysis and linkage mapping in pigeonpea (S. Yang *et al.*, 2006; S. Y. Yang *et al.*, 2011; Yohane *et al.*, 2022). Large-scale SSR markers for pigeonpea were developed by deep transcriptome sequencing by Dutta *et al.* (2011). They assembled 43 324 transcriptome shotgun assembly (TSA) contigs from two separate pools of cDNAs from pigeonpea varieties Asha and UPAS 120, designed 2877 genic-SSR markers and validated 550 of these for amplification. These were used to evaluate genetic relationship among cultivars and wild *Cajanus* species (Dutta *et al.*, 2011; Sarkar *et al.*, 2017). Genomic SSR markers were developed from 88 860 BAC-end sequences, and 842 polymorphic loci were identified (Bohra *et al.*, 2011). Genomic-SSR markers were also developed from the NIPB-draft of pigeonpea genome (N. K. Singh *et al.*, 2012). A search for class I (Temnykh *et al.*, 2001) and hypervariable (H. Singh *et al.*, 2010) SSRs led to design and validation of 370 highly polymorphic HASSR markers (Dutta *et al.*, 2013).

The results of 20 different QTL mapping studies in pigeonpea are compiled in Table 2. Numbering of linkage group (LG)/chromosome (Chr) in these studies is not uniform, and therefore we harmonized it by placing all the markers identified in these studies to their corresponding physical map position in the 11 chromosomes of 750 Mbp T2T reference genome assembly, where chromosomes are numbered according to their decreasing physical size as per the norm (NCBI Ac. No. GCA_000230855.3). A total of 68 QTLs including redundant intervals have been mapped for 20 traits, of which 10 QTL are validated in multiple studies and hence are suitable for MAS (Table 2). A genome wide association study (GWAS) of 94 pigeonpea genotypes using 6144 DArT and 768 single nucleotide polymorphism (SNP) markers showed association of determinate growth habit with 19 SNP and 6 DArT markers (Mir *et al.*, 2013). A follow-up study with candidate genes in 142 varieties, bi-parental QTL mapping, and expression profiling revealed association of determinacy with *CcTFL1* gene on LG9 (Chr6) (Mir *et al.*, 2014). The role of *CcTFL1* gene in determinacy has been validated and a 10 bp indel marker has been developed (R. K. Saxena *et al.*, 2017b; Mendapara *et al.*, 2023; K. Kumar *et al.*, 2025). Varshney *et al.* (2017) performed GWAS of 292 pigeonpea genotypes by whole genome resequencing to identify genomic regions associated with domestication and agronomic traits.

SNPs are the markers of choice for their high abundance, biallelic nature, and amenability to automation. Large-scale SNPs were identified by alignment of TSA contigs of pigeonpea varieties Asha (Ac. no. EZ647865-EZ683068) and UPAS 120 (Ac. no. EZ617718-EZ674864) assembled by Dutta *et al.* (2011), and multiplex assays of 768 and 1536 SNPs were developed for Illumina's GoldenGate platform. These were used in mapping two major QTL regions, each for multiple co-localized ideotype type traits including plant height (*qPH4.1*, *qPH5.1*) primary branching (*qPB41.1*, *qPB5.1*), secondary branching (*qSB5.1*), number of pods (*qPD4.1*, *qPD5.1*), flowering time, (*qFL4.1*, *qFL5.1*), and maturity time (*qMT4.1*, *qMT5.1*), of which *qPH5.1* and *qFL4.1/qMT4.1* located on Chr4 and Chr11, respectively, were validated in independent studies (Sreeshma, 2023; Kumawat *et al.*, 2012; P. G. Patil *et al.*, 2018; S. Singh *et al.*, 2020). A 48-plex GoldenGate SNP assay was used for diversity analysis of 256 pigeonpea genotypes by Roorkiwal *et al.* (2013). An interspecific linkage map of *C. cajan/C. scarabaeoides* with 910 markers was developed using KASP SNP assays (R. K. Saxena *et al.*, 2012), whereas an intraspecific linkage map of Asha/UPAS120 with 932 markers was developed by integrating SSR, GoldenGate SNP and ddRAD SNP markers (Arora *et al.*, 2017).

High-density linkage maps of pigeonpea have been developed using genotyping by sequencing (GBS) and SNP chip arrays. R. K. Saxena *et al.* (2017a, b, c) used GBS to map QTLs for SMD, FW resistance, and determinacy (Table 2). They validated one of the marker–trait associations for FW resistance on LG11 (Chr5) identified earlier by V. K. Singh *et al.* (2016) using QTL-seq which is a cost-effective technique for rapid identification of QTL and candidate genes (Sugihara *et al.*, 2022). It was used to find marker–trait associations for days to flowering on Chr7 and Chr8, and leaf shape on Chr1 (K. Kumar *et al.*, 2022; V. K. Singh *et al.*, 2022). A GWAS with 89 genotypes showed association of FW resistance with HASSR18 on Chr7 (P. G. Patil *et al.*, 2017), validating a previously mapped QTL at this position on LG2 (V. K. Singh *et al.*, 2016). Gnanesh *et al.* (2011) used 3000 SSR markers in QTL mapping for SMD resistance but with poor resolution

Table 2. Molecular mapping of 20 ideotype traits in 20 different studies identifying 68 QTL including redundant intervals.

Trait	QTL/gene	Marker interval/peak (LG/Chr)[a]	Chromosome position in T2T reference genome of cv Asha (NCBI Ac No. GCA_000230855.3)[b]	Reference, mapping population, marker system
Determinacy (DT, Det, TFL)	*CcTFl1*	*CcTFL1*–CcM0126 **(LG9)** *CcTFL1* allele-specific SNP	54 536 702 (**Chr6**)	Mir *et al.* (2014) ICPA 2029/ICPR 2447 (F_2) 142 varieties AM panel **CAPS, SSR, ARM-PCR**
	qDt1	S3_24127385–S3_21274904 (**LG3**) *CcTFL1* gene-based 10 bp indel marker	54 536 702 (**Chr6**)	R. K. Saxena *et al.* (2017b) ICP 5529 and ICP 11605 (F_2) 262 varieties validation panel **GBS-SNP**.
	CcTFL1	*CcTFL1* gene-based 10 bp indel marker (**LG3**)	54 536 702 (**Chr6**)	Mendapara *et al.* (2023) 10 cultivars and 3 species **PCR amplicon sequencing**
	qDet3.1	*CcTFL1* gene-based 10 bp indel marker (**LG3**)	54 536 702 (**Chr6**)	Kumar *et al.* (2025) ICPL 20338/Mal 3 (F_2), 146 genotype Mini core set **GBS-SNP**
Plant height (PH)	*qPH4.1* *qPH5.1*	*ASNP1310* – ASNP2099 **(LG4)** ASSR100 – ASSR206 **(LG5)** AX-165378601–AX-165373146 (**LG5**)	2 727 294 (***Chr6***)–25 865 338 (**Chr11**) 59 351 622–13 745 417 (**Chr4**) 57 284 461–60 197 279 (**Chr4**)	Kumawat *et al.* (2012) Pusa Dwarf/HDM04-1 (F_2/F_3) **SSR, GoldenGate SNPs**
Primary branches (PB)	*qPB4.1* *qPB5.1*	*ASNP1664* – ASSR295 **(LG4)** ASSR206 – ASNP242 **(LG5)**	36 659 559 (***Chr6***)–41 825 195 (**Chr11**) 13 745 417–3 042 588 (**Chr4**)	Sreeshma (2023) Pusa Dwarf/GT288 (F_2/F_3) **62k SNP chip/KASP markers**
Secondary branches (SB)	*qSB5.1*	ASSR100 – ASSR206 **(LG5)**	59 351 622–13 745 417 (**Chr4**)	
Number of pods (PD)	*qPD3.1* *qPD4.1* *qPD5.1*	ASNP64 – ASNP882 **(LG3)** ASNP2099 – *ASNP269* **(LG4)** ASSR100 – ASSR206 **(LG5)**	11 640 755–11 103 836 (**Chr1**) 25 865 338 (**Chr11**)–33 745 786 (***Chr6***) 59 351 622–13 745 417 (**Chr4**)	
Days to flowering (FL/IF/DOF/DFF)	*qFL4.1* *qFL5.1*	*ASNP1310* – ASNP2099 **(LG4)** ASSR100 – ASSR206 **(LG5)**	2 727 294 (***Chr6***)–25 865 338 (**Chr11**) 59 351 622–13 745 417 (**Chr4**)	
Days to maturity (MT/DM)	*qMT4.1* *qMT5.1* *qMT10.1*	ASNP2099 – *ASNP269* **(LG4)** ASSR100 – ASSR206 **(LG5)** ASNP2262 – ASNP2402 **(LG10)**	25 865 338 (**Chr11**)–33 745 786 (***Chr6***) 59 351 622–13 745 417 (**Chr4**) 1 829 971–1 467 343 (**Chr8**)	
FL, IF, DFF MT, DM, PB, DT	*qFL (IF/DFF)* *qMT (DM)* *qPB* *qDT*	ASSR295 (**LG4**) ASSR295 (**LG4**), ASSR390 (**LG2**) ASSR8 (**LG1**) *CcTFL1* SNP (**LG9**)	41 825 195 (**Chr11**) 41 825 195 (**Chr11**), 13 008 815 (**Chr8**) 55 130 445 (**Chr5**) 54 536 702 (**Chr6**)	Patil *et al.* (2018) 95 varieties AM panel **Genic SSR, ARM-PCR**
DOF/DFF	*qDOF/qDFF*	SNP 812678807:41 scaffold NW_017988637.1	45 402 471 (**Chr8**)	Kumar *et al.* (2022) 142 varieties AM panel **GBS-SNP**
Primary branches (PB)	*qPB3.1* *qPB5.1*	SCP-3333_576 – *CSCSP-1895_352* **(LG3)** CSCSP-14348_476 – SCP-14083_1762 (**LG5**)	51 047 634 **(Chr5)**–74 856 814 (***Chr1***) 60 445 810–51 025 653 (**Chr4**)	S. Singh *et al.* (2020) Pusa Dwarf/HDM04-1 (RIL) **62K SNP array**
Pod bearing length (PBL)	*qPBLm3.1* *qPBLp2.1* *qPBLp7.1* *qPBLp7.2*	DRDRP-209_577 – *DRDRP-159_1581* **(LG3)** SCP-11875_4471 – SCP-6166_1773 (**LG2**) SCP-6058_3471 – CSCSP-248_411 **(LG7)** SCP-3492_834 – *SCP-15353_1301* **(LG7)**	4 444 963 **(Chr9)**–42 249 995 (***Chr2***) 61 361 970–63 618 302 (**Chr5**) 8 475 289–8 409 157 (**Chr3**) 5 071 228 **(Chr3)**–65 693 221 (***Chr2***)	

(*continued*)

Table 2. Continued

Trait	QTL/gene	Marker interval/peak (LG/Chr)[a]	Chromosome position in T2T reference genome of cv Asha (NCBI Ac No. GCA_000230855.3)[b]	Reference, mapping population, marker system
	qPBLp7.3	SCP-1543_308 – SCP-15324_117 (**LG7**)	28 078 052–28 075 115 (**Chr3**)	
	qPBLp10.1	CSCSP-14172_2899–DRDRP-710_2488 (**LG10**)	17 454 486–16 677 754 (**Chr8**)	
Seeds per pod (SP)	*qSP3.1*	CSCSP-12895-48 – CSCSP-14596-3162 (**LG3**)	43 139 655–51 759 526 (**Chr6**)	
	qSP5.1		13 423 473–13 411 551(**Chr4**)	
	qSP10.1	CSCSP-15851-436 – CSCSP-6821-4504 (**LG5**)	10 872 622–76 822 822 (**Chr4**)	
		CSCSP-10917-684 – DRDRP-720-1470 (**LG10**)		
Seed wight (SW)	*qSW*	AX-123669406 (**Chr7**)	15 248 550 (**Chr5**)	Ujinwal *et al.* (2025)
Seed coat colour (SCC)	*qSCC*	AX-165370277 (**Chr2**)	43 318 633(**Chr10**)	287 varieties AM panel
		AX-165369586 (**Chr5**)	27 031 921 (**Chr1**)	**62K SNP array**
		AX-165343070 (**Chr11**)	1 101 853 (**Chr10**)	
Seed protein content (TPC)	*qTPC*	AX-165344137 (**Chr6**)	15 350 918 (**Chr10**)	
		AX-165358192 **(Chr11)**	34 341 988 (**Chr11**)	
		AX-165359399 **(Chr11)**	62 545 204 (**Chr5**)	
Phenolic content (PhC)	*qPhC*	AX-165372742 (**Chr11**)	62 754 200 (**Chr4**)	
		AX-165378002 (**Chr2**)	6 128 630 (**Chr9**)	
Cleistogamy (CL)	*qCl3.2*	Affx-123306383 – *Affx-123348752* **(LG3)**	13 326 037 (**Chr11**)–11 585 329 (***Chr6***)	P. Yadav *et al.* (2019) ICPL99010/CP 5529 (RIL)
Seed size (SS)	*qSS6.1*	Affx-123348721– Affx-123312002 (**LG6**)	39 686 812–18 400 594 (**Chr11**)	**56K SNP array**
FL leaf shape (LS)	*CcLG03 CcLG08*	9 SNPs 19.22–20.74 Mb **(LG3)**	58 649 524 (**Chr7**)	V. K. Singh *et al.* (2022)
		201 SNPs 6.69–8.88 Mb **(LG8)**	67 556 870 (**Chr1**)	ICP 5529/ICP 11605 (F_2) **GBS-SNP QTL-seq**
Fertility restorer A4 CMS	*qRf8.1*	S8_6388803 – S8_647438 (**LG8**)	16 153 030–16 066 708 (**Chr1**)	K. B. Saxena *et al.* (2018b) and R. K. Saxena *et al.* (2018a) ICPA2039/ICPL87119 (F_2) **GBS-SNP**
	qRf8.1	Affx-123357076 – Affx-123360361 **(LG8)**	12 762 522–12 190 242 (**Chr1**)	R. K. Saxena *et al.* (2020b) ICPA 2039/ICPL 87119 (F_2) **56K SNP array**
FW resistance	*qFW*	HASSR18 (**LG1**)	52 908 628 (**Chr7**)	Patil *et al.* (2017) 89 Genotypes (MTA panel) **SSR (HASSR)**
	qFW6.1	S6_22726005 – S6_23553522 (**LG6**)	15 025 885–45 543 841 (**Chr2**)	R. K. Saxena *et al.* (2017c)
	qFW11.1	S11_37262913 – S11_37133265 **(LG11)**	51 985 491–51 856 875 (**Chr6**)	ICPB 2049/ICPL99050 (RIL)
	qFW11.2	S11_20607023 – S11_16809228 **(LG11)**	62 725 054–54 248 502 (**Chr5**)	ICPL20096/ICPL 332 (RIL)
	qFW7.1	S7_6202998 – S7_4645510 **(LG7)**	42 729 963–37 062 591 (**Chr6**)	ICP8863/ICPL 87119 (F_2)
	qFW11.4	S11_7119684 – S11_10698013 **(LG11)**	63 805 954–50 159 536 (**Chr2**)	**GBS-SNP**
	C.cajan_0707	nsSNP 27 426 866 (**LG2**)	46 103 158 (**Chr7**)	V. K. Singh *et al.* (2016)
	C.cajan_07124	nsSNP 27 861 114 (**LG2**)	46 545 311 (**Chr7**)	ICPL 20096/ICPL 332 (RIL)
	C.cajan_02962	nsSNP 32 606 065 (**LG11**)	55 074 853 (**Chr5**)	11 varieties (MTA panel)
	C. cajan_03203	nsSNP 35 228 097 (**LG11**)	43 353 151 (**Chr5**)	**GBS-SNP, QTL-seq**
SMD resistance	*C.cajan_0707*	nsSNP 27 324 239 (**LG2**)	45 328 296 (**Chr7**)	
	C.cajan_07124	nsSNP 27 324 261 (**LG2**)	45 328 274 (**Chr7**)	
	C.cajan_02962	nsSNP 2 014 125 (**LG8**)	1 366 472 (**Chr8**)	
	C. cajan_03203	nsSNP 19 958 128 (**LG11**)	61 524 227 (**Chr5**)	
	qSMD11.1	S11_30004779 – S11_36027138 **(LG11)**	80 268 354–38 155 699 (**Chr3**)	R. K. Saxena *et al.* (2017a)
	qSMD3.1	S3_18837756 – S3_5324938 **(LG3)**	60 945 848–6 989 375 (**Chr6**)	ICPL20096/ICPL 332 (RIL)
	qSMD7.1	S7_14725598 – S7_7547477 **(LG7)**	4 865 846–29 596 731 (**Chr4**)	ICPL 20097/ICP 8863 (RIL)
	qSMD11.3	S11_16365686 – S11_5757417 **(LG11)**	16 434 210–52 164 031 (**Chr8**)	

(*continued*)

Table 2. Continued

Trait	QTL/gene	Marker interval/peak (LG/Chr)[a]	Chromosome position in T2T reference genome of cv Asha (NCBI Ac No. GCA_000230855.3)[b]	Reference, mapping population, marker system
				ICP8863/ICPL 87119 (F_2) **GBS-SNP**
	qSMD1	CcM1982 – CcM1447 **(LG9)**	87 030 515–42 606 123 (**Chr1**)	Gnanesh *et al.*, 2011
	qSMD2	CcM0588 – CcM2781 **(LG9)**	90 350 547–60 405 730 (**Chr1**)	ICP 8863/ICPL 20097 (F_2)
	qSMD3	CcM2149 – CcM0468 **(LG2)**	1 866 442–67 807 260 (**Chr5**)	TTB 7/ICP 7035 (F_2)
	qSMD4	CcM1825 – CcM1895 **(LG7)**	55 497 401–27 497 664 (**Chr8**)	**SSR-SNP**
	qSMD5	CcM0970 – CcM2485 **(LG1)**	18 818 732–14 063 805 (**Chr2**)	
	qSMD6	CcM0416 – *CcM2337* **(LG3)**	3 324 255 (**Chr01**)–31 407 570 (***Chr11***)	
	smdCc04	*Ccsmd04* gene-based 21 bp indel, and KASP markers snpCC00149, snpCC00150 (**Chr4**)	28,689,495 (**Chr2**)	Rangari *et al.* (2025) ICP8863/ICPL87119 (RIL) **GBS-Indel, QTL-seq, KASP**

[a]LG/Chr numbers in different studies are not uniform. [b]Chromosome number and position harmonized by BLAST search of the marker sequences in the T2T reference genome assembly of pigeonpea cv. Asha. Validated QTLs are shown underlined; conflicting QTL Chr flanking markers are shown in italic. ARM, amplification-refractory mutation system PCR; CAPS, cleaved amplified polymorphic sequence; CMS, cytoplasmic male sterility; Chr, chromosome; Det, determinacy; DFF, days to 50% flowering; DM, days to maturity; DOF, days of flowering; DT, determinacy; FL, flowering time; FW, Fusarium wilt; GBS, Genotyping by sequencing; IF, initiation of flowering; KASP, kompetitive allele specific PCR; LG, linkage group; MTA, marker–trait association; MT, maturity time; PB, number of primary branches; QTL, quantitative trait locus; SMD, sterility mosaic disease; SNP, single nucleotide polymorphism; SSR, simple sequence repeat; TFL, terminal flower.

due to low polymorphism. R. K. Saxena *et al.* (2017a) validated one of these QTLs on LG2/LG11 (Chr8). Rangari *et al.* (2025) mapped a major QTL for SMD resistance on Chr2 using QTL-seq in a recombinant inbred line (RIL) population of Maruti/Asha and validated a *Ccsmd04* gene-based marker using resistant and susceptible cultivars (Table 2). R. K. Saxena *et al.* (2018a) mapped *qRf8.1* for A4-CMS fertility restoration on LG8 (Chr1) and validated PCR-based markers. They developed a 56 K genomic-SNP array and used it for fine mapping of *qRf8.1* to a 410 kbp region (R. K. Saxena *et al.*, 2018b, 2020b), and mapping QTLs for cleistogamy and seed size (P. Yadav *et al.*, 2019). A 62K genic-SNP array was developed by re-sequencing of 45 diverse pigeonpea varieties. It comprises 62 053 SNPs in 9629 genes, allows gene haplotype analysis due to multiple SNPs per gene, and was used in QTL mapping for yield-related traits in a RIL population and GWAS for seed quality traits in 287 varieties (S. Singh *et al.*, 2020; Ujinwal *et al.*, 2025).

There is a need to accelerate pigeonpea breeding by integration of MAS using the available donor lines and markers for ideotype traits (Fig. 6). The genetic and genomic resources described here will help identify and validate genes/QTLs for the remaining traits. Though significant progress has been made in finding marker–trait associations, there is a dearth of validated markers for use in breeding. There are no reports of doubled haploids in pigeonpea for rapid development of pure lines, but speed breeding platforms are available. Multiparent advanced generation inter-cross (MAGIC) and nested association mapping (NAM) populations have been developed, but are yet to be utilized for trait mapping or breeding (Cavanagh *et al.*, 2008; R. K. Saxena *et al.*, 2020a; Joshi *et al.*, 2022b). These populations have the advantage of enhancing allele frequencies, which is a major issue in GWAS for quantitative traits (McMullen *et al.*, 2009). Multiparent populations provide an accurate means of tagging traits, and lines combining superior alleles can be released directly as commercial cultivars.

Marker-assisted breeding and genetic engineering in pigeonpea

Marker-assisted backcross breeding (MABB) has been deployed for accelerated introgression of climate-resilience, nutritional quality, and biotic stress resistance in the genetic background of elite cultivars of rice, maize, and other crops (R. Singh *et al.*, 2016; S. L. Krishnamurthy *et al.*, 2020; J. Singh *et al.*, 2021; Saminadane *et al.*, 2024). However, there are no examples of MAS-derived varieties in pigeonpea despite significant progress in genome sequencing, genotyping assays, and QTL mapping of important agronomic traits (Table 2). This is partly due to paucity of validated markers, elite high-yielding recipient cultivars, and long crop duration. Genomic selection based on genomic-estimated breeding values (GEBVs) of markers is becoming feasible in crop breeding and may help in designing new pigeonpea varieties with cost-effective genome profiling (Y. Zhao *et al.*, 2015; Crossa *et al.*, 2017). It has already shown moderate to high accuracies in

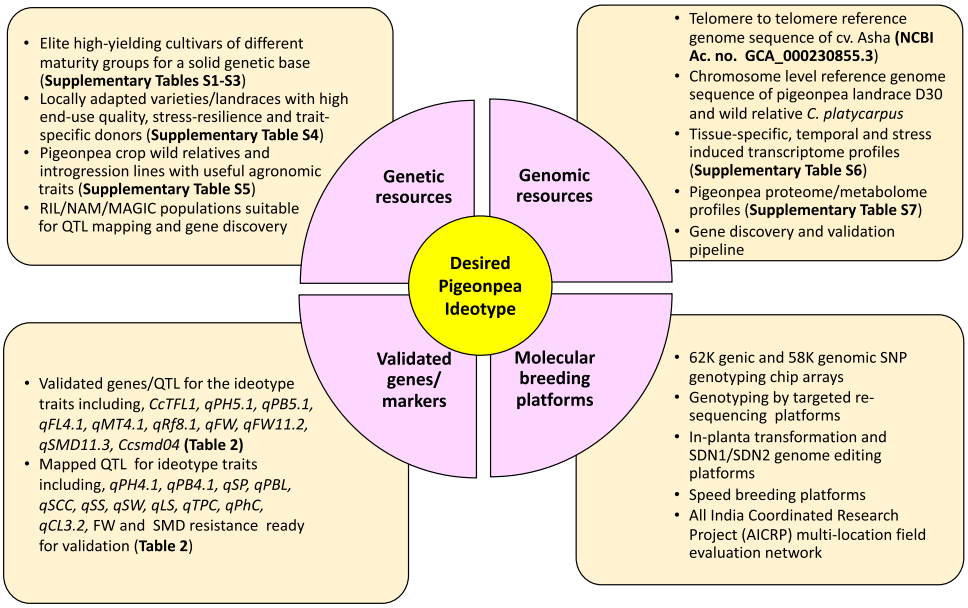

Fig. 6. A summary diagram of the available genetic and genomic resources for pigeonpea ideotype breeding. MAGIC, multiparent advanced generation inter-cross; NAM, nested association mapping; QTL, quantitative trait locus; RIL, recombinant inbred line; SDN, site-directed nuclease.

prediction of traits in maize, soybean, and chickpea (Jarquín *et al.*, 2014; Duhnen *et al.*, 2017; Li *et al.*, 2018; Barreto *et al.*, 2024). Genetic modification of pigeonpea for pod borer resistance using *cry1Ab*, *cry1Ac*, *cry1AcF*, and *cry2Aa* genes (K. K. Sharma *et al.*, 2006; Kaur *et al.*, 2016; Ghosh *et al.*, 2017; S. Singh *et al.*, 2018; Ramkumar *et al.*, 2020) and FW resistance using rice chitinase gene (S. M. Kumar *et al.*, 2004) has been achieved. Bt-pigeonpea lines with validated Bt-genes *cry2Aa* and *cry1AcF* are presently undergoing biosafety evaluation through contained open field trials (Ramkumar *et al.*, 2020). P. Mishra *et al.* (2017) did comparative evaluation of pigeonpea transgenic lines with *cry2Aa* and *cry1AcF* genes and found no significant difference in nutritional composition analyses. Proteome analysis of GM and non-GM seed proteins showed no significant changes in protein profiles, although minor changes in the expression of a few proteins were observed. CRISPR–Cas9 based genome editing is an exciting new breeding tool for developing non-GM varieties with desired agronomic and nutritional quality traits, and has already been deployed successfully in other crop plants (Nagamine and Ezura, 2022). Furthermore, India has granted exemption from GMO-like stringent bio-safety regulation for the genome-edited plants of SDN1 and SDN2 categories (https://dbtindia.gov.in/sites/default/files/SOPs%20on%20Genome%20Edited%20Plants_0.pdf). ICAR has initiated a large network project on genome editing for genetic improvement of crops, including pigeonpea. Meanwhile, MAS has great potential for accelerating the ideotype breeding in pigeonpea with the available genetic and genomic resources.

Conclusion

Pigeonpea has a rich germplasm collection from which trait donor lines have been identified and used in conventional breeding. Genes and QTLs for plant ideotype traits have been mapped using DNA markers but the utilization of these markers in accelerating varietal development to meet the needs of stakeholders is yet to materialize. Several factors contribute to this: (i) complex genetics of the desired traits including yield, quality, and stress resistance, (ii) limited validation of the identified markers, (iii) long generation time for testing and deployment of the MAS products, (iv) poor funding and research attention to pigeonpea. However, there is optimism for the future of MAS in pigeonpea, thanks to the advances in genomics and new breeding technologies such as MABB, GS, and genome editing (GEd). The T2T reference genome assembly of cv. Asha provides a robust platform for identifying high-confidence genes and markers. While MAS is not yet a practical reality in pigeonpea, the groundwork laid by mapping studies positions it for future breakthroughs. The following actions are needed for gene discovery, marker development, and utilization in pigeonpea breeding: (i) re-orientation of the breeding programme to meet the needs and requirements of stakeholders, (ii) conservation and utilization of landraces and wild *Cajanus* spp. with superior adaptive traits for climate-resilience and ideotype breeding, (iii) identification of genes underlying useful agronomic traits in the crossable gene pool, (iv) pigeonpea pangenome and high throughput genotyping/phenotyping platforms to facilitate next generation breeding, (v) enrichment of pigeonpea proteome and

metabolome database for understanding the underlying mechanisms of agronomic and quality traits, (vi) GEd for knocking out/in the regulators of useful traits using SDN1 and allele replacement using SDN2, since these are exempt from the GM-like stringent regulation, and (vii) a database of the genetic and genomic resources, including a catalogue of validated genes and markers to facilitate information access for research, innovation, and utilization. GEd could be used in future for direct replacement of the alleles of interest, bypassing the limitations of MAS, such as insufficient recurrent parent genome recovery, residual heterozygosity, and negative linkage drag. This review will help in devising strategies for accelerating molecular breeding of pigeonpea ideotype.

Supplementary data

The following supplementary data are available at *JXB* online.

Table S1. Short duration pigeonpea varieties released in India

Table S2. Medium duration pigeonpea varieties released in India

Table S3. Long duration pigeonpea varieties released in India

Table S4. Trait donor varieties and landraces of pigeonpea

Table S5. Trait donor wild related species of pigeonpea

Table S6. Transcriptome profiling of pigeonpea and wild related species

Table S7. Proteome profiling of pigeonpea and its wild relatives

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Author contributions

AS and NKS conceived and wrote the manuscript; others contributed to different sections as follows: MR: physical position of markers on the T2T reference genome and species geographical distribution figure; PM and VR: proteome profiling; KG: transcriptomics; RJ: DNA markers; IPS, KD, and RSR: conventional breeding; AS: stakeholder preference. All authors reviewed and accepted the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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Data availability

The NIPB_CcT2T_4 Telomere-to-telomere reference genome assembly of pigeonpea cv. Asha has been published at the NCBI genome database under BioProject No. PRJNA68667, GenBank Ac. No. GCA_000230855.3.

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