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REVIEW ARTICLE

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Pigeonpea improvement: An amalgam of breeding and genomic research

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Abstract

In the past five decades, constant research has been directed towards yield improvement in pigeonpea resulting in the deployment of several commercially acceptable cultivars in India. Though, the genesis of hybrid technology, the biggest breakthrough, enigma of stagnant productivity still remains unsolved. To sort this productivity disparity, genomic research along with conventional breeding was successfully initiated at ICRISAT. It endowed ample genomic resource providing insight in the pigeonpea genome combating production constraints in a precise and speedy manner. The availability of the draft genome sequence with a large-scale marker resource, oriented the research towards trait mapping for flowering time, determinacy, fertility restoration, yield attributing traits and photo-insensitivity. Defined core and mini-core collection, still eased the pigeonpea breeding being accessible for existing genetic diversity and developing stress resistance. Modern genomic tools like next-generation sequencing, genome-wide selection helping in the appraisal of selection efficiency is leading towards next-generation breeding, an awaited milestone in pigeonpea genetic enhancement. This paper emphasizes the ongoing genetic improvement in pigeonpea with an amalgam of conventional breeding as well as genomic research.

KEYWORDS

determinacy, genome sequence, hybrid technology, mini-core collection, photo-insensitivity, pigeonpea, trait mapping

1 | INTRODUCTION

The neglected crop of previous years, to core commercial crop of today, pigeonpea (*Cajanus cajan* [L.] Millspaugh) is a multipurpose food legume, serving as a lifeline to resource-poor farmers in tropical and subtropical regions of Asia, Africa, and Latin America. Globally, pigeonpea is cultivated in an area of 6.97 mha with a production and yield of 5.05 mt and 724 kg/ha, respectively (FAO STAT, 2016). The complexity of yield enhancement in pigeonpea has lessened the scope of breeding high-yielding cultivars. However, the cytoplasmic male-sterile system has evolved as a game changer in breaking the yield plateau by exploiting potential "Heterosis". Along with hybrid breeding, efforts of restructuring the plant type by emphasizing on short duration, determinant, photo and thermo insensitive lines aided in introducing the crop to newer niches. Genomic intervention in the past gave an insight of structural and functional aspects of pigeonpea genome complementing the conventional breeding. Availability of the draft genome sequence and enormous molecular markers helped in locating quantitative trait loci (QTLs) in a speedy manner. The recent development of modern genomic tools comprising of next-generation sequencing technologies, genomic selections, genome-assisted breeding has opened new avenues in pigeonpea breeding. In this review, efforts have been made to throw an insight on the status of pigeonpea breeding accosting parallel conventional and genomic research.

2 | ASCENDANTS OF CULTIVATED PIGEONPEA

Todays cultivated form, *C. cajan* has evolved from an inter-specific hybridization event between *Cajanus scarabaeoides* and *Cajanus cajanifolius* (Pundir and Singh, 1985). The whole genome re-sequencing studies also confirm the close relationships between *C. cajanifolius* and cultivated pigeonpea (Saxena et al., 2014; Varshney, Saxena, & Jackson, 2017; Varshney, Saxena, Upadhaya, et al., 2017). The genus *Cajanus* comprises of 32 species and belongs to the subtribe *Cajaninae* (Bohra et al., 2010; Pazhamala et al., 2015; Van der Maesen, 1990), of which only *C. cajan* is the domesticated species (Bohra et al., 2010; Pazhamala et al., 2015; Rao, Phillips, Mayeux, & Phatak, 2003). *Cajanus cajan* occupies the primary gene pool, whereas the wild progenitors are placed in the secondary and the tertiary gene pool based on their cross-compatibility with the cultivated species (Bohra et al., 2010; Pazhamala et al., 2015).

3 | GENETIC RESOURCES: CORE AND MINI-CORE COLLECTION

Pigeonpea germplasm resource comprises of 13,771 accessions deposited at the ICRISAT genebank, India (Gowda, Upadhyaya, Sharma, Varshney, & Dwivedi, 2013; Pazhamala et al., 2015), 11,221 accessions collected at National Bureau of Plant Genetic Resources (NBPGR), India (Pazhamala et al., 2015; Singh et al., 2014), 4,116 accessions at U.S. Department of Agriculture (USDA), USA, 1,288 accessions at Kenya Agricultural Research Institute's National Genebank of Kenya (KARI-NGBK), Kenya (Singh, Tyagi, & Pandey, 2013; Pazhamala et al.,2015) and 433 accessions at National Plant Genetic Resources Laboratory, Philippines (Upadhyaya et al.,2016).

Unfortunately, in spite of the rich germplasm reserve, its utilization in pigeonpea improvement is very limited and remained unexplored (Majumder & Singh, 2005; Pazhamala et al., 2015). To accost these issues, ICRISAT has defined a representative sub-sets of pigeonpea germplasm in the form of core collection comprised of 1,290 accessions, mini-core collection of 146 accessions (Gowda et al., 2013; Pazhamala et al., 2015) and genotype-based reference set (Upadhyaya, Reddy, Gowda, Reddy, & Singh, 2006; Upadhyaya et al., 2016). These collections represent more than 80% of the diversity existing in the entire germplasm collection and are ideal resources for studying genetic diversity, population structure and association mapping (Reddy, Upadhyaya, Gowda, & Singh, 2005; Upadhyaya et al., 2006; Gowda et al., 2013; Pazhamala et al., 2015). Extensive multidisciplinary evaluation of core /mini-core collection at ICRISAT has led to the identification of promising accessions for sterility mosaic disease (24), wilt (6), wilt + SMD (5), pod borer (10), salinity (16), water logging (23), high yield (54), high zinc (15) and iron (15) content, whereas NARS identified trait-specific germplasm for early maturity (8), high seed yield (2), wilt (39), SMD + wilt (24) from mini-core collection (Upadhyaya et al., 2016). The ICRISAT genebank has maintained 555 accessions representing 67 wild species from six genera (Upadhyaya et al., 2011). Thus, wealth from the wild has been extensively utilized by the researchers to develop need based varieties and hybrids in pigeonpea (Kumar, Priyanka, Lall, & Lal, 2011; Sharma, Upadhyaya, Varshney, & Gowda, 2013; Upadhyaya et al., 2013; : Pazhamala et al., 2015).

4 | CURRENT LIMITATIONS

Breeding in pigeonpea has always been the biggest bet for breeders. The inherent crop specific constraints are detailed below:

4.1 | Lack of genetic diversity

The polymorphic survey of sampled *Cajanus* accessions indicated the lack of genetic diversity within the primary gene pool. This has left no option for breeders, rather than utilizing the wild relatives from secondary, tertiary and quaternary gene pools using appropriate gene transfer techniques. Despite the high genetic diversity in the wild relatives, its use has been limited as no proper information on the presence of useful traits is easily available and an extended period of research is needed whenever utilized (Goodman, 1990). The combination of poor agronomic traits, incomplete characterization and limited collections (Saxena et al., 2014) adds on to the lagging genetic enhancement with the intervention of wild relatives.

4.2 | Photosensitivity

Pigeonpea requires shorter days and long hours of darkness for flower induction (Silim, Coe, Omanga, & Gwata, 2006; Vales et al., 2012). Interaction of day and night temperature with prevailing photoperiod has a pivotal role in flower induction. This restricts pigeonpea adoption beyond 30°northern and southern latitudes (Saxena, 2008). Wallis, Byth, and Saxena (1981) showed an inverse correlation between earliness and photosensitivity whereas Saxena (1981) confirmed no possibility of breeding late maturing photo-insensitive cultivars in pigeonpea. Both photoperiod and low-temperature sensitivity (Turnbull, Whiteman, & Byth, 1981) has limited the expansion of pigeonpea across higher altitudes and latitudes, narrowing its use in alternative cropping system (Vales et al., 2012).

4.3 | Linkage drag

A tight association between desirable traits with undesirable plant/seed characters often comes in the way of transferring the target genes into cultivated types. For instance, transferring the high protein genes from *C. scarabaeoides* and *Cajanus albicans* to the cultivated type took 12–14 generations for selecting a high protein, productive phenology and high yield (Saxena & Sawargaonkar, 2016).

4.4 | Lack of funds

Lack of systematic public and minimal or no industrial funding support to pigeonpea research and development is the major reason for the sluggish development of varieties with the limited genetic gains in past. The principal founder of Microsoft Corporation, Mr. Bill Gates also highlighted on funding and support of private sector for research and development in pigeonpea during his visit to ICRISAT (Varshney, Saxena, Upadhaya, et al., 2017; Varshney, Saxena, & Jackson, 2017).

5 | RECENT BREEDING APPROACHES

5.1 | Stress resistance

5.1.1 | Disease resistance

The major diseases in pigeonpea are fusarium wilt, sterility mosaic and phytophthora blight. Fusarium wilt resistance is governed by a single dominant gene (Pawar & Mayee, 1986) and accounts for yield loss ranging from 30%–100%. ICP 8863 (Maruti), the first released wilt resistant variety and ICPL 87119 (Asha), till today, are widely cultivated for wilt resistance in India. Recently, ICRISAT identified ICPL 20109, ICPL 20096, ICPL 20115, ICPL 20116, ICPL 20102 and ICPL 20094 as resistant genotypes (Sharma et al., 2016) after an extensive screening of 976 breeding as well as germplasm lines in wilt-sick plots. On contrary to conventional breeding, Saxena, Kale, et al. (2017) identified 3 QTLs qFW11.1,qFW11.2 and qFW11.3 for FW resistance by using a genotyping-by-sequencing approach from 3 RIL population (PRIL B, PRIL C, and F_2 Population), respectively. Phenotyping of hundreds of lines in wilt-sick plots across various location yielded in two RAPD markers (Kotresh et al., 2006), four SCAR markers (Prasanthi, Reddy, Rekha Rani, & Naidu, 2009) and six SSR markers (Singh et al., 2013; : Pazhamala et al., 2015) for FW resistance.

Fusarium wilt is one of the major diseases, inflicting pigeonpea productivity in Eastern and Southern Africa (ESA) too. The virulence pattern existing in ESA is entirely different from that of Asia. The germplasm/cultivars from ESA are offering greater resistance to fusarium wilt. After years of screening for wilt resistance in ESA at wilt-sick plots in Kenya, Malawi and Tanzania a number of germplasm lines were identified with FW resistance.

Sterility mosaic disease (SMD) is caused by *Pigeonpea sterility mosaic virus* (PPSMV), transmitted by a mite (*Aceria cajani*) owing to 100% crop yield loss if infested severely. Four independent loci, two duplicate dominant genes (Sv_1 and Sv_2) and two duplicate recessive genes (sv_3 and sv_4) are responsible for the inheritance of resistance for sterility mosaic disease (Saxena, 2008). SMD is expressed only when one dominant allele at locus 1 or 2 and homozygous recessive genes at locus 3 or 4 are present (Saxena, 2008). Although, the application of sprays in order to control mite populations can limit the spread of the disease, identification, and introgression of genomic segments attributing disease resistance through genomics-assisted breeding (GAB) programme would be an important strategy for the development of disease-resistant pigeonpea varieties (Saxena, Kale, et al., 2017). Genotyping-by-sequencing approach was used for simultaneous identification and genotyping of SNPs, and the candidate genomic region identified on CcLG11 was the promising QTL for molecular breeding in developing superior lines with enhanced resistance to SMD (Saxena, Kale, et al., 2017). Six QTLs explaining phenotypic variation were identified on LG7 and LG9 after extensive phenotyping for SMD resistance (Gnanesh et al., 2011).

Phytophthora drechsleri f.sp. *cajani* is a soil-borne fungus which survives as dormant mycelium in soil and infected plant debris. It is controlled by a single dominant gene Pd1 (Saxena, 2008). Phytophthora blight of pigeonpea is sporadic in nature, but occasionally assumes epidemic proportions in places of heavy and frequent rainfall. High incidence is usually associated with poor surface drainage (Bisht, Kannaiyan, & Nene, 1988). Pal, Gerewal, and Sarbhoy (1970) estimated yield losses due to phytophthora blight to be 98% since the affected plants dry up rapidly. Several screening methods have been developed, but screening in sick plots emerged as the best accounting for large-scale screening of germplasm (Singh & Chauhan, 1992). *Cajanus platycarpus* and *Cajanus sericeus* found to be resistant to P2 isolate but found susceptible to P3 isolate (Reddy, Sarkar, Nene, & Raju, 1991). BDN 627, Sehore 1971, ICPL 1871, ICPL 84052, ICPL 84023 and ICPL 88009 emerged as resistant lines after an extensive screening of 258 genotypes (Gupta, Singh, Reddy, & Bajpai, 1997). Recently at ICRISAT, ICP 11376-5, ICP 12730, ICP 12751, ICP 12755, ICPL 20093, ICPL 20100, ICPL 20101, ICPL 20104, ICPL 20105, ICPL 20109 were identified as resistant lines

for phytophthora (Pande, Sharma, Mangla, Ghosh, & Sundaresan, 2012). Gupta et al. (1997) reported the monogenic dominant nature of resistance and the involvement of minor genes in the resistance against phytophthora. Genomic intervention to identify the resistant gene and associated marker for phytophthora blight has been initiated at ICRISAT.

5.1.2 | Insect resistance

Helicoverpa armigera is the most devastating pest of pigeonpea for ages. Hence developing a resistant source for this pest is an ideal seed borne solution to enhance its productivity. However, the resistant source of Helicoverpa is not available among the cultivated species. Gene pyramiding with two different insecticidal genes and tissue-specific expression to reduce the risk of developing insect resistance is another attractive option to combat this pest for durable resistance. Expression of a chimeric cry1AcF (encoding cry1Ac and cry1F domains) gene in transgenic pigeonpea has been demonstrated towards resistance to *H. armigera* (Ramu et al., 2012). Apart from this, an advanced generation population from the cross utilizing "*Cajanus acutifolius*" a wild relative from the secondary gene pool as the pollen parent has shown considerable resistance for pod borer damage (Jadhav, Mallikarjuna, Sharma, & Saxena, 2012; Mallikarjuna, Sharma, & Upadhyaya, 1997).

The bruchid (*Callosobruchus maculatus* F.) resistance is another important trait for pigeonpea seeds under storage as resistance to pest has not been observed in cultivated pigeonpea. F_1 hybrids developed from the cross involving *Cajanus lanceolatus* showed delayed bruchid lifecycle owing to the antibiosis mechanism of resistance to bruchids (Mallikarjuna, Saxena, Byre Gowda, & Varshney, 2017; Srikanth, Marri, Kollipara, Rao, & Mallikarjuna, 2017).

Pod trichomes too play a pivotal role in the plant defence system. The orientation, density, type and length of wild pigeonpea species were dominant over trichome characteristics of the released cultivars (Aruna, Manohar Rao, Reddy, Upadhyaya, & Sharma, 2005).

5.1.3 | Terminal drought tolerance

Though efforts are made to understand the mechanism of drought tolerance in pigeonpea, the influence of seasonal variation on occurrence and intensity of drought has not yet been clearly defined (Saxena, Hingane, Choudhary, & Bharathi, 2015). The severe moisture stress not only limits the productivity but also restricts the symbiotic N fixation in pigeonpea (Kumar et al., 2014). Apart from yield and yield-related traits, physiological parameters like leaf area, dehydration tolerance, relative water content and osmotic adjustments too play a vital role in combating drought stress. Hence, while breeding for drought resistance in pigeonpea, agronomic traits such as pods/plant, seeds/pod, seed size, seed yield/plant (Choudary, Sultana, Pratap, Nadarajan, & Jha, 2011) coupled with the deep root system are primely focused.

In tune with conventional breeding, Sinha et al. (2016) identified candidate drought tolerant genes from the available genomic resources. The expression analysis of 51 drought-responsive genes has provided a set of 10 genes that belong to U-box proteins, Cation / H (+) antiporter proteins, uncharacterized proteins and universal stress proteins A-(uspA) like protein. The identified genes pave way for understanding the molecular mechanism involved in drought tolerance (Sinha et al., 2016). Varshney et al. (2012) identified 111 proteins which were homologous to drought-responsive universal stress proteins (Pazhamala et al., 2015). CcCYP is the candidate gene identified for drought stress coupled with salinity (Sekhar, Priyanka, Reddy, & Rao, 2010; Pazhamala et al., 2015).

5.1.4 | Water logging

ICRISAT has developed an excellent screening technology for water-logging tolerance and identified a number of genotypes which exhibit high levels of tolerance to the extended periods of water logging (Sultana et al., 2012). Among the tolerant genotypes ICPB 2043, ICPB 2039 and ICPB 2047 are known male-sterility maintainers and ICPL 87119, ICPL 149 and ICPL 20125 are known fertility restorers. This has made breeder's job easy. However, before using the tolerant lines in a hybrid breeding programme, their assessment for other agronomic traits is essential. Since the resistance to water logging is governed by a single dominant gene (Perera, Pooni, & Saxena, 2001; Sarode, Singh, & Singh, 2007) its incorporation in the productive A/B lines will be resource efficient and allows the development of water-logging hybrids with greater frequency. Advanced generation lines developed from the cross employing *C. acutifolius* when screened under the water-logging condition reported the formation of lenticels in the region above the water surface. This special character increases the survival rate of pigeonpea lines prone to water logging (Hingane et al., 2015; Mallikarjuna et al., 2017).

5.1.5 | Salinity

Soil salinity hampers the growth and development of crop due to the accumulation of salts on the soil surface, mostly under irrigated and dryland agriculture (Choudary et al., 2011). Higher NaCl /Na_2SO_4 content in the soil affect crop yield by adversely affecting physiological as well as a biochemical pathway. Salinity delays days to 50% flowering by 1–2 weeks and prolongs the peak period of flowering and reduces the number and weight of the seeds (Promila & Kumar, 2000).

The wild relatives of pigeonpea, *C. scarabaeoides*, *C. albicans* and *C. platycarpus* showed a wide range of variation in their salinity tolerance. The transfer of salinity tolerance from *C. albicans* to *C. cajan* would be feasible as the high level of salinity tolerance in this wild species is expressed as a dominant genetic trait (Choudary et al., 2011).

5.2 | Game changer: cytoplasmic male-sterility systems

Reddy and Faris (1981) were the first to make an attempt to breed a CMS line in pigeonpea using cytoplasm of a wild relative of

pigeonpea (*C. scarabaeoides*). Intensive selection and subsequent backcrossing resulted in the identification of a promising CMS line (Saxena, Rao, Singh, & Remanandan, 1996). It was believed that the interaction of wild cytoplasm with cultivated nuclear genome would produce male sterility. So far, nine such systems namely *C. sericeus* (A_1), *C. scarabaeoides* (A_2), *Cajanus volubilis* (A_3), *C. cajanifolius* (A_4), *C. cajan* (A_5), *Cajanus lineatus* (A_6), *C. platycarpus* (A_7), *Cajanus reticulatus* (A_8) and *C. lanceolatus* (A_9) have been reported in pigeonpea with varying degree of success (Singh, Saxena, & Varshney, 2017; Singh, Sameer Kumar, et al., 2017). Out of these, A_4 cytoplasm has been promising because of its stability under various agro-climate zones and availability of good maintainers and restores. The F_1 hybrids developed from this CMS produce excellent pollen load and pod set.

5.2.1 | Criteria in CMS system

The purity of parents and hybrids

The grow out test is the only way so far used to test the purity. But, the time lapse to grow out test due to the long duration of the crop is bothersome in pigeonpea. Hence, SSR base purity assessment kit has been developed for assessing the purity of the hybrids (Saxena, Ravikoti, & Sultana, 2010; Saxena, Saxena, & Varshney, 2010). Initially, a set of two simple sequence repeat (SSR) markers was identified for testing the hybridity of ICPH 2438. Subsequently, after the screening of 3072 SSR markers on the parental lines, a set of 42 diagnostic markers were identified for purity assessment of the hybrid ICPH 2671. In order to save time and costs, the set of 42 markers has been grouped into eight multiplexes. With the help of these markers, reliable detection of off-types in the commercial hybrid seed lots can now be undertaken by the public and private seed companies (Kumar, Singh, et al., 2016).

Naked Eye Polymorphism (NEP) a phenotypic marker, aiding in the identification of pure hybrid seed, has been developed at ICRISAT. Saxena, Sultana, et al. (2011) identified "obcordate leaf" as a polymorphic marker and incorporated it into A and B lines. This marker, controlled by a single recessive gene, can be easily recognized within a month from sowing. The hybrids developed by crossing the parents involving normal and obcordate leaf types will always have normal leaves and the unwanted sibs will have obcordate leaves. Such off-types can be detected within a month from sowing. This approach of hybrid breeding should be promoted to help in maintaining seed quality of female parents and hybrids.

Identification of stable restorers and maintainers

Fertility restoration in pigeonpea is governed by two dominant genes. Presence of these two dominant genes makes a hybrid fully fertile or stable across the environment. The advances made in the fields of genomics and marker-assisted plant breeding (Varshney et al., 2012) can hasten the process of transferring Fr gene into non-restorers economically. In this direction, a significant progress has been made by constructing a consensus genetic map derived from six inter-specific mapping populations, involving three mapping populations segregating for Fr genes. The consensus map comprised of 339 simple sequence repeat (SSR) loci spanning a distance of 1,059 cM. In three mapping populations, a total of four major QTLs namely QTL-RF-1, QTL-RF-2, QTL-RF-3 and QTL-RF-4 for fertility restoration were identified showing up to 24% of phenotypic variation. This consensus genetic map can be used as a reference for developing new genetic maps to facilitate marker-assisted selection to accelerate hybrid breeding (Bohra et al., 2012).

5.2.2 | CMS based hybrids

GTH1 is the world's first CMS-(A_2 cytoplasm) based hybrid developed at SDAU (Sardarkrushinagar Dantiwada Agricultural University), S K Nagar, Gujarat in 2004. But, this hybrid failed to gain its stake hold due to the problems associated with the stability of fertility restoration caused by high G x E interactions. Thus, world's first commercial pigeonpea hybrid is ICPH 2671(A_4) released in 2010 by the government of Madhya Pradesh which had 47% yield advantage over national check Maruti (Kumar, Wani, et al., 2016). Later in 2014, OUAT (Odisha University of Agriculture and Technology) released ICPH 3762(A_4) which registered 20%–67% yield advantage over local checks owing to FW and SMD resistance. In 2015, Professor Jayashankar Telangana State Agriculture University, Hyderabad released ICPH 2740 which showed a superiority of 42% over national check Asha (Kumar, Wani, et al., 2016). Highly vigorous, disease-resistant pigeonpea hybrids had led to a renaissance in pigeonpea cultivation.

5.3 | Future breeding thrust

5.3.1 | Temperature-sensitive male-sterility system

The reversion of male sterility to fertility and the vice versa has been reported in a number of crop species (Kaul, 1988). Various environmental factors such as photoperiod, temperature and specific stresses alter the expression of genes controlling male sterility/fertility. The recent success in two line breeding in hybrid rice triggered the latter in breeding a temperature-sensitive male-sterility system in pigeonpea (Saxena, 2014). Such genotypes when grown under <24°C, turn male fertile to produce self-pollinated seeds; hence, such male-sterile lines will not require any maintainer line. The same line, when grown under high (>25°C) temperature regime, will remain male sterile; and hence can be used for large-scale F_1 hybrid seed production when cross-pollinated by insects (Saxena, 2014).

5.3.2 | Earliness & photo-insensitivity

Prevailing cultivars of pigeonpea cannot fit in preceding or proceeding cropping systems due to extended duration and photo-sensitivity. Hence, photo-insensitivity coupled with earliness is the desired trait of interest for the breeders. In this regard, super-early pigeonpea with defined traits of earliness, photo-insensitivity, impressive per day productivity, stress escape mechanism, niche to fit well in

wheat–pulse cropping pattern as well as rice fallows emerged as a new intervener in pigeonpea breeding (Shruthi et al., 2017). Faster generation turn over, with faster introgression of traits eases the study on the genetics of biotic and abiotic stress by developing mapping population within the short span of time (Vales et al., 2012). Extensive test crosses and backcrosses are carried out at ICRISAT to explore the conceivable heterosis for greater and stable yield at newer niches.

5.3.3 | Plant type

The two plant types Determinate (DT) and Indeterminate (IDT) exist in pigeonpea (Mir et al., 2013). Short-statured DT types cease their growth once they reach flowering. Whereas, vigorous IDT types continue the growth even after flowering. Though IDT is a dominant trait preferred by pigeonpea growers, continuous flowering followed by non-synchronous harvesting draws the attention on DT type breeding. High initial vigour, tolerance to drought & water logging and ease in mechanical harvesting in DT type are found advantageous over IDT type. Thus, to avoid this ambiguity, Saxena, Obala, et al. (2017) studied the inheritance of IDT growth habit over DT growth habit. They used Indel-derived markers to differentiate DT/IDT lines and reported that CcTFL1 is a candidate gene for growth habit in pigeonpea. These efforts will be useful in marker-assisted backcross breeding programme and allow early generation selection efficiency in crossing programme to select both DT and IDT lines.

Mir et al. (2014) reported CcTFLI as a candidate gene for determinacy explaining 45%–60% phenotypic variation for determinacy. Whole-genome scanning approach using SNP and DArT assays has been used to unravel the mechanism of transition from indeterminate growth habit to determinate growth habit in pigeonpea (Mir et al., 2013; : Mir et al., 2014). This helps in understanding the pigeonpea domestication process. Further, faster manipulation in growth habit and flowering time will be favored in this climate-smart breeding era.

5.3.4 | Protein content

The protein content of pigeonpea, in general, varies around 20%–22%. Protein content is mainly controlled by additive genetic action (Saxena, 2008). Extension of hybrid parent research in the direction of breeding high protein A-lines can help in developing hybrids with 25%–30% yield advantage and high (26%–27%) protein content. Saxena and Sawargaonkar (2016) reported that newly bred pigeonpea lines have protein between 28%–30% and yield good as cultivars. An estimate of protein yield showed that the cultivation of high protein lines in one hectare will yield an additional 100,000 g protein for the farming families living under subsistence level.

5.3.5 | Cleistogamous flower

"Natural out-crossing" considered as a boon in hybrid breeding, is also considered as a genetic contaminant in varietal breeding. The outcrossing extent in pigeonpea is up to 25%–30% (Saxena & Sharma, 1990). To maintain the true to type especially in partially out-crossed species, it needs a lot of resources in terms of isolation distance, installation of insect-proof cages and labour charges for rouging and seed cleaning operations. In this context, a novel flower trait called cleistogamy is identified at ICRISAT. Genetic purity of a variety can be maintained through the incorporation of partial cleistogamy into desirable cultivars. Considering these facts attention was paid to a natural mutant with wrapped flower morphology or cleistogamy (Saxena et al., 1994). Cleistogamy trait is governed by a single recessive gene and very easy to transfer in the background of commercial lines. A partial cleistogamous line ICPL 87154 was developed earlier with low natural outcrossing (<1%) (Kumar, Singh, et al., 2016; Kumar, Wani, et al., 2016).

6 | GENOMIC INTERVENTION

ICRISAT in collaboration with national/international partners is leading the world in pigeonpea genomic studies. In 2012, pigonpea became the first orphan and non-industrial legume crop to have a draft genome sequence. Unraveled genomic resources are currently utilized for trait mapping and molecular breeding making pigeonpea a resource-rich legume crop. A large set of Simple Sequence Repeat markers (Bohra et al., 2011; Dutta et al., 2011; Mir, Rather, Bhat, Parray, & Varshney, 2017; Saxena, Ravikoti, & Sultana, 2010; Saxena, Saxena, & Varshney, 2010), Diversity Array Technology markers (Yang et al., 2006, 2011), Single Feature Polymorphism (Saxena, Sultana, et al. (2011); Saxena, Cui, et al. (2011)) and Single Nucleotide Polymorphism Genotyping platforms (Saxena et al., 2014; Varshney et al., 2012) have been developed for generating low,moderate and high density genetic maps in pigeonpea. These molecular markers and genetic maps provide greater opportunity to discover genes/QTLs responsible for important targeted traits leading to genetic improvement of the crop. In addition to this, association mapping, marker-based QTL mapping, candidate gene-based association mapping, transcriptomics and whole-genome sequencing has been used to identify markers and candidate genes responsible for traits like flowering time, fertility restoration Wilt and SMD resistance, determancy (Mir et al., 2013), yield as well as phenology in pigeonpea (Mir et al., 2017).

Modern genomic tools like next-generation sequencing (NGS) technology, genome-wide-genetic-markers, transcriptome/genome assemblies enabled to establish a wide range of genomic resources supporting pigeonpea breeding. Whole mitochondrial genome sequence paved new avenue for a better understanding of cytoplasmic male-sterility systems and hybrid breeding in pigeonpea. New generation mapping populations like multiparent advanced generation intercross (MAGIC) and nested association mapping (NAM) population not only ensures the best utilization of high-throughput genotyping/sequencing platforms, but also offers several advantages over conventional (biparental) mapping populations in terms of

greater resolution and allelic richness aiding in family-based QTL study and Linkage-linkage disequilibrium analysis (Bohra et al., 2017).

6.1 | Genomic research: future prospects

6.1.1 | Genetic diversity via sequencing/ re-sequencing

Limited genetic diversity is the impending danger in genetic improvement of pigeonpea. It is high time to introduce novel genetic variation through the intervening mutation, landraces and wild relative in today's systematic breeding programmes. However, the linkage drag associated with favourable alleles restricts the satisfactory gene transfer from wild to cultivated forms. In this context, the available NGS technology and draft genome sequence in pigeonpea provide a great opportunity for exploring nucleotide-level diversity in cultivated, landraces and wild species accessions and its relationship with phenotypic diversity (Varshney et al., 2012). Re-sequencing of germplasm accessions will provide a better understanding of existing genetic diversity, associating gene(s) with phenotypes and exploiting natural genetic diversity to develop superior genotypes (Varshney, Saxena, Upadhaya, et al., 2017; Varshney, Saxena, & Jackson, 2017).

6.1.2 | Advanced trait mapping approaches

The traditional QTL mapping approach involves identification of parental polymorphisms and genotyping of the populations with the polymorphic markers in a time consuming and resource intensive manner (Abe et al., 2012). On the other hand is bulked segregant analysis (BSA), where marker screening on the extreme bulks and parents provides trait-associated markers. Thus, NGS-based BSA approaches would be anticipated in future for rapid and accurate trait mapping.

6.1.3 | Next-generation breeding

Currently, in pigeonpea, very few genomic inputs like marker-based purity testing in hybrids and parents, DNA fingerprinting, genome-assisted breeding for introgression of SMD and FW resistance in elite varieties is employed at ICRISAT (Singh, Sameer Kumar, et al., 2017; Singh, Saxena, & Varshney, 2017). The available draft genome, re-sequencing data, NGS bio-informatics advances, phenotyping platforms coupled with a recent drop in marker genotyping cost enables breeders to select appropriate allele combination at an early stage and facilitate successful introgression from wild to elite cultivars without the hindrance of linkage drag (Singh, Sameer Kumar, et al., 2017; Singh, Saxena, & Varshney, 2017). Genomic selection in the pigeonpea hybrid breeding programme would improve the chances of breeding high-yielding hybrids and parental lines. A faith of leap comprising conventional breeding with genomic inputs of NGS,high-throughput genotyping for early generation screening, marker-assisted backcrossing (MABC) and marker-assisted selection (MAS) is anticipated in coming days to take pigeonpea breeding a step ahead.

7 | SUMMARY

Enormous variability and plasticity of the pigeonpea crop, provided an opportunity for breeding varieties and hybrids for reducing crop duration, improving seed quality and overcoming the constraints of major diseases like fusarium wilt and sterility mosaic. These milestones have helped to increase the production and area of pigeonpea, in spite of stagnant yield/ha. Exploitation of heterosis for yield, breeding for agro-ecological adaptation and restructuring plant type for increased harvest index are major possible ways for achieving a breakthrough in yielding ability. The development of the A_4 CMS system has provided the opportunity for the commercialization of pigeonpea hybrids. High levels (30%–60%) of hybrid vigour observed over the standard cultivars and easy methods for producing hybrid seed have attracted a number of private and public seed companies. Larger emphasis on development of TGMS lines, short duration hybrids, early and photo-insensitive types, determinate plant types is an added advantage to secure substantial productivity. Complementary support via genomic interference with next-generation sequencing, genome-wide selection, trait mapping is a reason behind the renaissance in pigeonpea breeding in today's climate-smart breeding. Thus, this paper summarized the key role of conventional as well as genomic research in pigeonpea breeding.

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CONFLICT OF INTEREST

The authors declare no conflict of interest for the submitted manuscript/publication.

AUTHORS CONTRIBUTION

Sameer Kumar CV and Saxena R K designed the article. Saxena KB imparted the knowledge on pigeonpea improvement in Asia and Africa. Ganga Rao NVPR shared information on pigeonpea popularization and improvement of pigeonpea in eastern and southern Africa. Upadhyaya HD and Reddy KN provided inputs on genetic resource maintenance in pigeonpea. Hingane AJ, Sharma Mamta, Sharma Shivali shared the inputs on early duration improvement, disease screening and pre-breeding in pigeonpea in Asia, respectively. Varshney RK and Saxena RK provided inputs on genomic resource development in pigeonpea. Jaganmohan Rao P, Prasanthi L, Sudhakar C, Nagesh Kumar MV and Singh IP catered the information on pigeonpea improvement in India. Mose Siambi, Silim SN, Lyimo SD, Rose Ubwe and Makenge M supported with the information on pigeonpea improvement in Tanzania. Kananji GAD (Malawi), Kimurto PK(Kenya), Manuel Amane(Mozambique), Kanenga K(Zambia), Yuventino Obong(Uganda), Emanuel Monyo[1],

Ojiewo Chris shared the ongoing pigeonpea research in Africa. Shruthi HB drafted the manuscript. Saxena KB, Ganga Rao NVPR, Sameer Kumar CV, Saxena RK, Sobhan Sajja and Shruthi HB revised the article. All the authors have read and approved the final manuscript.

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