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Review article

Exciting journey of 10 years from genomes to fields and markets: Some success stories of genomics-assisted breeding in chickpea, pigeonpea and groundnut

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ABSTRACT

Legume crops such as chickpea, pigeonpea and groundnut, mostly grown in marginal environments, are the major source of nutrition and protein to the human population in Asia and Sub-Saharan Africa. These crops, however, have a low productivity, mainly due to their exposure to several biotic and abiotic stresses in the marginal environments. Until 2005, these crops had limited genomics resources and molecular breeding was very challenging. During the last decade (2005–2015), ICRISAT led demand-driven innovations in genome science and translated the massive genome information in breeding. For instance, large-scale genomic resources including draft genome assemblies, comprehensive genetic and physical maps, thousands of SSR markers, millions of SNPs, several high-throughput as well as low cost marker genotyping platforms have been developed in these crops. After mapping several breeding related traits, several success stories of translational genomics have become available in these legumes. These include development of superior lines with enhanced drought tolerance in chickpea, enhanced and pyramided resistance to Fusarium wilt and Ascochyta blight in chickpea, enhanced resistance to leaf rust in groundnut, improved oil quality in groundnut and utilization of markers for assessing purity of hybrids/parental lines in pigeonpea. Some of these stories together with future prospects have been discussed.

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1. Introduction

Chickpea (*Cicer arietinum*), pigeonpea (*Cajanus cajan*) and groundnut (*Arachis hypogaea*) with high nutrition and protein values are the leading legume crops grown in marginal environments in Asia and sub-Saharan Africa. These legume crops play a significant role in ensuring nutritional food security in many developing countries in Asia and Africa. Despite the significance of these legume crops in providing protein rich food in the vegetarian diet, the productivity of these legume crops over past decades remained low. This was mainly due to exposure of the crops to several biotic and abiotic constraints in marginal environments. Recent abrupt changes in the climatic conditions are expected to make this situation worst in coming future [1]. Conventional breeding approaches have been focusing on increasing yield in these legumes. Therefore, there is a scope for enhancing crop productivity using modern breeding approaches. Due to availability of very limited genomic resources and unaffordable high-costs associated with genomics research, genomics-assisted breeding (GAB) approaches were not used in these legume crops until 2005. As a result these crops were often referred as 'orphan crops'.

During the last decade, significant progress has been made in the development of genetic and genomic resources in these legumes [2]. Recent advances in next-generation sequencing (NGS) and high-throughput technologies coupled with strategic partnership with different organizations facilitated development of large-scale molecular markers. These markers have been used to construct several dense and comprehensive genetic maps, inter- and intra-specific genetic maps and identification of various markers associated with traits of interest to breeders. In several cases, candidate genomic regions for targeted traits have been introgressed in elite breeding lines [3]. In brief, NGS based approaches have been proven cost-effective, precise and fast forward way for crop improvement. The progress made in all these legume crops have been recently documented in some recent articles [3,4]. This article is mainly focused on the major research efforts led by ICRISAT with its research partners on development of genomic resources, trait mapping and molecular breeding in chickpea, pigeonpea and groundnut. Future requirements and prospects have also been presented to accelerate translation of genomics research in breeding for enhancing genetic gains in these legume crops.

2. Genomic resources

2.1. Molecular markers

The last decade (2005–2015) has witnessed the development of large-scale genomic resources in chickpea, pigeonpea and groundnut. Simple sequence repeat (SSR) markers, most preferred markers for breeding, were available in very limited number in these crops until 2005. For instance only 10 SSR markers were available in pigeonpea. However, ICRISAT along with its partners has developed several thousand SSR markers in each of these crops. At present, >2,000 SSR markers are available in chickpea, >3,000 in pigeonpea and >2,500 in groundnut (Table 1). These SSRs were developed using one or combination of following approaches namely: (i) SSR-enriched or size-selected DNA libraries, (ii) bacterial artificial chromosome-end sequences (BESs), (iii) SSR mining from ESTs (expressed sequence tags). In addition to SSRs, ICRISAT in collaboration with DArT Pty Ltd, Australia has also developed diversity arrays technology (DArT) arrays with 15,360 features each for chickpea, pigeonpea and groundnut [5] (Table 1). Similarly, single nucleotide polymorphism (SNP) markers, that were not available in these legume crops in 2005, have been developed in tens of thousands number in the last 10 years. SNP markers have been developed using following approaches: (i) alignment of Sanger ESTs [6,7] (ii) allele-specific sequencing [8–11] and (iii) sequencing of parental lines using NGS approaches [12–14] (Table 1). After availability of genome sequences (see later), re-sequencing of germplasm collection has enhanced the number of SNPs to several millions at least in chickpea and pigeonpea.

Table 1
Advances in the genomic resources during last decade from 2005 to 2015 in targeted legumes.[a]

Features	Chickpea		Pigeonpea		Groundnut	
	2005	2015	2005	2015	2005	2015
Molecular markers						
SSR markers	++	+++	+	+++	+	+++
SNP markers	No	+++	No	+++	No	++
DArT markers	No	+++	No	+++	No	+++
Maps						
Genetic maps	+	+++	No	++	+	+++
Physical maps	No	+	No	No	No	+
Bin maps	No	+	No	No	No	No
Assembly						
Genome	No	+++	No	++	No	++
Transcriptome	No	+++	No	++	No	++
Marker genotyping platforms						
KASP assays	No	+++	No	+++	No	++
GoldenGate	No	++	No	++	No	++
Affymetrix	No	+++	No	+++	No	+++
Trait mapping						
Biotic stress	+	+++	No	+++	+	++
Abiotic stress	+	+++	No	++	No	+
Other traits	+	+++	No	+	+	++
Products						
Superior lines	No	+++	No	No	No	+++
Marker-based purity assessment kit	n.a.	n.a.	No	++	n.a.	n.a.

n.a. = not applicable.
[a] one, two and three + sign indicate availability in moderate, good and excellent quantity, respectively.

The success of any marker system depends on its throughput and cost of marker assays. After the generation of huge genomic resources in three legume crops, the next step was to develop cost-effective marker assays for various applications (Table 1). Kompetitive Allele Specific PCR (KASP) assays have been developed for 2,005 SNPs in chickpea [9], 1,616 SNPs in pigeonpea [11] and 90 SNPs in groundnut [15]. To use these SNP markers in breeding applications, Golden-Gate assays with a possibility to undertake genotyping of 768 SNPs have been developed. Also, VeraCode assays for genotyping 96 SNPs in chickpea and 48 SNPs in pigeonpea have also been developed [16]. Very recently, 60K SNP chip for each of three legume crops is also being developed using Affymetrix SNP platform for accelerating genetics and breeding applications in these legume crops.

2.2. Genome sequencing and re-sequencing

With the advent of NGS technologies, the cost of genome sequencing has been drastically reduced. As a result, draft genome

sequences have become available for many important crops. For assembling genome sequence, ICRISAT took the lead and floated genome sequencing consortia e.g. International Initiative on Pigeonpea Genomics (IIPG, www.icrisat.org/gt-bt/iipg/Home.html) and International Chickpea Genome Sequence Consortium (ICGSC, www.icrisat.org/gt-bt/ICGGC/Homepage.htm) for sequencing and assembling genome sequences of pigeonpea and chickpea, respectively. In the case of groundnut, ICRISAT collaborated with the partners in International Peanut Genome Initiative (IPGI, http://www.peanutbioscience.com/peanutgenomeinitiative.html) for decoding draft genome for both the diploid progenitors while co-led with colleagues from China another initiative Diploid Progenitor Peanut A-genome Sequencing Consortium (DPPAGSC) for sequencing the A-genome progenitor.

By using whole genome shotgun sequencing approach, ICRISAT-led IIPG completed the sequencing of pigeonpea genotype Asha by using the Illumina sequence technology [17]. A total of 237.2 Gb of sequence data was generated using NGS technology and assembled 605.78 Mb into scaffolds representing ~73% of 833 Mb pigeonpea genome. In fact, pigeonpea became the second legume crop after soybean and the first non-industrial legume crop for which a genome sequence was available in 2012. This was the first report on genome sequencing from any CGIAR centre as a lead for any plant species.

Like above, ICRISAT-led ICGSC completed the genome sequencing of CDC Frontier, a kabuli chickpea variety in 2013 [18]. In total, 153.01 Gb of sequence data was generated using Illumina sequencing of 11 genomic libraries and assembled 544.73 Mb of genomic sequence in scaffolds representing 73.8% of the total genome (738.09 Mb). Re-sequencing of 90 accessions was also reported along with the genome sequence. This important research breakthrough was announced by the then Secretary, Agriculture (Development & Cooperation), Ministry of Agriculture, Government of India, along with the then Director General, ICRISAT, the then Deputy Director General (Crop Science), Indian Council of Agricultural Research (ICAR) and the Project Coordinator (me).

In the case of groundnut, ICRISAT collaborated with the US-led initiative IPGI to decode the genomes of two diploid progenitors. The progenitors representing A-genome (*Arachis duranensis*, accession V14167) and B-genome (*A. ipaensis*, accession K30076) together represent the tetraploid genome of cultivated groundnut (*A. hypogaea*). In this context, a total of 216 Gb whole genome shotgun sequencing data were generated and were assembled into ten pseudomolecules for each genome. The sequencing of genomes revealed 1.1 Gb genome size for A-genome progenitor (*A. duranensis*) and 1.38 Gb for B-genome progenitor (*A. ipaensis*) (http://peanutbase.org/genomes). In addition to above, under the framework of DPPAGSC, the genome sequence draft of the probable groundnut A-genome progenitor, *A. duranensis* (accession PI475845) was generated with 1.07 Gb genome size, very close the genome size estimated by the IPGI (1.1 Gb).

In addition of sequencing genomes of all three legume crops, re-sequencing of large number of genotypes including cultivated and wild genotypes, parental lines, reference sets, and released varieties of these legumes has been initiated at ICRISAT. In the case of pigeonpea, whole genome re-sequencing of reference set collection of 292 lines, 104 parental line of pigeonpea hybrids including cytoplasmic male sterlity (CMS), maintainer and restorer lines and 21 parental lines of different mapping populations has been completed and data analysis is underway. In the case of chickpea, 90 cultivated and wild genotypes of chickpea [18], 35 parental lines of different mapping populations, ~400 chickpea lines including 300 lines from chickpea reference set and 100 elite varieties have been sequenced. Most importantly, "The 3,000 Chickpea Genome Sequencing Initiative" was started by ICRISAT in 2014 with an objective to capture the genetic variation present in germplasm collection and to identify the superior alleles for the target traits. In addition to generating sequence data, the set of 3,000 accessions has already been phenotyped at 6 locations in India by ICRISAT and other partner institutes like International Center for Agricultural Research in the Dry Area (ICARDA), Indian Institute of Pulses Research (IIPR), Kanpur; Rajasthan Agricultural Research Institute (RARI), Durgapura; Junagadh Agricultural University (JAU), Junagadh and RAK College of Agriculture (RAKCA), Sehore in India (Fig. 1).

Due to unavailability of draft genome sequence of the cultivated (tetraploid genome) genotype and large genome size in case of groundnut, exome sequencing has been planned on a set of 250 lines including elite lines, landraces and wild relatives. Nevertheless, as a part of DPPAGSC, re-sequencing data was generated for four synthetic tetraploids and their six diploid parents (two A-genome, four B-genome including the probable B-genome progenitor, *A. ipaensis*).

In brief, the availability of the genome sequence and re-sequencing data of diverse lines of all the three legumes has provided access for genes and alleles in their genomic context to the global research community.

2.3. Genetic and physical maps

Above mentioned molecular markers have been used for developing different kinds of genetic maps. In the case of chickpea, a high-density genetic map was developed on an inter-specific mapping population (ICC 4958 × PI 489,777) with 1,291 loci spanning a distance of 845.56 cM [19]. With the development of large-scale KASP assays, a second generation genetic map of 1,328 marker loci, including 625 novel CKAMs (Chickpea KASP Assay Markers), 314 TOG-SNPs (Tentative orthologous genes- single nucleotide polymorphisms) and 389 published marker loci with an average inter-marker distance of 0.59 cM was developed [9]. Additionally, two genetic maps comprising 241 and 168 loci and spanning 621.51 cM and 533.03 cM distance were developed for ICC 4958 × ICC 1882 and ICC 283 × ICC 8261 intra-specific populations [20]. The average inter-marker distances of 2.71 and 3.27 cM were observed for ICC 4958 × ICC 1882 and ICC 283 × ICC 8261 maps respectively. A consensus map of 352 loci and 771.39 cM length was also developed using molecular markers from above mentioned crosses [20]. Further, genotyping-by-sequencing (GBS) methodology was employed on RIL population ICC 4958 × ICC 1882 and 828 novel single-nucleotide polymorphisms (SNPs) were identified. The SNP markers along with previously used SSR markers generated a high-density linkage map comprising 1,007 marker loci and spanning a distance of 727.29 cM [21]. Moreover, low coverage based whole genome re-sequencing, called as skim sequencing [22], was carried out on the RIL population of ICC 4958 × ICC 1882, which resulted in the identification of >50 K SNPs. These SNPs were subjected to parent dependent sliding window based bin mapping and 1610 true recombination bins were identified. An ultra-high density linkage map of 973.54 cM distance was developed using recombination bins as markers. An average inter-marker distance of 0.66 cM was observed in this study that was lower than other studies conducted on intra-specific mapping populations (0.94–7 cM) in chickpea. Very recently, two dense genetic maps comprising of 2,177 loci for population involving kabuli type genotypes while 3,625 loci involving desi type genotypes also have been developed in a separate study [23]. Such a highly saturated map can be used for targeted QTL mapping, QTL cloning and identification of candidate genes for important agronomic traits in chickpea. In addition to genetic map, physical map was also developed for the reference chickpea genotype (ICC 4958) using BAC libraries targeting 71,094 clones (~12× coverage) [24]. The developed physical map was also linked with genetic maps and genome sequence through sequencing of BAC-ends and/or mapped

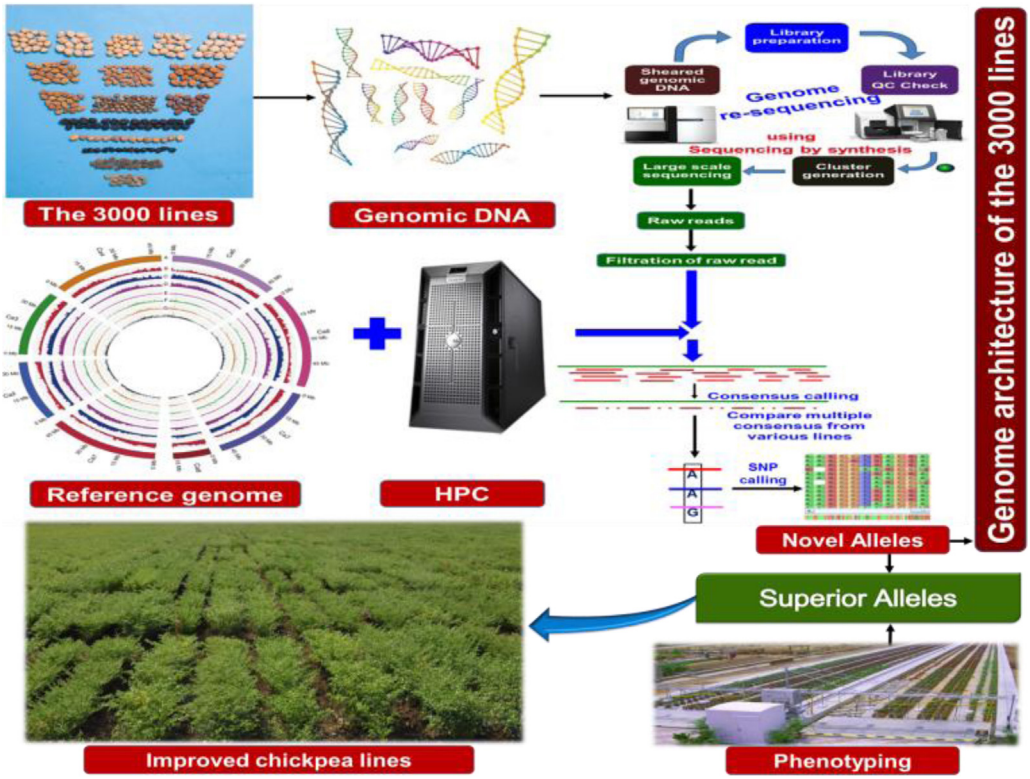

Fig.1. The 3,000 Chickpea Genome Sequencing Initiative for mining favorable alleles for chickpea improvement. The figure shows the flow of planned work that begins with generation of re-sequencing and phenotyping data on 3,000 chickpea genotypes. The re-sequencing data will be analyzed for better understanding the chickpea genome and identification of structural variations in the germplasm collection. These structural variations together with phenotyping data will be analyzed for establishing marker-trait associations for agronomically important traits. The associated structural variations can be deployed for accelerating development of improved cultivars using genomics-assisted breeding.

SSR markers derived from BAC-end sequences. The developed integrated map will be useful for molecular detection of targeted traits.

In the case of pigeonpea, the first reference genetic map was developed using an inter specific population (ICP 28 × ICPW 94) comprising 79 F_2 plants with 239 SSR markers spanning a map distance of 930.9 cM over 11 linkage groups [25]. Further, genotyping of the same mapping population with DArT markers resulted in the development of DArT based paternal and maternal specifc maps with 122 and 172 loci, respectively [26]. With the development of 1616 KASP assays for pigeonpea, a dense genetic map comprising 875 SNP loci with an average inter-marker distance of 1.11 cM has been developed [27]. Likewise, six intra-specific F_2 populations developed for diverse traits were also used for the development of low to moderate density linkage maps. These six intra-specific maps were further utilized for the development of a consensus map, which is comprised of 339 SSR loci with 1,059 cM of genetic distance [28]. Presently, ~20 mapping populations, including RILs, ILs, and F_2s developed for different targeted traits are being genotyped through GBS approach for the development of high-density linkage maps in pigeonpea.

In the case of groundnut, the first SSR-based genetic map was developed with 135 loci using a recombinant inbred line (RIL) population [29]. Later the map was updated to 191 SSR mapped loci [30]. Two more SSR based genetic maps were developed with 56 marker loci (TAG 24 × GPBD 4) and 45 marker loci (TG 26 × GPBD 4) [31,32]. Availability of large number of SSR markers further facilitated further improvement of these two genetic maps with 188 (TAG 24 × GPBD 4) and 181 (TG 26 × GPBD 4) marker loci [33]. Moreover, by using three other RIL populations developed from the crosses TAG 24 × ICGV 86031, ICGS 44 × ICGS 76 and ICGS 76 × CSMG 84-1, a consensus genetic map with the 293 marker loci onto 20 linkage groups covering genome distance of 2,840.8 cM was constructed [34]. In order to achieve more density, by using 10 RILs and one back cross population [*A. duranensis* × (*A. ipaensis* × *A. duranensis*)], 897 marker loci (895 SSRs and 2 CAPS) were mapped on 20 linkage groups spanning a total map distance of 3607.97 cM [35]. This consensus genetic map was further improved by adding mapped loci from other five mapping populations. This resulted in development of a more saturated and dense consensus map with 3,693 marker loci covering 2,651 cM anchored on 20 consensus LGs corresponding to the A and B genomes [36]. This map was also used to refine genome assembly of A and B genomes of IPGI. In addition to above, in collaboarton with USDA-ARS, Tifton (Baozhu Guo), improved genetic linkage maps were developed for S-population (SunOleic 97R × NC94022) with 206 (1780.6 cM) and T-population (Tifrunner × GT-C20) with 378 (2,487.4 cM) marker loci [37] which were then further saturated to 426 and 248 marker loci, respectively.

3. Trait mapping

To make the best use of available genomic resources in breeding applications, several breeding related traits have been mapped in these legume crops. For instance, in chickpea, the yield is severely affected by drought and biotic stresses like Fusarium wilt (FW) and Ascochyta blight (AB). In order to dissect the complex nature of drought tolerance and to identify the markers associated with yield under drought stress, two intra-specific mapping populations namely ICCRIL03 (ICC 4958 × ICC 1882) and ICCRIL04 (ICC 283 × ICC 8261) segregating for drought tolerance related root traits were used. Based on genotyping data for 241 loci and 168 loci for ICCRIL03 and ICCRIL04, respectively, and using extensive

phenotyping data (20 drought tolerance related traits collected in 1–7 seasons at 1–5 locations in India), QTL analysis was performed and 45 robust main-effect QTLs (M-QTLs) were identified [20]. A "*QTL-hotspot*" region harboring 12 major QTLs for drought tolerance related traits explaining up to 58.20% phenotypic variation was identified on the linkage group 4. However, this region was estimated to be 29 cM on the genetic map and 7.74 Mb on the physical map. Subsequently, by using genotyping-by-sequencing (GBS) approach, this region were further refined to 14 cM [21]. Recently, a comprehensive association mapping approach using whole genome scanning and candidate gene-based approach identified 312 marker trait associations (MTAs) for drought and heat responsive traits in chickpea [38]. Some markers-associated with drought tolerance were found present in the "*QTL-hotspot*" region confirming the promising nature of the "*QTL-hotspot*" region. For fine mapping of this region, a combination of two complementary approaches, namely sliding window based bin mapping approach and GWAS based gene enrichment analysis of skim sequenced data of RIL population (ICCRIL03) splits the "*QTL-hotspot*" in two sub-regions viz. "*QTL-hotspot_a*" and "*QTL-hotspot_b*" of 139.22 and 153.36 Kb sizes [39]. To identify QTLs for FW and AB resistance in chickpea, two mapping populations (C 214 × WR 315) and (C 214 × ILC 3279) were developed. Comprehensive analysis of genotyping and phenotyping data identified two novel QTLs for FW that explained 10.4–18.8% of phenotypic variation and six QTLs explaining up to 31.9% of phenotypic variation for resistance to AB [40]. Similarly QTLs have also been identified for botrytis gray mould [41]. Some other QTL mapping reports are also available from other institutes on resistance to FW [42–44], AB [45–50] and rust [51] and several agronomic and yield related traits [42,44,52–55].

In the case of pigeonpea, FW and sterility mosaic disease (SMD) are major yield constraints. QTL analysis for identification of markers associated with SMD provided six QTLs using ICP 8863 × ICPL 20,097 and TTB 7 × ICP 7035 mapping populations. Of these QTLs, one QTL (*qSMD4*) explaining 24.72% of the phenotypic variance was identified on CcLG07 [56]. However, for more precise identification of the candidate gene/ genomic regions for molecular breeding for FW and SMD resistance, NGS based trait mapping approaches have been utilized. Bi-parental mapping population namely PRIL_B (ICPL 20096 × ICPL 332) segregating for FW and SMD resistance was developed at ICRISAT and phenotyped at three different locations (ICRISAT, Patancheru; ANGRAU, Tandur and UAS-Gulbarga) in two different years. In this context, sequencing-based bulked segregant analysis (Seq-BSA) approach combined with the non-synonymous substitution approach (nsSNPs) approach has identified the genomic regions associated with FW and SMD resistance (unpublished data). Similarly, NGS based QTL-seq approach has also been found promising for identification of genomic regions for days to flowering and obcordate leaf shape (an important morphological trait in hybrid pigeonpea breeding) (unpublished). In addition, marker-trait association has been established for some agronomic traits like number of pods per plant, plant height, plant types and primary branches per plant in two other studies [57,58]. To achieve a breakthrough in pigeonpea productivity, cytoplasmic-nuclear male sterility (CMS) (designated as A_4 cytoplasm, derived through the introgression from wild relative *Cajanus cajanifolius*) system based pigeonpea, hybrid breeding was initiated at ICRISAT. In this context, based on the information of 34 mitochondrial genes [59], *nad7* gene has been found associated with A_4 CMS in pigeonpea [60]. Additionally, *nad7* gene-based markers associated with the A_4 CMS trait have also been developed for detection of CMS seed purity.

In the case of groundnut, with the availability of several mapping populations segregating for different targeted traits as well as large number of molecular markers, linkage mapping based marker analysis has been undertaken to identify the QTLs for large number of biotic, abiotic and quality traits. For drought tolerance related traits by using multi-environment phenotyping data, 153 main-effect and 25 epistatic QTLs were identified [29,30,34]. On the other hand, 13 major QTLs were detected for resistance to LLS with phenotypic variance explained (PVE) in the range of 10.27–67.98% and 7 major QTLs for resistance to rust with PVE up to 82.62% in two RIL populations from TAG 24 × GPBD 4 and TG 26 × GPBD 4 crosses [33]. Recently, in collaboration with the University of Georgia, Tifton campus (Baozhu Guo), major QTLs for early leaf spot, late leaf spot and tomato spotted wilt virus with PVE of up to 15%, 17% and 29%, respectively have been identified in S and T- populations. Enhancing oil content and quality has become another possible way to provide benefits to farmers [32,36,61]. The first QTL study of the oil quality traits was done in the RIL population of TG 26 × GPBD 4 and identified one major QTL with PVE of 10.2% [32]. Recently, four major QTLs for oil content were identified in two RIL (S and T) populations with PVE up to 14.18% [37]. In addition, trait mapping has also been conducted for resistance to *Aspergillus falvus* invasion [62], Aphid vector for groundnut rosette disease [63], tomato spotted wilt virus [64,65], agronomic traits e.g seed weight, pod weight, number of branches, plant height, plant biomass [62,66]. Also to conventional trait mapping, sequenced-based trait mapping approaches has also been initiated for identification of candidate genes/genomic regions for rust and late leaf spot resistance (unpublihsed). In addition to trait mapping through linkage mapping, a comprehensive marker-trait association study was conducted in the groundnut reference set for 50 important agronomic, disease and quality traits. The above analysis resulted in identification of 524 MTAs for 36 traits with wide PVE range (5.81–90.09%) [67].

4. Molecular breeding

Large-scale genetic and genomic resources together with traits associated markers developed during last decade have made it possible to integrate molecular breeding approaches in chickpea and groundnut improvement. The transfer of targeted traits has been completed in 2–3 years through marker-assisted backcrossing (MABC) as opposed to 6–8 years needed with conventional methods. MABC has been deployed for several traits in these legume crops. Although some success stories on molecular breeding are available in soybean for some traits like resistance to soybean cyst nematode [68], rust [69], soybean mosaic disease [70,71] and multiple diseases [72,73] and common bean for disease resistance [74–76], a very few reports on molecular breeding were available until recently in ICRISAT mandate legume crops. For instance, in the case of groundnut, improved lines have been developed for nematode resistance [77,78], high oleic/linoleic acid ratio [78,79] and in the case of chickpea, very recently, improved lines with enhanced resistance to AB have been developed [80]. In these legume crops, translational genomics is being used extensively for developing improved lines at ICRISAT. In a short period of time, five success stories of translational genomics that are reaching to fields and markets have become available. These cases have been documented as following and given in Table 2.

4.1. Drought tolerance in chickpea

In context of chickpea, '*QTL-hotspot*' region containing QTLs explaining up to 58.20% of PVE for several drought tolerance related traits was targeted for enhancing drought tolerance in elite chickpea varieties. For instance, the '*QTL-hotspot*' region was introgressed in leading chickpea variety JG 11 through MABC [81]. Multi-location trials of a set of 29 MABC lines have identified several superior lines with higher yield, as compared to the JG 11, in both rainfed and irrigated conditions. In parallel, '*QTL-hotspot*'

Table 2
Details of molecular breeding products released and/or under pipeline at ICRISAT

Crop	Cultivars targeted for QTL introgression/ hybrids for purity assessment	Trait	Current status	Reference
Chickpea	JG 11	Drought tolerance	Several introgression lines were developed and some superior lines are in multilocation trials.	[81]
	C 214	Fusarium wilt and Ascochyta blight resistance	Several introgression lines were developed and some superior lines are in multilocation trials	[83]
Groundnut	ICGV 91114, JL 24 and TAG 24	Leaf rust resistance	Several introgression lines were developed and some of them are in replicated trials for enhancing seeds and for testing in multilocation trials.	[84]
	ICGV 06110, ICGV 06142 and ICGV 06420	Oil quality	Introgression lines with two mutant alleles, namely *ahFAD2A* and *ahFAD2B* have been developed.	[85]
Pigeonpea	ICPH 2671 and ICPH 3438	Hybrid purity	SSR based hybrid seed testing purity kits have been developed.	[25,86]
	ICPA 2039 and ICPB 2039	CMS seed purity	Gene based makers for seed purity analysis of A_4 CMS seeds have been developed.	[60]

genomic region has been transferred in two more leading chickpea varieties (Chefe and KAK 2) by using MABC approach [82]. Similar efforts to introgress this genomic region (‘*QTL-hotspot*’) in other elite cultivars is underway at Indian Agricultural Research Institute (IARI, New Delhi), Indian Institute of Pulse Research (IIPR, Kanpur), Egerton University in Kenya and Ethiopian Institute of Agricultural Research.

4.2. Fusarium wilt and Ascochyta blight resistance in chickpea

Fusarium wilt (FW) and Ascochyta blight (AB) are two major constraints to chickpea production therefore, stepwise MABC approach was adopted to develop dual resistance C 214, an elite chickpea cultivar. To develop resistant lines, *foc1* locus for FW and two quantitative trait loci (QTL) regions, ABQTL-I and ABQTL-II, for AB were targeted for introgression. Foreground selection with six markers linked to *foc1* and eight markers linked to both QTL regions was used for selection of plant with desirable alleles in different segregating generations. In addition to foreground, background selection was performed for selection of plant with high recurrent parent genome recovery, with evenly distributed 40 SSR markers. After three backcrosses and three rounds of selfing, 22 BC_3F_4 lines were generated for FW and 14 MABC lines for AB [83]. Phenotyping of these lines has identified three resistant lines for FW and seven resistance lines for AB. The multi-location phenotyping of identified theses lines for disease resistance and for their agronomic traits are underway for identification of suitable lines for possible release as superior varieties.

4.3. Rust resistance in groundnut

Rust is one of the major scourging diseases that causes 40–55% losses in pod yield in commonly grown but susceptible cultivars in Maharashtra, Karnataka, Tamil Nadu and Andhra Pradesh regions of India. To cope with this problem, it was necessary to introgress leaf rust resistance genes/genomic regions in susceptible varieties through MABC. Some elite and farmer-grown varieties, namely ICGV 91114, JL 24 and TAG 24 are/have become susceptible to rust. Therefore, these varieties were targeted for introgression of the major QTL for rust resistance from GPBD 4, a rust-resistant variety. The introgression of the major QTL in targeted varieties was deployed using one dominant (IPAHM103) and three co-dominant (GM2079, GM1536, GM2301) linked markers. After undertaking three backcrosses and one round of selfing, 200 introgression lines were obtained. Field evaluation of these 200 lines under stress conditions have identified 81 introgressed lines (ILs) with improved rust resistance. In comparison to their respective recurrent parent (targeted variety), these ILs showed increased pod yields (56–96%) in the same environmental condition [84].

4.4. Oil quality in groundnut

Among different quality traits, oil quality in groundnut is of high importance. This trait is useful for markets and health benefits in addition to enhancing shelf life of the groundnut products. Therefore, two approaches namely MABC and marker-assisted selection (MAS) were adopted to enhance the oil quality traits in three groundnut varieties, namely ICGV 06110, ICGV 06142 and ICGV 06420. The SunOleic 95R carrying two *FAD2* mutant alleles responsible for oil quality traits was used as donor. After one backcrossing followed by selfing of BC_1F_1 and F_1 generated 82 MABC and 387 MAS derived introgression lines (ILs) with increased oleic acid in the range of 62–83% [85].

4.5. Hybrid purity assessment in pigeonpea

To enhance the cultivation of pigeonpea hybrids, which has reported significant increases in yields, by giving 30–35% higher yields compared to local varieties, high quality hybrid seeds is of primary requirement. Traditional ‘grow-out-test’ based on the morphological traits are time consuming and are environment dependence. To overcome this disadvantage, the SSR based hybrid purity kits have been developed for rapid assessment of purity of hybrid and parental lines for two hybrids namely, ICPH 2438 and ICPH 2671 [25,86]. Very recently, hybrid seed purity testing kits have also been developed for five more hybrids including one leading pigeonpea hybrids (ICPH 2740) and four promising hybrids (ICPH 4503, ICPH 3762, ICPH 3933, and ICPH 2751). SSR markers of these kits amplify only one specific allele in their respective parents and both alleles in true hybrids. For example, for the hybrid ICPH 2438, SSR marker CCB4, amplifies 228 bp fragment in ICPA 2039 (CMS line or female parent) and 220 bp fragment in ICPR 2438 (male or restorer parent), while the true hybrid (F_1) seeds show both alleles (228 bp and 220 bp). In the case some seeds of hybrids show only one allele or other allele than the parental genotypes, those seeds are considered as impure hybrid seeds.

In addition to hybrid seed purity testing kit, marker for A_4 CMS (nad7a_del) seed purity has also been developed and validated in a

range of A_4 derived CMS lines and large seed lots [60]. This marker amplifies 150 bp fragment in A_4 CMS lines and 160 bp fragment in their cognate maintainer lines and can be visualized on 3.5% agarose gel. The developed CMS associated gene based marker is capable of detection of <2% of adulteration on low-cost agarose gel system. These high-throughput markers based hybrid and parental lines purity testing kits have been made freely available to private seed companies and public organizations. This will help them to detect the purity of the F_1s/ parental lines seeds, which can avoid traditional grow-out tests and save one full crop season.

5. Summary and outlook

Although these legumes crops together with some other legume crops used to be called "orphan legume crops" earlier especially in context of availability of limited genomics resources, recent advances in genomics research have put these legume crops in the category of "genomic resources rich crops". The last decade has also witnessed tremendous progress in the area of translation of the massive genomic information in development of products that are reaching to farmers' fields as well as markets. For realizing the full potential of translational genomics especially by National Agricultural Research System (NARS) partners, I would suggest following four areas to be strengthened:

5.1. Specialized and big size populations

An important area of research that is yet to be addressed is development and utilization of specialized genetic populations with a broad genetic base as the genetic diversity in the elite and/or adapted germplasm of these legumes is very narrow. Such populations include multi-parents advanced generation intercross (MAGIC) [87–99], advanced backcross [90] and chromosome segment substitution lines (CSSL) [91,92]. In the case of MAGIC populations, genome of the founder parents is re-shuffled in different combinations [87–89]. These MAGIC lines are useful for high-resolution genetic mapping and identification of target genomic regions in addition to using them in breeding programs. MAGIC populations have been developed in several crops like wheat [93–95], maize [96], barley [97], rice [98]. Some efforts have been initiated to develop MAGIC population in chickpea [88,89]. In the case of advanced backcross populations, genomic segments from a wild species are introgressed in the genetic background of elite cultivars [90]. These populations after undertaking phenotyping in the BC_2 or BC_3 generations are also used for QTL analysis. In the case of CSSLs, each line consists of one or few homozygous chromosome segments derived from the donor parent (mainly wild species or a landrace) in the genetic background of the recurrent parent i.e. elite cultivar [99]. Each line exhibits effect of the introgressing chromosome segment from the donor line. Therefore, the effect of each chromosome segment on a trait can be evaluated without genetic interactions among QTLs. In addition, genetically fixed CSSLs can serve as important breeding materials. In the case of groundnut, both advanced backcross population [100] as well as CSSLs have been developed [101], however such efforts need to be intensified in these legume crop.

5.2. Next generation phenotyping

While looking back in the area of crop breeding, it is clear that before the advent of marker technology, selection of plant lines for breeding was solely based on phenotyping. Because of availability of molecular markers linked with traits, genotyping based selection of lines, mainly in the framework of MAS and MABC, started in many crops in the decade of 1990–2000. With the decreasing cost in the genotyping, while the phenotyping costs did not decrease much, the last five years (2010–2015) have seen the extensive use of markers in selection of lines in breeding (Fig. 2). However for successful deployment of MABC, it is essential to have reliable and precise effect QTLs for the given trait that obviously depends on the quality of phenotyping. In brief, more accurate and precise phenotyping strategies are necessary to empower high-resolution linkage mapping and GWAS and for training genomic selection models in crop improvement. Therefore, Cobb et al. [102] proposed to establish next generation phenotyping to increase the accuracy, precision and throughput of phenotypic estimation at all levels of biological organization while reducing costs and minimizing labor through automation, remote sensing, improved data integration and experimental design. Robust and field-relevant trait phenotyping systems are needed to characterize the full suite of genetic factors that contribute to quantitative phenotypic variation across cells, organs and tissues, developmental stages, years, environments, species and research programs.

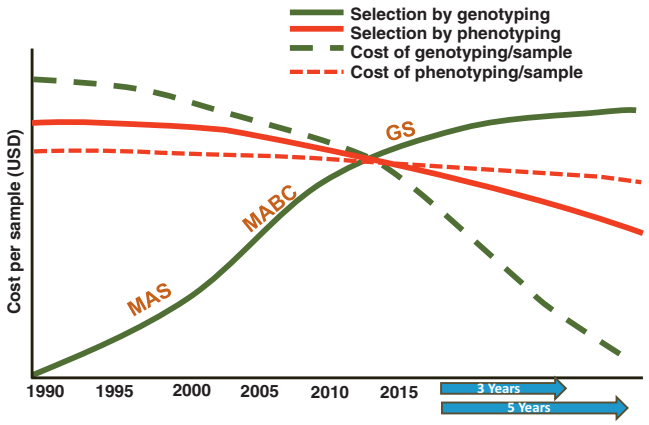

Fig. 2. Trends in genotyping and phenotypic selection in crop breeding. The selection of lines (plants) in breeding during 1990s was mainly based on phenotypic screening. However with the development/ availability of diagnostic markers and reduction in genotyping costs, selection of lines in breeding started based on genotyping from 1990s onwards. As the costs on phenotyping did not decrease in the last 20 years or so, there was a sharp decrease in the cost on genotyping. As a result, genotyping based selection of lines increased a lot in many breeding programs in recent years. With anticipation of further cost reduction in sequencing and genotyping technologies, it is anticipated that selection of lines in breeding programs will be predominantly based on genotyping/ sequencing in the framework of genomic selection (GS).

5.3. Forward breeding and genome-profiling based selection

As mentioned above, MABC approach has been used in project mode in several crops. It is important to note that reduction in genotyping costs is expected to be steeper in coming years (Fig 2). Therefore, breeding programs will have use of markers in basically two approaches. In the first approach breeders may start to use the diagnostic markers in early generations and therefore with the reduction in genotyping costs, it will be possible to screen large-scale populations. This will help in enhancing selection intensity and therefore genetic gain. Furthermore, it can be anticipated that selection of plants may start to move based on genome-wide markers based profile mainly in the framework of genomic selection (GS) [103]. In the GS approach, selection of lines is based on breeding values estimated on the basis of genome-wide marker profile data. The approach gained popularity in developing lines with enhanced genetic gain [104]. Therefore, molecular breeding will have a shift from MAS to forward breeding and/ or GS [103]. In this context, ICRISAT has also initiated efforts in undertaking forward breeding and deployment of GS in all three legume crops in recent years.

5.4. Empowering capacity of NARS partners

Although documented success stories are very encouraging and motivating, a huge yield gap still exists between potential and the actual yield in these legume crops. To fill this yield gap, acceleration of the integration of molecular breeding approaches in breeding programs especially at NARS partners is essential. Majority of NARS partners have a tendency to deploy GAB approaches when they have sophisticated genotyping facilities available at their institutes [105]. However, in my opinion, they do not need to essentially worry about in-house genotyping facilities. They can avail genotyping or sequencing through outsourcing which is both time- as well as cost-effective mainly due to scale of economies. However NARS partners need to be trained in data analysis and translational genomics in agriculture. Therefore, development of user-friendly decision support tools e.g., pipelines in graphic user interface and their deployment is essential [106].

In brief, availability of genomic tools, low-cost genotyping platforms together with specialized genetic populations and precise phenotyping and empowered and equipped NARS partners with appropriate decision support tools will be accelerating translation of genomics research for enhancing genetic gains in the mentioned legume crops. This will help in developing better and faster products for both farmers and markets.

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