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Chapter 8

Forward Breeding for Efficient Selection



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Abstract Global food security is the *numero uno* priority in the current global situation, threatened by a number of challenges catalyzed by accelerated climate change and population growth. Crop improvement coupled with the modern plant breeding approaches, such as genomic-assisted breeding, is a proven solution to meet the food security. One of the key mandates in the modern plant breeding program is to combine the power of genomic selection into the breeding pipeline employing a low-cost genotyping solution. Several SNP marker-based platforms are now available depending on the objectives and field of application; despite the

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availability of different platforms, the public sectors face challenges in terms of funding and accessibility to the latest technology when compared to private sectors. Shared genotyping platform coupled with open breeding informatics involving different stakeholders with active support from donors will address several constraints faced by the public breeding program. Here, we summarize the available forward breeding genomic resources in the space of low-mid-density genotyping platform with special emphasis on shared services for four crop groups:

1. Wheat (cereal)
2. Potato (roots, tubers, and bananas (RTB crops))
3. Groundnut (grain legumes)
4. Vigna species (legumes)

Keywords Forward breeding · Genomics-assisted breeding · Marker-assisted selection · Single-nucleotide polymorphism · Genomic selection · Wheat · Potato · Groundnut · Vigna · Cowpea · Mung bean · Black gram

8.1 Introduction

Global food security is the *numero uno* priority in the current global situation, threatened by a number of challenges catalyzed by accelerated climate change and with the expected global population growth to bypass 9.75 billion figures, where more than 2.5 billion people reside in Africa by 2050 (FAOSTAT (2022)). Crop improvement coupled with the modern plant breeding approaches is one of the proven solutions to meet the food security along with number of other factors including, but not limited to exploiting the natural variations. Next-generation breeding, such as genomic-assisted breeding (GAB), employing molecular markers has a significant impact and is considered as a practical way forward to accelerate the crop improvement with specific focus to improved crop yield (Razzaq, Ali, et al. 2021). Importance of GAB is evident from the commitment made by the Consultative Group on International Agricultural Research (CGIAR) with its 2030 Research and Innovation Strategy (Action Area 3) to support the breeding optimization pipelines and implementation of GAB approaches (CGIAR 2021). Methods of plant breeding was positively changed by the implementation of molecular marker technology especially after the boom of the genomic sequencing era that enhanced the pace of crop improvement. From the era of restriction fragment length polymorphisms (RFLPs) to simple sequence repeats (SSRs) to single-nucleotide polymorphisms (SNPs), the marker technology rapidly advanced, and currently, SNPs is considered as the most advanced and commonly used marker systems in plant breeding application (Bohar et al. 2020). One of the key mandates in the modern plant breeding program is to combine the power of genomic selection (GS) into the breeding pipeline. Low-cost genotyping solution, which is affordable and meaningful, makes the practical application of GS integration. Many genotyping platforms are available, among which SNP genotyping method utilizing the high-throughput multiplexed approach is a predominantly used genotyping method, such as genotyping-by-sequencing (GBS). Though GBS is a preferred choice, it lacks

practical suitability, such as requirement of imputation to fill the missing data, and in turn requires a complex bioinformatics to suit the multiyear data interpretation. Diversity Arrays Technology's DArTag (Diversity Arrays Technology, Bruce, Australia), Integrated DNA Technologies' rhAmpSeq (Integrated DNA Technologies, Coralville, IA, USA), and Illumina's AmpliSeq (Illumina, San Diego, CA, USA,) are some of the commercially available pooled and multiplexed sequencing technology targeting the specific SNPs. Though the available platforms demand a high up-front cost for designing, they have a comparative advantage with GBS in terms of repeatability, heterozygotes identification, and requirement of less bioinformatics support (Sneller et al. 2021).

Several SNPs' marker-based platforms are now available, depending on the objectives and field of application such as the following: high-density SNP genotyping platforms (HDSG) for discovery studies and linkage mapping; medium-density SNP genotyping platforms (MDSG) for GS and background studies; and low-density SNP genotyping platforms (LDSG), such as Kompetitive Allele Specific PCR (KASP), for forward breeding application through marker-assisted selection (MAS), marker-assisted backcrossing (MABC), and quality control (QC) analysis (Roorkiwal et al. 2020). Despite the availability of different platforms, the public sectors face challenges in terms of funding and accessibility to latest technology when compared to private sectors. To tackle such situation, Xu et al. suggested that there should be coordinated efforts by the scientific community, particularly in developing countries backed by big donors, such as Bill and Melinda Gates Foundation (BMGF). These efforts, especially in the field of modernization of plant breeding through establishment of public–private partnerships, will improve the international crop improvement system (Xu et al. 2017; Cobb et al. 2019). Shared genotyping platform coupled with open breeding informatics involving different stake holders with active support from donors, such as BMGF, will address several constraints faced by the public breeding program. CGIAR's strategic approach in this direction includes the development of world-class shared genotyping service through High-Throughput Genotyping Project (HTPG) (<http://cegsb.icrisat.org/high-throughput-genotyping-project-htpg/>), the Genomics Open-Source Breeding Informatics Initiative (GOBii) (<http://gobiiproject.org/>), and the Excellence in Breeding (EiB) (<https://excellenceinbreeding.org/>) platform led by the CGIAR institutes with the able funding of the BMGF (Bohar et al. 2020). HTPG facilitated low-cost and high-throughput genotyping for CGIAR and National Agricultural Research Systems (NARS) led by ICRISAT (2016–2020) and further transitioned to genotyping/sequencing tools and services module of EiB platform through service provider, Intertek AgriTech (<http://www.intertek.com/agriculture/agritech/>) (Bohar et al. 2020).

EiB has been coordinating and supporting the use of genotyping by NARS and has launched shared genotyping services, such as EiB-LDSG and EiB-MDSG, for the benefit of national, CGIAR, and other breeding programs. Currently, the EiB shared services is functional with all CGIAR centers and their partner programs in rice, wheat, maize, several millets, legumes, and several other crops, which are readily deployable in the breeding programs with continuous addition of new crops and marker resources. These services are targeted at CGIAR and NARS

breeding institutions, aggregating demand across institutions to offer high-quality, low-cost genotyping with faster turnaround time of 10–15 business working days. Implementation of shared services is one among the six requests from the funder consortium Crops to End Hunger (CtEH), whose overall objective is to modernize CGIAR breeding programs and networks ensuring those programs deliver the highest possible rate of genetic gains in farmers' field (Hunt et al. 2021). The EiB-LDSG service (formerly HTPG) based on KASP platform, which is cost-effective up to 200 markers, is suited for applications including specific trait screening (foreground selection), QC, and MAS. The markers available for use in EiB-LDSG can be accessed at <https://excellenceinbreeding.org/module3/kasp>, which is continuously updated and improved (EiB-LDSG 2022). The EiB-MDSG service is a DArTag genotyping method with a density of up to 4000 markers, primarily suited to GS applications, but can also be used for diversity studies, DNA fingerprinting, and MABC for background recovery analysis (EiB-MDSG 2022).

Success stories and publications incorporating the HTPG, EiB-LDSG, and/or EiB-MDSG are reported in several crops, such as groundnut (Parmar et al. 2021), potato (Kante et al. 2021; Sood et al. 2022), cassava (Le Thuy et al. 2021), sorghum (Mwamahonje et al. 2021), and banana (Garcia Oliveira et al. 2021). Here, we summarize the available forward breeding genomic resources in the space of low-mid-density genotyping platform with special emphasis on the resources available with EiB genotyping shared services for four crop groups: (1) wheat (cereal), (2) potato (roots, tubers, and bananas (RTB crops)), (3) groundnut (grain legumes), and (4) *Vigna* species (legumes).

8.2 Genomic Resources and Forward Breeding in Wheat

Wheat is a key food staple that provides around 20% of protein and calories consumed worldwide. The demand for wheat is projected to continue to grow over the coming decades, particularly in the developing world to feed an increasing population and, with wheat being a preferred food, continuing to account for a substantial share of human energy needs in 2050 (Wageningen 2016). Current annual genetic gains for grain yield of about 1% are being realized in the CIMMYT Global Wheat Program (GWP) for a number of target populations of environments (Crespo-Herrera et al. 2017, 2018; Honsdorf et al. 2018; Gerard et al. 2020). Thus, higher-yielding, more productive varieties continue to be released in developing countries, resulting in enhanced productivity (Lantican et al. 2016). In addition to grain yield improvement together with yield stability, key breeding objectives of the program (similar to others) are resistance/tolerance to biotic and abiotic stresses, end use, and nutritional quality characteristics. In order to keep up with the pressing future demands of wheat production and to adapt to changing environmental factors, wheat breeders overall and at CIMMYT are constantly turning to new and emerging technologies and breeding strategies. For example, advanced genetics and genomics tools are progressively deployed and related operating processes optimized (Fig. 8.1) (Dreisigacker et al. 2016, 2021).

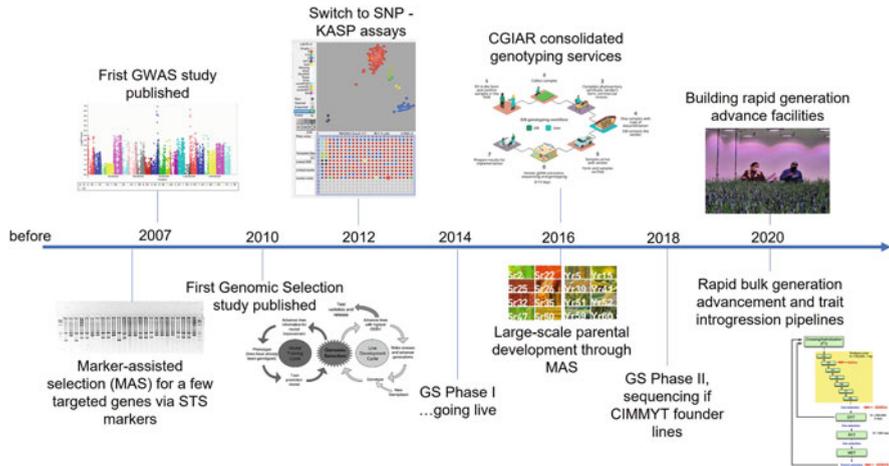


Fig. 8.1 Implementation of genetic and genomic tools in the CIMMYT Global Wheat Program

Marker-assisted forward and backcross breeding are approaches that can be successfully deployed in crops, mainly when (i) a target trait is rather difficult to manage in the field because it is expensive or time-consuming to measure, has low penetrance, or has complex inheritance; (ii) trait selection depends on specific environments or host developmental stages; (iii) recessive alleles during backcrossing need to be maintained or for speeding up backcross breeding in general; and (iv) pyramiding multiple monogenic traits or several QTL for single traits is looked for (Miedaner and Korzun 2012). However, often the number of markers per trait with enough information content about their relevance and usefulness to a breeding program is low. To increase response to selection using marker-assisted forward and backcross breeding in wheat, markers related to genes for disease resistance, end use, and nutritional quality are mainly used, because they show reasonable effect size. In the CIMMYT GWP, the targeted development of rust-resistant wheat germplasm is probably the most important example for which markers are adopted. The aim is to develop elite breeding lines that carry a combination of non-race-specific adult-plant resistance genes and race-specific genes, to avoid applying extremely high selection pressure on the pathogen that might endanger the avirulence of individual genes in developing countries. Rust research in the GWP has mapped and officially designated several rust genes (reviewed by Lan and Basnet 2016). Multiple pleiotropic non-race-specific genes (including *Lr34/Yr18/Sr57/Pm38*, *Lr46/Yr29/Sr58/Pm39*, and *Sr2/Yr30/Lr27/Pm*) are present in the CIMMYT wheat germplasm pool and build the basis of resistance against the three rusts (Singh et al. 2014). A larger number of race-specific stem and yellow rust resistance genes not present in CIMMYT germplasm have recently been introgressed into a set of elite genetic backgrounds via MABC to develop new parental lines (Table 8.1). In addition to rust, resistance to fusarium head blight (FHB) and *Septoria tritici* blotch are targets for forward breeding. For example, recombinant inbred lines that have the resistant *Fhb1* and *Sr2* alleles in coupled

Table 8.1 List of rust resistance genes introgressed via MAS for parental development

| Trait | Source | Gene |
|------------------------------------|---|---------------------------------------|
| Pleiotropic adult-plant resistance | RL6077/AOC-YR | <i>Lr67/Yr46/Sr55/Pm46</i> |
| | SUJATA | <i>Lr67/Yr46/Sr55/Pm46, YrSuj-7BL</i> |
| Stem rust resistance genes | SWSR22T.B. | <i>Sr22</i> |
| | KACHU/3/WHEAR//2*PRL/2*PASTOR | <i>Sr25</i> |
| | SHORT SR26 TRANS./4/3*CHIBIA//PRLII/CM65531/3/MISR 2/5/2*BAJ #1 | <i>Sr26</i> |
| | SR32 | <i>Sr32</i> |
| | W3763-SR35 | <i>Sr35</i> |
| | SR47 | <i>Sr47</i> |
| | SR50 | <i>Sr50</i> |
| Stripe rust resistance genes | ALPOWA | <i>Yr39</i> |
| | CHUAN NONG 19 | <i>Yr41</i> |
| | BLANCA GRANDE 515 | <i>Yr5, Yr15</i> |
| | SUMMIT 515 | <i>Yr5, Yr15</i> |
| | YR51#5515-1 | <i>Yr51</i> |
| | KOELZ W 11192:AE | <i>Yr52</i> |
| | YR57#5474-6 | <i>Yr57</i> |
| | IRAGI | <i>Yr59</i> |
| LALBMONO1*4/PVN | <i>Yr60</i> | |

phase linkage in the background of the cultivar HARTOG were crossed with CIMMYT bread wheat lines and selected with molecular markers for both genes in addition to the use of pseudo-black chaff (PBC) as a phenotypic marker for the selection of *Sr2* (He et al. 2020). The *Fhb1*-resistant allele has previously been absent in CIMMYT germplasm as the gene is usually tightly linked in repulsion phase (the case where each homologous chromosome has one dominant and one recessive allele from the two genes) on chromosome 3BS and CIMMYT wheat breeding focused much time and energy on stem rust resistance. Durum wheat (*Triticum turgidum* subsp. *durum*) is also an important crop worldwide, while its production runs secondary to that of bread wheat. One aspect to consider is the relatively restricted food functionalities of durum wheat, primarily attributed to its kernel texture and gluten strength limitations (Morris et al. 2019). During the last few years, soft kernel durum was crossed with CIMMYT elite durum lines to produce soft kernel progeny with a high degree of genetic variance for milling and baking quality. Selection for the novel soft kernel types was routinely supported with associated KASP markers.

Breeding in Mexico routinely utilizes two crop seasons per year that cuts the breeding time by about half but also allows selection for a range of traits at contrasting field sites that have distinct daylength and temperature regimes. MAS is deployed in both crop-seasons. In 2020, a field greenhouse and rapid-generation advance (RGA) greenhouse facility at the CIMMYT Toluca research station were

constructed. Donor parents derived from the previous parental development pipelines are now used and crossed with selected elite lines for rapid introgression, pyramiding, and trait augmentation through RGA. The scaling-up marker-assisted forward and backcross breeding in the public sector has long been hampered by high genotyping costs and insufficient data management support. And still, the cost of genotyping for several high-throughput SNP platforms is inversely proportional to sample quantity, which in the case of smaller public sector organizations that have low individual demand partly impedes the routine deployment of molecular markers. In 2016, the HTPG project supported by the BMGF developed a shared industrial-scale service of low-density SNP genotyping serving the CGIAR and partner breeding programs. A low-cost, fast turnaround service (EiB-LDSG) was established by EIB platform. EiB-LDSG is routinely used in the CIMMYT GWP. Information on the wheat markers that are routinely applied is also available at <https://excellenceinbreeding.org/module3/kasp>.

8.3 Genomic Resources and Forward Breeding in Potato

To come up with a satisfactory variety, potato breeders must concentrate their efforts on selecting for a multitude of traits besides yield. Depending on the breeding program, goals as many as 12 traits have been proposed (Bonierbale et al. 2019). Although stacking of multiple genes is complicated in highly heterozygous tetraploid potato, it is possible to make progress through a dedicated MAS procedure (Bradshaw 2017; Stefańczyk et al. 2020; Rakosy-Tican et al. 2020). Furthermore, MAS facilitates the traits-based selection without heavy phenotypic evaluation at early stages, as compared to conventional breeding methods. In International Potato Center (CIP), the main breeding targets were for decades centered on disease resistance and climate resilience to achieve varieties that are productive under stressful conditions. The main diseases of potato in the breeding target areas of CIP are late blight (LB) caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, potato virus Y (PVY), potato virus X (PVX), and potato leaf roll virus (PLRV). Molecular markers have been identified to trace the presence of many genes that provide control to these diseases (Nie et al. 2016; Fulladolsa et al. 2015; Ottoman et al. 2009; Whitworth et al. 2009; Tiwari et al. 2013), and significant time and cost savings can be achieved by using them instead of traditional phenotyping. We had calculated that the use of MAS for *Rladg* gene that provides resistance to PLRV (Mihovilovich et al. 2014; Velásquez et al. 2007) can save up to 88% of the costs as compared to phenotypic assays (RTB. 2019). This is particularly valuable for traits such as PLRV resistance that is extremely difficult to measure because the virus is phloem limited and thus infection assays require the use of vector insects or grafting to indicator plants (Mihovilovich et al. 2014). The *Rladg* assay that was developed at CIP is a gel-based SCAR marker (Mihovilovich et al. 2014) that is well suited for the screening of a relatively small number of samples. However, this screening method is not ideal for screening in the early breeding stages when

thousands of clones would be evaluated. Furthermore, a breeding program is usually interested in screening for more than one single trait, and therefore, screening for multiple markers in a single assay is more efficient. KASP offers an excellent cost-efficient option for breeding programs to develop custom sets of low-density markers for purposes, such as QC or MAS (Semagn et al. 2014; Caruana et al. 2021). Therefore, at CIP we started to convert some of the most important trait markers for our breeding program into KASP markers. The first trait markers converted and validated are two markers for PVY resistance and two for LB resistance (Kante et al. 2021). The PVY markers were designed for the *Ryadg* gene that is the main source of PVY resistance in CIP breeding populations (de Herrera et al. 2018). Based on high assay power and low error rate, the new markers work very efficiently in CIP breeding program (Kante et al. 2021). The LB markers were discovered in GWAS studies using CIP breeding germplasm and located in or near the QTL in chromosome 9 that has been shown to contain *R8* resistance gene (Lindqvist-Kreuzer et al. 2014, 2021; Jiang et al. 2018). These markers have a variable performance, depending on the germplasm they are applied to, but have consistently good performance in the populations targeting LB as a main trait (Kante et al. 2021; M. Gastelo, pers. Comm). These markers are available at <https://excellenceinbreeding.org/module3/kasp> through EIB-LDSG. Other markers well worth pursuing as a KASP assay for disease resistance traits in CIP germplasm include at least gene *Rx* for PVX resistance and *Rladg* for PLRV resistance.

Another useful application for KASP markers is identity verification with the help of a set of QC markers. QC marker sets have been reported for maize, rice, and sweet potato (Gemenet et al. 2020a; Ndjiondjop et al. 2018; Semagn et al. 2012). Mislabeled genotypes at any stage of the breeding process are problematic and should be avoided as they waste time and resources and negatively affect genetic gains (Gemenet et al. 2020a). We selected a set of SNP markers from the SolCAP Infinium array that had discriminatory power to differentiate CIP breeding germplasm. Using the tetraploid calls, it was possible to discriminate full and half sibs with as few as 20 SNP markers (Kante et al. 2021). Several cases of mislabeling were discovered when this set of markers was applied to test the identity of clones across different stages (Kante et al. 2021). Although the KASP assay for a relatively low number of markers is cost-efficient, there is a need to carefully define the best approach for routine use of these markers in the breeding program. At the very least, the CIP breeding program will strive to verify the identity of the progenitors in the crossing block and the advanced clones that are shared with partners for variety evaluation.

The rate of progress in genetic gains by recurrent selection in potato is largely limited by the number of vegetative generations needed to complete all phenotyping (Bradshaw 2017). GS and genomic estimations of breeding values are a powerful tool that can shorten the breeding cycle of potato and lead to increased genetic gains for several traits (Ortiz 2020). Most studies published in potato GS up to date have utilized hybridization-based Illumina SNP SolCAP array (Stich and Van Inghelandt 2018; Enciso-Rodriguez et al. 2018; Endelman et al. 2018) or GBS (Sverrisdóttir et al. 2017; Caruana et al. 2019; Byrne et al. 2020). SolCAP array is a relatively

expensive assay keeping in mind that not all markers are applicable across different breeding populations (Slater et al. 2014). GBS can be more affordable particularly if sequencing depth is kept at a moderate level, but it is computationally intensive (Gemenet et al. 2020b). However, if one wishes to utilize the allele dosage information in the GS model, it is advisable to consider sequencing depth of 60–80x so that the different heterozygous states can be called reliably in autotetraploid potato (Uitdewilligen et al. 2013).

Targeted sequencing with selected SNP across the genome is therefore an attractive option to reduce the number of markers to a more manageable level allowing for a sufficient sequencing depth (Slater et al. 2014). DArTag is a targeted Diversity Arrays Technology (DArT, <http://www.diversityarrays.com>), genotyping method where a single oligonucleotide is used to capture selected SNPs or indels. Further advantage of this system is that the sequencing of the fragments allows for identification of other polymorphisms beyond the originally targeted SNP/indel and thus a capture of additional haplotypes. Tetraploid calls can be obtained from the raw read counts, even for samples with low read depth (<15). As part of the EiB-MDSG efforts, we developed such a reduced, but representative set of markers using previously available data points from the SolCAP SNP (Hamilton et al. 2011; Felcher et al. 2012) and SolSTW SNP (Uitdewilligen et al. 2013; Vos et al. 2015) genotyping efforts with CIP and Jeff Endelman’s Lab at the University of Wisconsin potato germplasm. The marker selection and primer design yielded a set of 2503 markers, with a number of markers per chromosome ranging between 177 and 272. In a standard DArTag assay, these markers have a mean median read depth of 164, which allows for successful dosage calling in tetraploid potato. Like the KASP marker set, the DArTag marker set is in public domain and available for all interested breeding programs through EiB-MDSG. The mid-density DArTag marker set will allow a cost-effective genotyping of the breeding material for genomic prediction. Further, the inclusion of two trait markers for *Ryadg* and *Rysto* into the panel will allow a characterization of the breeding material without necessarily increasing the genotyping costs. Inclusion of more trait markers is and will allow a one-time genotyping of clones through the breeding cycle, for trait characterization and genomic prediction. CIP clones from intermediate trials DArTag genotyping for GS can be done from tuber and/or leaf samples, assuring therefore a rapid availability of molecular data of the prediction population.

8.4 Genomic Resources and Forward Breeding in Groundnut

Groundnut or peanut (*Arachis hypogaea* L.) is an important food and oil crop, cultivated across the tropics and subtropics regions. Globally, it is cultivated on an estimated 29.6 million hectares of area, producing 48.86 million tons (FAOSTAT 2022; <http://www.fao.org/faostat/en/#data/QC>). Moreover, half of groundnut crop

produce is used to extract oil, with the remaining eaten raw or processed. Groundnut is often referred to as the “poor man’s almond” owing to its high nutritional content, like oil, protein, fiber, polyphenols, antioxidants, vitamins, and minerals. Gibbons began breeding work in groundnut around 1976. Groundnut breeding’s major goal is to develop cultivars having high-yielding, early maturity, adaptability to specific conditions and production systems, resilience or endurance to environmental challenges, disease and insect resistance, and improved nutritional quality. Efforts to enhance groundnut breeding via genomics have been very successful, over the previous decades. Availability of genomic resources, such as extensive whole-genome assemblies and transcriptome assemblies, high-density saturated genetic maps, and, most interestingly, linked markers with traits of interest, has eased routine breeding programs (Pandey et al. 2020). Modern-day advanced breeding strategies, such as GS, speed breeding, or RGA, are projected to boost groundnut genetic gains (Parmar et al. 2021). Here, we commence by highlighting recent advances in groundnut genomics, with an emphasis on next-generation technologies.

8.4.1 Genomic Resources in Modern Era

Recent groundnut genomic advancements have enabled the emergence of a diverse array of advanced genomic methods and technologies for crop improvement. The groundnut researchers have succeeded in terms of leveraging genetic resources, notably during the past decade (Fig. 8.2). A wide range of genomic resources, including reference genomes assemblies, genome-wide genetic markers, expression atlas, genotyping platforms (low, mid, and high density), QC panels, and diagnostic markers, have facilitated the translational genomics in groundnut research.

8.4.2 Reference Genomes Assemblies

A reference genome provides a standardized, important basis for genomic and genetic research. Utilizing advanced sequencing technologies, a well-assembled and annotated genome has been developed, which facilitates the understanding of complex genome structure, aids gene discovery, and helps in the exploiting genetic resources for faster crop improvement (Pandey et al. 2020). In 2016, IPGI through Peanut Genome Consortium (PGC) completed the sequencing of two diploid ancestors (*A. duranensis* V14167 and *A. ipaensis* K30076) of cultivated groundnut (Bertioli et al. 2016) in order to solve the complexity associated with assembling chromosomal pseudomolecules. Meanwhile, the Diploid Progenitor Peanut A-Genome Sequencing Consortium (DPPAGSC) sequenced both diploid progenitor species, *A. duranensis* (Chen et al. 2016) and *A. ipaensis* (Lu et al. 2018). Furthermore, with the advent of next-generation sequencing (NGS) technology, it aided research in further improving, refining, and developing high-quality reference

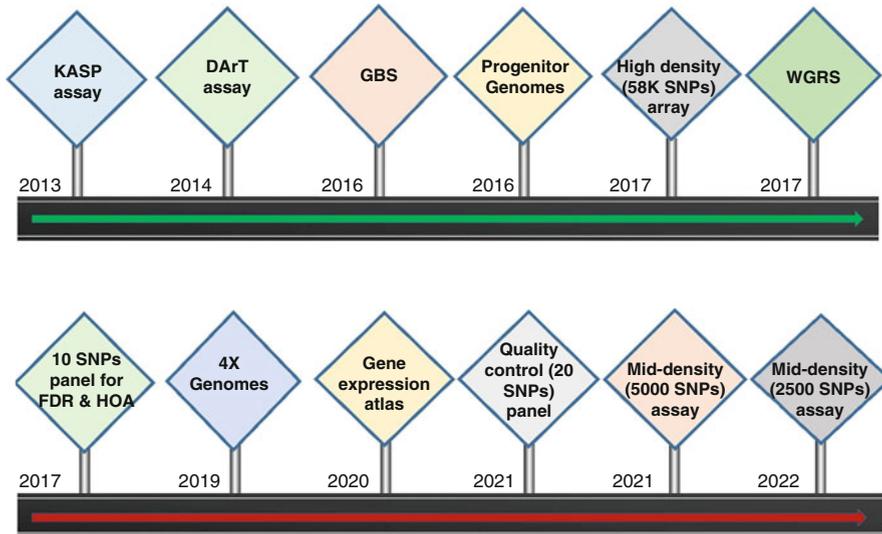


Fig. 8.2 A road map of significant developments in the field of groundnut genomics

genome assemblies for the cultivated tetraploid groundnut. In 2018, the genome assembly for the allotetraploid wild groundnut *A. monticola* was made publicly available (Yin et al. 2018). A major breakthrough among groundnut researchers took place with the availability of two reference genomes for subsp. *fastigiata* (Chen et al. 2019; Zhuang et al. 2019) and one for subsp. *hypogaea* (Bertioli et al. 2019). These reference genome assemblies revealed new knowledge on groundnut genes that have been impacted by domestication and breeding, highlighting breeding possibilities for future.

8.4.3 Whole-Genome Resequencing and Genome-Wide Markers

Adoption of NGS approaches enabled the discovery and deployment of a diverse array of molecular markers in groundnut. Both diploid genomes (*A. duranensis* and *A. ipaensis*) were mined for markers, resulting in the discovery of 135,529 and 199,957 SSRs, respectively (Zhao et al. 2017). Additional comparative diploid genome study between *A. duranensis* and *A. ipansis* detected 515,223 InDels, i.e., 269,973 insertions and 245,250 deletions (Vishwakarma et al. 2017). Furthermore, high-coverage WGRS data for 41 distinct genotypes have been generated, resulting in the finding of 98,375 SNPs in the A-subgenome and 65,407 SNPs in the B-subgenome (Pandey et al. 2017a; Clevenger et al. 2017). Notably, 58,233 high-quality informative SNPs were employed to develop high-density genotyping platform, “Axiom_*Arachis*” Array (Pandey et al. 2017a). Nowadays, it is commonly

utilized in groundnut molecular breeding routine activities for mapping traits of interest and detection of associated genomic regions. Additionally, 300 diverse accessions of the ICRISAT groundnut reference set have been sequenced in order to explore genome-wide structural changes, diversity, and marker trait association studies (see Varshney et al. 2019). Similar initiatives are ongoing in the USA and China for diverse groundnut sets. Likewise, significant use of WGRS data has resulted in the discovery of unique alleles, signature sequences, and related markers.

8.4.4 Gene Expression Atlas

NGS not only advances genome sequencing and novel genome assembly development, but it also enhances genome annotation advancement via the RNA sequencing (RNA-seq) strategy. A groundnut subsp. *hypogaea* gene expression atlas was generated (Clevenger et al. 2017). This investigation generated gene expression data from 22 groundnut tissues and reported 8816 putative homeologous genes, over 9000 alternative splicing events, and over 6000 non-coding RNA. Similarly, the second groundnut transcriptome map has been generated using RNA-seq of 39 samples from various tissues and environments. This map represents 91.73% of all annotated genes (Zhuang et al. 2019). Subsequently, a gene atlas for subsp. *fastigiata* has been employed by utilizing the same subspecies tetraploid genome (Sinha et al. 2020). Furthermore, genome annotation expansion facilitates the integration of proteome and metabolome atlases. These findings will help us to better understand genomes that have more RNA genes than protein-coding ones. Crop trait development and expression will be better understood if the genome, metabolome, and epigenome are all studied in greater depth.

8.4.5 Rapid and Cost-Effective Genotyping Assays

The current crop genomics scenario has been transformed by NGS technologies, which give a multitude of sequence information with significant increases in coverage, speed, and expense. Such advances have permitted the design of low- to high-throughput genotyping platforms. SNPs are regarded the ideal marker due to genome-wide uniform distribution and cost-effectiveness. For the present, efficient and cost-effective genotyping platforms are being developed in groundnut genomics, which will be used according to the study's objective. For example: (a) High-density genotyping platform ("Axiom_Arachis" 58 K SNP arrays) has been developed and utilized in several studies, marker trait analysis, dense genetic map construction, and QTL analysis. (b) A mid-density assay (2500–5000 SNPs) has been successfully deployed in genetic mapping; QTL analysis (Bomireddy et al. 2022) is suggested for performing GS, genetic diversity assessment, and background selection; using Agri-seq 5 K assay, genotyping of about 3000 lines has been done so

far in order to optimize genomic prediction in groundnut breeding. Similar DArT-seq assay with 2500 SNPs has been developed and ready for deployment through EiB-MDSG. And (c) low-density assay (10–100 SNPs) can be effectively utilized for QC assessment and purity testing of founder parents, hybridity confirmation, and early generation selection through EiB-LDSG. Panel of highly informative 20 SNPs has successfully tested for quality check among founder parents of IC-Asia, IC-WCA, IC-ESA, ICAR-DGR, and UAS-Dharwad breeding (Unpublished). So far, QC panel has effectively used in hybridity testing of more than 700 F₁ plants (IC-Asia, ICAR-DGR, and UAS-Dharwad) and for determination of homozygosity among advanced breeding lines.

All the abovementioned genotyping assays are successfully deployed in routine breeding activities. In future, such genotyping platforms will become more widely used in breeding programs around the world and pave a new era of genomics in molecular breeding.

8.4.6 Sequencing-Based Trait Mapping

New inventions in sequencing and high-throughput genotyping have accelerated trait discovery studies significantly while also enabling candidate gene identification at a fast pace. The substantial decrease in the cost of sequencing and the increased advent of high reference genomes in groundnut have facilitated sequence-based trait mapping more feasible and time-effective, over the past 2–3 years. In fact, right now, sequencing-based mapping is now accomplished out by either sequencing the entire populations or pooling samples exhibiting extreme phenotypes of the desired trait (Varshney et al. 2019). Inside this aspect, the low-to high-density sequencing methodologies are being employed to develop high-density genetic maps and improve trait mapping precision in groundnut. Recently, the GBS method is employed to develop high-density maps, to perform QTL mapping and detection of candidate genes (Pandey et al. 2017c; Han et al. 2018; Dodia et al. 2019). By using SLAF-seq technology, two high-density maps (with 2266 and 2808 SNP loci) have been constructed, for QTL mapping of quality and growth habit traits (Hu et al. 2018; Li et al. 2019), respectively. Similar approach has been successfully deployed to develop dense map (with 7184 SNPs), which facilitates to narrow down the co-localized regions associated with seed size traits, resulting in the detection of trait-linked candidate genes. Additionally, same genetic map has been used for testa color trait mapping (Zhuang et al. 2019). Association mapping of 158 groundnut diverse accessions with 17,338 polymorphic SNPs has allowed to identify marker trait association for agronomic traits (Zhang et al. 2017). To obtain large number of polymorphic SNPs, the WGRS approach has been deployed in RIL population (Tifrunner GT-C20), which enabled the generation of high-density genetic maps (8869 to 11,106 SNP loci), fine mapping of genomic region, and candidate gene discovery for ELS, LLS, and TSWV resistance (Agarwal et al. 2018, 2019). However, both WGRS and GBS platforms have been extensively deployed for mapping

traits and identification of QTLs in groundnut, but each has its own shortcomings. Recent methods for trait mapping (QTL-seq, Indel-seq, Seq-BSA, MutMap, and BSR-seq) generally rely on high- and low-bulk sample pooled sequencing, which exhibits extreme phenotypes related to the trait of interest under investigation. Among all, the “QTL-Seq” approach has been effective in identifying genomic regions and candidate genes in groundnut (Pandey et al. 2017b; Clevenger et al. 2018; Luo et al. 2019; Zhuang et al. 2019; Kumar et al. 2020; Zhao et al. 2020). Such research efforts have been facilitating the development of diagnostic markers and will help in pyramiding of QTLs associated with traits of interest in groundnut breeding.

8.4.7 Genomics-Assisted Breeding to Accelerate Groundnut Breeding

The groundnut researcher has taken several initiatives over the past decade to provide efficient genetic resources for crop improvement. Groundnut achieved the status of crop with the plentiful of genomic resources, which enable identification of genes and associated markers used in GAB. Based on the available genomic resources, diagnostic markers for high-oleic acid and resistance to nematode, rust, and LLS have been effectively generated in groundnut. The three GAB procedures, notably MAS or MABC, marker-assisted recurrent selection (MARS), and GS, have proven the most effective in groundnut. The development of a nematode-resistant variety, NemaTAM, was the first successful use of MAS (Simpson et al. 2003). Later, by pyramiding the nematode resistance and high-oleic trait, employing molecular markers linked with these traits, a high-oleic “Tifguard High O/L cultivar” has been developed (Chu et al. 2011). Following that, favorable alleles (*ahFAD2A* and *ahFAD2B*) for oleic acid content from the donor parent SunOleic 95R were transferred to ICGV 06110, ICGV 06142, and ICGV 06420 using MAS (Pasupuleti et al. 2016). Similarly, utilizing the MABC approach, high-oleate lines have been developed in ICGV 05141 (Bera et al. 2018), GPBD 4 (Ndeve et al. 2019), and ICGV 06100 (Bera et al. 2018). In another study, high-oleate lines have been developed through MABC utilizing favorable alleles from parents (KN176, DF12, and KX016) (Huang et al. 2019). Likewise, work has been done in developing cultivars resistant to foliar diseases (rust and LLS) together on high-oleic background (Janila et al. 2016; Bera et al. 2018; Shasidhar et al. 2020). There have certain attempts to combine high-oleic acid with foliar disease resistance in GPBD 4, G 2–52, TMV 2, and JL 24, in addition to ICGV 06189 variety (Bhat et al. 2022). Among the molecular breeding lines developed through marker-assisted backcrossing for high oleic acid (Janila et al. 2016), two Virginia bunch high oleic varieties namely Girnar 4 (ICGV 15083) and Girnar 5 (ICGV 15090) and two Spanish bunch high oleic varieties namely GG 39 (ICGV 16697) and GG 40 (ICGV 16688) are released for cultivation in India. More recently, two elite

varieties, GPBD 4 and G-252, have been improved for oleic acid content using MABC (Jadhav et al. 2021). Now, development of groundnut backcross lines has been made more precise and efficient using the available genetic resources for LLS and rust resistance (Pandey et al. 2020). The first effort has been made by utilizing SSR markers to enhance resistance for rust in three susceptible varieties, ICGV 91114, JL 24, and TAG 24 (Varshney et al. 2014). Using two to three backcrosses and selfing, 200 backcross lines were selected. From these, 81 lines were examined in the field and found to be more resistant to rust. As contrast to susceptible parents, these lines produced far more pod yield (56–96%) in affected environments (Pasupuleti et al. 2016). With GPBD 4 as the donor, various attempts have been made to develop LLS- and rust-resistant backcross lines in JL 24 (Yeri and Bhat 2016) and TMV 2 (Kolekar et al. 2017; Ramakrishnan et al. 2020). Two foliar disease resistance varieties namely Improved JL 24 (DBG 3) and Super TMV 2 (DBG 4) using donor source GPBD 4 (Bhat et al. 2022) were developed using marker-assisted selection and released for cultivation in Karnataka state of India. The most of lines are being tested in multiple locations or on large-scale farms in order to facilitate varietal development (Bhat et al. 2022).

8.5 Genomic Resources and Forward Breeding in *Vigna* Species

The genus *Vigna* with around nine domesticated crops, viz., mung bean (*Vigna radiata* (L.) R. Wilczek var. *radiata*), black gram, (*V. mungo* (L.) Hepper), cowpea (*V. unguiculata* (L.) Walp), moth bean (*V. aconitifolia* (Jacq.) Marechal), azuki bean (*V. angularis* (Willd.) Ohwi & H. Ohashi), rice bean (*V. umbellata* (Thunb.) Ohwi & H. Ohashi), creole bean (*V. reflexo-pilosa*), tuber cowpea (*V. vexillata* (L.) A. Rich), and bambara groundnut (*V. subterranean* (L.) Verdc.), is one of the important genera contributing toward food and nutritional security across the world (Takahashi and Tomooka 2020). Except for mung bean, cowpea, and black gram, the other species have limited progress on development of genomic resources and use of forward breeding approaches for crop improvement. The forward breeding approaches have been successfully proven efficient in enhancing selection accuracies and intensity for complex traits in many crops, thus helping breeders in selecting individuals with the most desirable traits of the product profile. The initial efforts used isoenzymes, random amplified polymorphic DNA (RAPD), and RFLP markers and later shifted to microsatellite markers derived from various *Vigna* species for the construction of genetic maps and to find QTLs associated with the traits of interests. The recent advancement in whole-genome sequence has strongly improved the access to molecular markers for these crops. Several thousands of SNP markers have been produced by GBS and WGRS, which are being used to assess the diversity at the genomic level and for developing new genomic resources including diagnostic markers and tools for deployment in breeding programs. The genomic resources

available in cowpea (Muñoz-Amatriaín et al. 2017; Boukar et al. 2019), mung bean (Kim et al. 2015), and black gram (Bisht and Singh 2013) are discussed in detail in earlier studies. The important genomic resources that are useful for the genetic improvement of important *Vigna* crops through forward breeding approaches are summarized below.

8.5.1 Cowpea

Cowpea (*Vigna unguiculata*), $2n = 22$ with a genome size of 620 MB, is one of the largely grown *Vigna* species in the dry agroecologies of the tropics in Latin America, Africa, and South Asia. The cultivated cowpea belonging to the cultivar group *Unguiculata* is divided into five cultivar groups, namely, *unguiculata*, *sesquipedalis* (yard-long-bean), *textilis*, *biflora*, and *melanophthalmus* (Padulosi and Ng 1997). Initial efforts for use of molecular markers for the cowpea improvement used RFLP (Fatokun et al. 1993), RAPD (Kaga et al. 1996; Simon et al. 2007), inter-simple sequence repeat (ISSR) (Ajibade et al. 2000), amplified fragment length polymorphisms (AFLPs) (Fang et al. 2007), and SSR (Gupta and Gopalakrishna 2010; Ogunkanmi et al. 2008) to characterize accessions belonging to the four subgenera of the genus *Vigna* and to study genetic diversity within cultivated as well as wild relatives of cowpea accessions. The world collection of landraces and African ancestral wild cowpea were characterized at molecular level with >1200 SNP markers. The study identified two major gene pools in cultivated cowpea in Africa, each with landraces mostly distributed in Western Africa (GP1) and Eastern Africa (GP2) (Huynh et al. 2013). GBS was used to discover more SNPs in cowpea that could be used to study genetic diversity, population structure, and phylogenetic relationships (Xiong et al. 2016).

Four QTLs on Vu01 with 24 to 95% PV associated with root-galling and egg masses per root system were reported most effective against resistance to root-knot nematode caused by *M. javanica* (Ndeve et al. 2019). The trait-specific SRR markers associated with different traits, such as seed size, pod fiber thickness, seed weight (Andargie et al. 2011), pod length (Kongjaimun et al. 2012), days to flower (Andargie et al. 2013), pod number per plant (Xu et al. 2013), and pod tenderness (Kongjaimun et al. 2012), were identified in different studies. Similarly, useful SNP markers were reported for cowpea bacterial blight (Agbicodo et al. 2010), foliar thrips (Lucas et al. 2012), leaf senescence (Xu et al. 2013), heat tolerance (Lucas et al. 2013a), seed size (Lucas et al. 2013b), aphid infestation (Huynh et al. 2015), and fusarium wilt (Pottorff et al. 2012) that could be deployed in the breeding programs. The microsatellite marker SSR1 was successfully used to transfer striga resistance gene from the breeding line IT93K-693-2 into three farmers' preferred varieties, viz., IT90K-372-1-2, KVx30-309-6G, and TN5-78 through MABC (Salifou et al. 2016). The resistance to three striga races SG1, SG3, and SG5 from IT97K-499-35 into an elite farmer preferred cowpea cultivar Borno Brown was successfully introgressed using three markers SSR-1, 61RM-2 and C42-26

(Omoigui et al. 2017). Around 28 introgression lines selected in the BC₁F_{2:4} generation with large seed size, brown seed coat color carrying marker alleles were evaluated in the field for resistance to striga resistance. The SSR-1 was identified as best for screening genotypes for striga resistance. A rare haplotype associated with large seeds at the *Css-1* locus was successfully stacked from an African buff seed-type cultivar IT82E-18 (18.5 g/100 seeds) into a blackeye seed-type cultivar CB27 (22 g/100 seed) (Lucas et al. 2015). The foreground and background selections using genome-wide SNPs identified introgression lines with very large seed size (28–35 g/100 seeds) and desirable seed quality traits. For bacterial blight, one major QTL on linkage group (LG) Vu09 (*qtlblb-1*) accounting for 30.58% phenotypic variation (PV) and two QTLs, i.e., *qtlblb-2* and *qtlblb-3* on LG Vu04 with 10.77% and 10.63%, PV, respectively, were reported (Dinesh et al. 2016). The major QTL on Vu09 was successfully introgressed from cultivar V-16 into the bacterial leaf blight susceptible variety C-152 through marker-assisted backcrossing (MABC) (Dinesh et al. 2016).

A set of informative SNP panel, i.e., Cowpea iSelect Consortium Array with 51,128 SNPs, was developed to facilitate researchers with useful genomic resources (Muñoz-Amatriaín et al. 2017). The array was further used to develop a mid-density marker platform for cowpea with 2602 SNP markers distributed evenly throughout 11 chromosomes. The SNPs for the mid-density panel were selected based on iSelect data from 2714 diverse cultivated cowpea accessions with more weightage on 184 most commonly used accessions in African breeding programs while selecting these SNPs. This mid-density array is quite suitable for marker-assisted breeding, genomic-based predictions, QTL studies, molecular diversity analyses, and germ-plasm management applications. KASP fluorescence-based methodology offers rapid and cost-effective genotyping useful for target trait screening, QC, and MAS in the breeding programs across several crops. The KASP assay-based SNP markers were developed and being used in cowpea for screening against resistance to aphid infestation (Huynh et al. 2015) and bacterial blight (Agbicodo et al. 2010) (Table 8.2). The SNP-based foreground and background selections with KASP genotyping platform were successfully used to combine drought tolerance along with nematode and striga resistance into Moussa local, a cowpea variety from Burkina Faso, using MABC (Batieno et al. 2016). Six promising families were identified based on MAS and preliminary field testing for yield under well-watered and water-stress, and striga resistance field trials demonstrated the high efficiency of using SNP markers for foreground and background selections to combine target traits (Batieno et al. 2016). Around 17 KASP-based SNP markers were used to determine parental diversity and to confirm hybridity of cowpea crosses (Ongom et al. 2021). These QC markers differentiated 222 cowpea parental genotypes with mean efficiency of 37.9% and a range of 3.4–82.8%, revealing unique fingerprints of the parents. These markers demonstrated an effective application of KASP-based SNP assay in fingerprinting, confirmation of hybridity, and early detection of true F₁ plants (Ongom et al. 2021).

Table 8.2 Diagnostic trait-specific and QC SNP markers available for KASP genotyping platform useful for forward breeding in cowpea and mung bean

| Target trait | SNP ID | Chr. | Position | SNP/ Indel | Favorable allele | Alternate allele | Reference |
|------------------------------------|-----------|-----------------------|-----------------------|------------|------------------|------------------|------------------------|
| Cowpea | | | | | | | |
| Aphid resistance | snpVU0031 | 2 | 25,345,278–25,345,401 | A/G | A | G | Huynh et al. (2015) |
| | snpVU0032 | 2 | 25,479,793–25,480,105 | A/G | A | G | |
| | snpVU0024 | 5 | 3,748,293–3,748,425 | A/T | A | T | |
| | snpVU0025 | 5 | 4,562,162–4,562,294 | C/G | C | G | |
| Bacterial blight | snpVU0041 | 3 | 992,603–993,420 | C/T | C | T | Agbicodo et al. (2010) |
| Quality control and hybridity test | snpVU0007 | 1 | 36,773,526–36,773,649 | T/C | – | – | Ongom et al. (2021) |
| | snpVU0011 | 2 | 22,941,996–22,942,128 | T/C | – | – | |
| | snpVU0018 | 4 | 16,415,787–16,415,919 | A/G | – | – | |
| | snpVU0019 | 4 | 24,230,438–24,230,570 | T/G | – | – | |
| | snpVU0001 | 5 | 399,824–399,956 | C/G | – | – | |
| | snpVU0002 | 5 | 43,326,556–43,327,417 | A/G | – | – | |
| | snpVU0009 | 6 | 30,511,313–30,511,445 | A/C | – | – | |
| | snpVU0010 | 6 | 34,246,871–34,247,003 | T/G | – | – | |
| | snpVU0003 | 7 | 4,914,544–491,665 | T/C | – | – | |
| | snpVU0004 | 7 | 39,680,298–39,680,430 | T/C | – | – | |
| | snpVU0008 | 8 | 34,271,840–34,271,972 | A/G | – | – | |
| | snpVU0012 | 9 | 29,111,205–29,111,337 | A/C | – | – | |
| | snpVU0013 | 9 | 37,010,557–37,010,817 | A/T | – | – | |
| | snpVU0016 | 10 | 37,900,312–37,900,440 | A/G | – | – | |
| snpVU0017 | 10 | 967,432–967,564 | C/G | – | – | | |
| snpVU0014 | 11 | 34,083,600–34,083,732 | A/G | – | – | | |

(continued)

Table 8.2 (continued)

| Target trait | SNP ID | Chr. | Position | SNP/ Indel | Favorable allele | Alternate allele | Reference |
|------------------------------|------------|------|-----------------------|------------|------------------|------------------|----------------------------|
| | snpVU0015 | 11 | 12,936,036–12,936,168 | T/C | – | – | |
| Mung bean^a | | | | | | | |
| Bruchid resistance | snpVR00001 | 5 | 5,178,332 | G/A | G | A | Schafleitner et al. (2016) |
| | snpVR00002 | 5 | 5,179,402 | T/C | T | C | |
| | snpVR00003 | 5 | 5,454,538 | T/C | T | C | |
| | snpVR00004 | 5 | 5,622,070 | G/A | G | A | |
| | snpVR00005 | 5 | 5,662,479 | G/A | G | A | |
| | snpVR00006 | 5 | 5,730,691 | G/A | G | A | |
| | snpVR00007 | 5 | 5,953,917 | A/T | A | T | |
| | snpVR00008 | 5 | 5,974,663 | C/T | C | T | |
| | snpVR00009 | 3 | 10,431,528 | T/A | T | A | |
| | snpVR00010 | 4 | 15,255,162 | T/G | T | G | |

^aSNPs for bruchid resistance in mung bean are being validated for their selection efficiency in the KASP platform

8.5.2 Mung Bean

Mung bean (*Vigna radiata* (L.) R. Wilczek var. *radiata*), an Asiatic *Vigna* species also known as green gram or moong, is grown in around 7.3 m ha worldwide with an average yield of 721 kg/ha (Nair and Schreinemachers 2020). It is one of the important food and cash crops in the rice-based farming systems of South and Southeast Asia with India and Myanmar together accounting for 60% of global produce of 5.3 m t. Other large producers are China, Indonesia, Thailand, Kenya, and Tanzania. The mung bean yellow mosaic disease (MYMD) and bruchid infestation are major biotic stresses initially focused to develop genomic resources for forward breeding approaches. The RAPD marker OPP 07₈₉₅ was identified to be linked with MYMD resistance using bulk segregant analysis (Dharajiya and Ravindrababu 2019). Two QTLs, i.e., qMYMIV2 and qMYMIV7, with 31.42–37.60% and 29.07–47.36% PV, respectively, were reportedly linked to MYMD resistance (Alam et al. 2014). Four SSR markers, viz., CEDG275, CEDG006, CEDG041, and VES0503, linked to these QTLs could be useful for MAS. Other markers VrD1, CEDG228, CEDG044, and STSbr1 (Singh et al. 2017a, b) and CEDG293, DMB-SSR008, and DMB-SSR059 (Singh et al. 2020) were also reportedly linked with MYMD. Five QTLs with PV that ranged from 10.11 to 20.04% for MYMD resistance were detected on an interspecific recombinant inbred line (RIL) population of mung bean and rice bean. Of these, QTL qMYMV4–1 on LG4 was identified in the same marker interval across years (Mathivathana et al. 2019). The inter-simple sequence repeat, I85420, and ISSR-anchored resistance gene analog markers I42PL-229 and I42PL-222 were successfully used for MAS of powdery mildew (PM) resistance in mung bean. Of these,

I42PL229 was used for negative selection, where I85420 and I42PL-222 were used for positive selection with around 94% selection accuracies when confirmed resistance using detached leaf assay (Chathiranrat et al. 2018). Diagnostic derived cleaved amplified polymorphic sequences (dCAPS1, 2, and 3) and cleaved amplified polymorphic sequences (CAPS) markers (CAPS1, 2, 3, 4, 6, 8, 9, 11, 12, 13, and 14) were reported for resistance to bruchid infestation on LG3, LG4, and LG5 with selection efficiency of over 93% (Schafleitner et al. 2016). Among these, 10 promising markers information used to design SNP markers and their KASP assay to deploy in the breeding program (Table 8.2). These markers are being validated for their selection efficiency using a diverse set of genotypes. The genomic regions qZn-4-3 and qFe-4-1 on LG4 between flanking markers PVBR82-BM210 and qZn-11-2 and qFe-11-1 on LG11 between flanking markers BM141-BM184 were reported for Zn or Fe concentration (Singh et al. 2017a, b). Around 43 SNPs were found to be highly associated with seven seed mineral concentrations traits, including Fe and Zn through genome-wide association study. A total of six genomic regions, one with Fe (five associated SNPs) and five with Zn (7 associated SNPs), were found to be associated with PV ranging from 13 to 22% (Wu et al. 2020).

8.5.3 *Black Gram*

Black gram is a highly nutritious grain legume crop, mainly grown in the South and Southeast Asian countries, including Afghanistan, Bangladesh, India, Myanmar, Pakistan, Sri Lanka, and Thailand, with India contributing over 70% of global black gram production (Kaewwongwal et al. 2015). The efforts of development linkage map in black gram during the initial years used RFLP and AFLP markers (Chaitieng et al. 2006; Gupta et al. 2008). The efforts were also made to identify and deploy SSR markers available in other crops, such as cowpea (Gupta and Gopalakrishna 2010), mung bean, adzuki bean (Gupta and Gopalakrishna 2009), and common bean (Souframanien and Reddy 2015). The discovery of NGS technologies such as Illumina paired-end sequencing resulted in 17.2 million paired-end reads, and 48,291 transcript contigs (TCS) were used for gene discovery and development of 1840 SSRs that could be used for developing linkage maps and linked molecular markers for target traits (Souframanien and Reddy 2015). In black gram, the efforts on identification of QTLs and molecular markers are limited to MYMD (Souframanien and Gopalakrishna 2006; Maiti et al. 2011; Gupta and Gopalakrishna 2013) and bruchid infestation (Souframanien et al. 2010; Somta et al. 2019). An ISSR marker, ISSR8111357, linked to the MYMD resistance gene with a 6.8 cM distance identified, was sequenced to design a sequence characterized amplified region (SCAR) primer to deploy for MAS (Souframanien and Gopalakrishna 2006). The SSR marker CEDG180 linked to MYMD resistance was also reported (Gupta and Gopalakrishna 2013). Two major QTLs governing resistance to MYMD disease in black gram reported on LG2 and LG10 with 20.90 and 24.90% PVE, respectively (Vadivel et al. 2021). The validation of these QTLs in

two other mapping populations identified as qmymv10_60 of LG10 with better selection efficiency could be useful for the MAS/MABC in black gram. Two loci, YR4 and CYR1, were identified associated with resistance to *Mung bean Yellow Mosaic India Virus* (MYMIV) in mung bean, of these CYR1 also co-segregated with MYMIV-resistant F₂, F₃ progenies of black gram (Maiti et al. 2011).

Two QTLs, viz., Cmrae1.1 and Cmrae1.2, were reported for bruchid adult emergence on LG3 and LG4, respectively (Souframanien et al. 2010). However, six QTLs were identified, with two QTLs (Cmrdp1.1 and Cmrdp1.2) on LG 1, three QTLs (Cmrdp1.3, Cmrdp1.4, and Cmrdp1.5) on LG 2, and one QTL (Cmrdp1.6) on LG 10, capturing 8.4 to 16.4% phenotypic variation for developmental period (Souframanien et al. 2010). The draft genome of black gram was sequenced using hybrid genome assembly with Illumina reads and third-generation Oxford Nanopore sequencing technology (Souframanien et al. 2021). It opens tremendous opportunities for the development of marker resources, along with the discovery of QTLs/genes and molecular markers for desirable traits. The genome analysis identified 42,115 genes with a mean coding sequence length of 1131 bp, of which around 80.6% are annotated. Besides, a total of 166,014 SSRs, including 65,180 compound SSRs, were also identified (Jegadeesan et al. 2021). The genome sequence of black gram is expected to provide greater insights and facilitate the identification of genes and QTLs linked to economically important traits for accelerating the genetic gain in black gram. The QTL qCm_PDS2.1 for percent damaged seeds and qVmunBr6.1 (24.32–28.76% PV) and qVmunBr6.2 (15.26–17.37%) for bruchid infestation severity progress mapped on LG 6 in mung bean. Two QTLs, i.e., qVmunBr6.1 and qVmunBr6.2, that are new loci for *C. maculatus* resistance in *Vigna* species will be useful for widening the genetic base of bruchid resistance in black gram (Somta et al. 2019). The SSR markers CEDG030 and CEDG248 were successfully used for hybridity test and ingression of MYMD resistance from rice bean to black gram (Sehrawat et al. 2016). Another successful example of the introgression of QTLs for MYMD resistance on LG2 and LG10 from resistant donor Mash 1008 into the popular black gram variety MDU 1 uses the MABC approach. Nine advanced backcross lines were identified with significant superior performances over recurrent parent MDU1 for yield and MYMD resistance (Subramaniyan et al. 2021).

8.6 Future Prospects

Despite the availability of several SNP markers, the public sectors face several challenges compared to private sectors when it comes to accessibility of these platform for implementation. Shared genotyping platform are expected to address several constraints faced by the public breeding program and will enable the implementation of genotyping tools into routine breeding operation. Availability of several LDSG-based trait and QC markers for forward breeding especially for QC and MAS and the MDSG-based medium density SNP panel will be useful for diversity studies, DNA fingerprinting, and MABC for background recovery analysis

and GS applications in wheat, potato, and groundnut crops. The *Vigna* species crops were previously considered to be an orphan crop due to the limited availability of genomic resources compared to other legume and cereal crops. However, the recent progress on draft genome sequencing of mung bean (Kang et al. 2014), cowpea (Lonardi et al. 2019), black gram (Jegadeesan et al. 2021), and azuki bean (Kang et al. 2015) would help in accelerating the development of genomic resources and varietal improvement through forward breeding in *Vigna* crops. Collecting and resequencing *Vigna* species from different geographical areas would help researchers investigate allelic variation in beneficial traits that can be mined from wild relatives. These new resources would also open the door to genomic research in other *Vigna* species. More focus should be given to bring the identified markers on a cost-effective genotyping platform, i.e., KASP for their deployment in the breeding program. Utilization of 100-150 SNPs using DArTag panels for QC in potato and sweet potato (polyploids in general) would help streamline the QC implementation in a cost-effective manner. The enhanced precision and selection intensities for different complex target traits using diagnostic cost-effective molecular markers would accelerate the rate of genetic gains in crops and help breeders in developing the market preferred varieties.

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