REVIEW ARTICLE

Genetics, genomics and breeding of groundnut (Arachis hypogaea L.)

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Abstract

Groundnut is an important food and oil crop in the semiarid tropics, contributing to household food consumption and cash income. In Asia and Africa, yields are low attributed to various production constraints. This review paper highlights advances in genetics, genomics and breeding to improve the productivity of groundnut. Genetic studies concerning inheritance, genetic variability and heritability, combining ability and trait correlations have provided a better understanding of the crop’s genetics to develop appropriate breeding strategies for target traits. Several improved lines and sources of variability have been identified or developed for various economically important traits through conventional breeding. Significant advances have also been made in groundnut genomics including genome sequencing, marker development and genetic and trait mapping. These advances have led to a better understanding of the groundnut genome, discovery of genes/variants for traits of interest and integration of marker-assisted breeding for selected traits. The integration of genomic tools into the breeding process accompanied with increased precision of yield trialing and phenotyping will increase the efficiency and enhance the genetic gain for release of improved groundnut varieties.

KEYWORDS
breeding, genetic maps, genetics, genomics, groundnut, molecular markers, QTL

1 INTRODUCTION

Groundnut (Arachis hypogaea L.), also known as peanut, is a member of genus Arachis and family Leguminosae (Krapovicks & Gregory, 1994). It is believed to have originated in the southern Bolivia to northern Argentina region of South America. The genus Arachis contains 80 species, and most of them are diploid (2n = 2x = 20) with only two allotetraploids. The cultivated groundnut is allotetraploid
hybridization between two wild species, Arachis duranensis (AA-genome, \(2n = 2x = 20\)) named as “A-genome ancestor” and Arachis ipaensis (BB-genome, \(2n = 2x = 20\)) named as “B-genome ancestor” and subsequent chromosome doubling. Based on the patterns of reproductive and vegetative branching and on the pod morphology, the cultivated species is divided into two cultivated subspecies that is A. hypogaea subsp. hypogaea and A. hypogaea subsp. fastigiata. The subspecies are further divided into botanical varieties. The subsp. hypogaea is divided into hypogaea (virginia) and hirsuta, while the subsp. fastigiata is divided into fastigiata (valencia), vulgaris (Spanish), peruviana and aequatoriana (Krapovickas & Gregory, 1994).

Groundnut is grown in more than 100 countries covering over 26 million (M) hectares (ha) area in 2014 with a global production of about 44 M metric tons and an average yield of about 1,655 kg/ha (FAOSTAT 2017). Asia (58.3%) and Africa (31.6%) accounted for about 90% of the world’s production with China (16.6 M tons), India (6.6 M tons) and Nigeria (3.4 M tons) being the top three largest producing countries (FAOSTAT, 2017). The groundnut seed contains 22% to 30% protein and 35% to 60% oil and is a rich source of dietary fibre, minerals, vitamins and bioactive compounds, hence contributing to household nutrition. It is suitable for making nutrient-dense foods for alleviating malnutrition in vulnerable groups such as pregnant and breastfeeding women and children under 2 years, particularly in developing countries (Anim-Somuah, Henson, Humphrey, & Robinson, 2013). The haulms and groundnut cake are important sources of animal feed. In addition, groundnut has the ability to fix atmospheric nitrogen benefitting the succeeding crop. As a cash crop, it is frequently traded locally, regionally and globally, significantly contributing to rural household cash income and national economy. In the west and central Africa (WCA), for example, groundnut accounts for up to 50% or more of rural household cash income in many countries—46% in Mali, 54% in Nigeria, 66% in Niger and 80% in Senegal (GAIN 2010; Ndjeunga et al., 2010). In Asia and Africa, a large number of women and youth are engaged in the cultivation, processing and marketing of groundnut, thereby contributing to their economic participation and empowerment. In Nigeria, for example, almost all the small-scale groundnut oil processing is controlled by women. In Mali, about 85% of groundnut fields are owned by women (Ndjeunga et al., 2010).

Groundnut productivity significantly varies among regions with Africa having the lowest mean yield of around 965 kg/ha (FAOSTAT 2017). In Asia, the productivity is relatively better with an average yield of 2,370 kg/ha. On the other hand, in the USA and other developed countries, groundnut yields are high with a yield over 3,300 kg/ha. In general, groundnut productivity has significantly increased over the last five decades with a global yield average increasing from 849 kg/ha in 1961 to 1655 kg/ha in 2014, which is attributed to significant advances in genetics, genomics, breeding and crop management. This paper reviews the advances in understanding the genetics of important traits, genome sequences, molecular marker development, QTL analysis, genetic resources, breeding for specific traits and integration of genomic tools into groundnut breeding process to enhance the genetic gain and improve the productivity of the crop.

2 GENETICS

Detailed reviews on groundnut genetics covering inheritance, cytogenetics, combining ability, genotypic and phenotypic coefficients of variation, heritability, genetic gain, genotype-by-environment interactions and trait correlations were published (Knauff & Wynne, 1995; Nigam, 2014; Reddy, 1988). Qualitative and quantitative inheritances of traits have been reported. Generally, majority of morphological (e.g., growth and branching, leaf, pod and seed traits), quality (e.g., protein and oil) and disease resistance (leaf spots, rust) traits were reported to have predominantly qualitative inheritance (e.g., Asibu et al., 2008; Gangadhar & Nadaf, 2016; Jakkeral, Nadaf, Gowda, & Bhat, 2013; Pattanashetti, Gowda, & Girija, 2008; Upadhyaya & Nigam, 1994, 1998, 1999). But quantitative inheritances were also reported for some of the traits such as oil content and quality (Aruna & Nigam, 2009; Dwivedi, Pande, Rao, & Nigam, 2002; Khedikar et al., 2010; Pandey, Wang, et al., 2014; Sarvamangala, Gowda, & Varshney, 2011; Shasidhar et al., 2017; Sujay et al., 2012; Wilson et al., 2017). Most of the economically important traits such as yield, maturity and drought tolerance traits are quantitatively inherited (Knauff & Wynne, 1995; Nageswara Rao, Talwar, & Wright, 2001; Ravi et al., 2011; Upadhyaya, 2005; Upadhyaya & Nigam, 1998). The presence of genetic and nongenetic variances was reported for various traits (Dwivedi, Nigam, Chandra, & Ramraj, 1998; Janila, Ramaiyah, et al., 2013; John, Reddy, Reddy, Sudhakar, & Reddy, 2011; Pattanashetti et al., 2008; Upadhyaya, Gopal, Nadaf, & Vijayakumar, 1992).

Low-to-high genotypic and phenotypic coefficients of variation, broad-sense heritability, genetic advance and genetic advance as percentage of mean were reported for various traits including grain and pod yield, days to 50% flowering and plant height, shelling percentage, specific leaf area (SLA) and SPAD chlorophyll meter readings (SCMR), number of pods per plant and 100-seed weight (e.g., John, Vasanthi, Sireesha, & Krishna, 2013; John et al., 2011; Padmaja, Eswari, BrahmeswaraRao, & Madhusudhan Reddy, 2013; Padmaja, Eswari, BrahmeswaraRao, & Prasad, 2015; Patil, Punewar, Nandanwar, & Shah, 2014; Songsri et al., 2009; Thirumala Rao, Venkanna, Bhdaru, & Bharathi, 2014; Upadhyaya, 2005). In the case of trait correlations, grain and pod yield were reported to be positively correlated among themselves and with traits such as shelling percentage, biomass production, 100-seed weight, number of pods per plant and dry haulm yield (e.g., Padmaja et al., 2013, 2015; Thirumala Rao et al., 2014) and also with drought-related traits such as harvest index (HI), SCMR and SLA (e.g., Songsri et al., 2009; Upadhyaya, Sharma, Singh, & Singh, 2011). On the other hand, negative correlations were reported for grain and pod yield with early leaf spot (ELS) resistance parameters, days to first flowering and days to 50% flowering (Gaikpa, Akromah, Asibuuo, Appiah-Kubi, & Nyadanu, 2015; Padmaja et al., 2013). For quality traits,
negative correlations between protein content and oil content and between oleic acid and linoleic acid were reported (Sarvamangala et al., 2011).

3 | GENOMICS

Limited genomic resources existed for groundnut prior to 2005 (Pandey et al., 2012). However, significant advances have been made in recent years in genome sequencing, development of molecular markers, construction of genetic maps and quantitative trait locus (QTL) analyses. Various marker systems including RFLP (restriction fragment length polymorphism), RAPD (random amplification of polymorphic DNA), AFLP (amplified fragment length polymorphism), DArT (diversity array technology), SSR (simple sequence repeat) and SNPs (single-nucleotide polymorphisms) were developed (Pandey et al., 2012; Varshney, 2016) and have been utilized for genetic diversity analyses, constructing genetic maps, mapping of traits of breeding interest and marker-assisted breeding. The emphasis has been more on SSR and SNP markers for usefulness and practical reasons. SSR markers are codominant, more informative and easy to score in the tetraploid genome, while SNP markers are highly amenable to high-throughput genotyping approaches (Bertioli et al., 2014; Pandey et al., 2012). Consequently, a large number of expressed sequence tag (EST)-based SSR markers ranging from 26 (Hopkins et al., 1999) to 6455 (Peng, Gallo, Tillman, Rowland, & Wang, 2016) have been reported. Similarly, large numbers of SNP markers have been developed including 8486 candidate SNPs from a screening of sequences of 17 genotypes assembled along with sequences from the reference ‘Tifrunner’ transcriptome (Alves et al., 2008; GCP 2011), which was used to construct 1536-SNP GoldenGate assay (Nagy et al., 2012). Another 768-SNP Illumina GoldenGate assay was developed at the University of California-Davis (Pandey et al., 2012). These assays were found very informative for genotyping diploid species, but limited use for tetraploid species (Bertioli et al., 2014; Pandey et al., 2012). Zhou et al. (2014) reported the development of 53,257 SNPs for tetraploid species. Additional SNPs have become available including 62 SNPs (Hong et al., 2015), 263,840 SNPs and indel variants (Chopra et al., 2015), 11,902 SNPs (Peng et al., 2016) and 6965 SNPs (Peng et al., 2017). Besides, 96 SNP markers were converted to competitive allele-specific PCR (KASP) SNP markers to develop KASP assays designated as GKMAs (groundnut KASP assay markers) for use in LGC’s KASP genotyping service (Khera et al., 2013). Similarly, easy-to-use KASP markers linked to root-knot nematode (RKN) resistance loci were developed and validated in a tetraploid context (Leal-Bertioli et al., 2015).

Genetic maps were constructed to understand the groundnut genome structure and organization and to identify QTLs for traits of breeding interest. Different marker systems such as RFLP (Halward, Stalker, & Kochert, 1993), RAPD (Garcia, Stalker, Schroeder, Lyerly, & Kocher, 2005), AFLP (Herselman, Thwaites, Kimmens, & Seal, 2004), SSR (Moretzsohn, Barbosa, Alves-Freitas, Teixeira, & Leal-Bertioli, 2009), SNP (Bertioli et al., 2014) and DArT (Shasidhar et al., 2017) were employed to construct the genetic maps, but the majority of maps were based on SSR markers from biparental populations (Table 1). Earlier SSR-based genetic maps had lower marker density (e.g., 135 markers, Varshney et al., 2009), but as more and more SSR markers have become available, the genetic maps were improved with more dense maps developed recently (e.g., 1,469 markers—Shirasawa et al., 2013). SNP and other markers were integrated into some of the genetic maps. Besides, six consensus maps were developed, the first with 175 loci (Hong et al., 2010) and the latest with 3,693 loci (Shirasawa et al., 2013), which are useful for the characterization of the groundnut genome. Specifically, the construction of the consensus map by Shirasawa et al. (2013) from 16 segregating populations of diverse genetic backgrounds has enabled mapping a larger number of loci with greater genome coverage than in any of the genetic maps from the single populations and was useful to determine the relative position of common markers across different mapping populations. While many genetic maps were developed with a focus on mapping maximum number of loci onto a single map (e.g., Foncêka et al., 2009; Hong et al., 2008, 2010; Shirasawa et al., 2013; Wang et al., 2012), majority of them were developed with a focus on facilitating QTL analysis (trait mapping) and development of diagnostic markers for marker-assisted breeding. QTL analysis studies to date have reported the identification of more than 1,380 small and major effect QTLs (Table 2) for various traits including agronomic and yield component traits (e.g., Luo, Xu, et al., 2017; Selvaraj et al., 2009), quality traits (e.g., Sarvamangala et al., 2011; Shasidhar et al., 2017), biotic stress resistance (e.g., Khedikar et al., 2010; Kolekar et al., 2016; Pandey, Wang, et al., 2017; Pandey, Khan, et al., 2017; Zhou et al., 2016) and abiotic stress resistance mainly for drought-related traits (e.g., Leal-Bertioli et al., 2016; Varshney et al., 2009).

Another significant advance in groundnut genomics has been the release of the draft genome sequences of the 1.1 Gb genome size for A-genome progenitor (A. duranensis, accession V14167) and 1.38 Gb for B-genome progenitor (A. ipaensis, accession K30076) (Bertioli et al., 2016). In addition, the draft genome sequence of another A-genome progenitor accession (A. duranensis, accession P475845) was generated with 1.07 Gb genome size which provided greater insights into the genome architecture and genes related to important traits such as geocarpy, oil biosynthesis and allergens (Chen, Li, et al., 2016). In the case of cultivated tetraploid genotype, a high-quality genome assembly of ‘Tifrunner’, an important US variety with good market and growth characteristics and resistance to several diseases, was released in December 2017 (https://peanutbase.org/peanut_genome). The draft genome sequences have enabled large-scale genomewide discovery of 515,223 indels (Vishwakarma et al., 2017) and SSRs including 105,003 SSRs in the A-genome (Chen, Li, et al., 2016), 135,529 SSRs in the A-genome (Zhao et al., 2017), 199,957 SSRs in the B-genome (Zhao et al., 2017), 84,383 in the A-genome (Luo, Ren, et al., 2017) and 120,056 in the B-genome (Luo, Ren, et al., 2017). Further, a high-throughput genotyping platform, an Axiom_Arachis SNP array with 58K genomewide SNPs, was developed from the analysis of DNA resequencing and RNA
| Genome | Population | Population size | Marker loci mapped | Marker type | LGs | Total map distance (cM) | References |
|--------|------------|-----------------|--------------------|-------------|-----|------------------------|------------|
| AA     | A. stenosperma × A. cardenasii | 87 F2 | 132 | RFLP | 11 | 1,063.00 | Halward et al., 1993; |
|        | A. stenosperma × (A. stenosperma × A. cardenasii) | 44 BC1F1 | 206 |
|        | RAPD, RFLP | 11 | 800 | Garcia et al., 2005; |
|        | A. duranensis (K7988) × A. stenosperma (V10309) | 93 F2 | 204 | SSR | 11 | 1,230.89 | Moretzsohn et al., 2005; |
|        | A. duranensis (K7988) × A. stenosperma (V10309) | 93 F2 | 369 | SSR, anchor, AFLP, NBS profiling, SNP, RGA-RFLP SCAR | 10 | – | Leal-Bertioli et al., 2009; |
|        | A. duranensis (PI 475887) × A. duranensis (Grif 105036) | 94 F2 | 1,724 | SNP, SSR, SSCP, RGC | 10 | 1,081.30 | Nagy et al., 2012; |
| BB     | A. ipaënsis (K30076) × A. magna (K30097) | 93 F2 | 149 | SSR | 10 | 1,294.00 | Moretzsohn et al., 2009; |
|        | A. ipaënsis (K30076) × A. magna (K30097) | 94 RILs | 798 | SSR, TE | 10 | 461.00 | Shirasawa et al., 2013; |
|        | K 9484 (PI 298639) × GKBSPSc 30081 (PI 468327) in A. batizocoi | 94 F2 | 449 | SSR | 16 | 1,278.60 | Guo et al., 2012; |
| AABB   | Florunner × TxAG-6 ([A. batizocoi K9484 × (A. cardenasii GKP10017 × A. diogoi GKP10602)[4] ×] | 78 BC1F1 | 370 | RFLP | 23 | 2,210.00 | Burow, Simpson, Starr, & Paterson, 2001; |
|        | Florunner × TxAG-6 ([A. batizocoi K9484 × (A. cardenasii GKP10017 × A. diogoi GKP10602)[4] ×] | 78 BC1F1 | 91 | SSR | 22 | 1,321.90 | Wilson et al., 2017; |
|        | ICG 12991 × ICGV-SM 93541 | 60 F2 | 12 | AFLP | 5 | 139.4 | Herselman et al., 2004; |
|        | ICG 12991 × ICGV-SM 93541 | 88 BC1F1 | 298 | SSR | 21 | 1,843.70 | Foncéka et al., 2009; |
|        | Yueyou 13 × Zhenzhuhei | 142 RILs | 131 | SSR | 20 | 679.00 | Hong et al., 2008; |
|        | Yueyou 13 × Zhenzhuhei | 318 RILs | 135 | SSR | 22 | 1,270.50 | Varshney et al., 2009; |
|        | Yueyou 13 × Zhenzhuhei | 318 RILs | 191 | SSR | 22 | 1,785.40 | Ravi et al., 2011; |
|        | Yueyou 13 × Zhenzhuhei | 142 F4:6 | 132 | SSR | 19 | 684.90 | Hong et al., 2010; |
|        | Yueyou 13 × Zhenzhuhei | 84 F4:6 | 109 | SSR | 21 | 540.69 | Hong et al., 2010; |
|        | Yueyou 13 × Fu 95-5 | 136 F4:6 | 46 | SSR | 13 | 401.70 | Hong et al., 2010; |
|        | Yueyou 13 × J11 | 268 RILs | 56 | SSR | 14 | 462.24 | Khedikar et al., 2010; |
|        | Yueyou 13 × J11 | 266 RILs | 188 | SSR | 20 | 1,922.40 | Sujay et al., 2012; |
|        | Yueyou 13 × J11 | 266 RILs | 289 | SSR, TE | 20 | 1,730.80 | Kolekar et al., 2016; |
|        | TG 26 × GPBD 4 | 146 RILs | 45 | SSR | 8 | 657.90 | Sarvamangala et al., 2011; |
|        | TG 26 × GPBD 4 | 146 RILs | 181 | SSR | 21 | 1,963.00 | Sujay et al., 2012; |
|        | ICGS 44 × ICGS 76 | 188 RILs | 82 | SSR | 15 | 831.40 | |
| Genome                          | Population  | Population size | Marker loci mapped | Marker type | LGs | Total map distance (cM) | References                                      |
|--------------------------------|-------------|-----------------|--------------------|-------------|-----|------------------------|------------------------------------------------|
| ICGS 76 × CSMG 84-1            | 177 RILs    | 119             | SSR                | 20          |    | 2,208.20               | Gautami, Pandey, et al., 2012; Qin et al., 2012; |
| SunOleic 97R × NC94022         | 352 RILs    | 172             | SSR, CAPs          | 22          |    | 920.70                 | Pandey, Wang, et al., 2014; Qin et al., 2012;   |
| Tifrunner × GT-C20             | 94 F2       | 318             | SSR                | 21          |    | 1,674.40               | Wang et al., 2012;                               |
| YI-0311 × Nakateyutaka         | 186 F2      | 326             | SSR, TE            | 19          |    | 1,332.90               | Shirasawa et al., 2012;                          |
| Satonoka × Kintoki             | 94 F2       | 1,114           | SSR, TE            | 21          |    | 2,166.40               | Shirasawa et al., 2012;                          |
| A. hypogaea “Runner” IAC 8865  | 91 RILs     | 1,469           | SSR, TE            | 20          |    | 1,442.00               | Shirasawa et al., 2013;                          |
| Zhonghua 5 × ICGV 86699        | 166 RILs    | 1,685           | SNP, SSR           | 20          |    | 1,446.70               | Zhou et al., 2014;                               |
| VG 9514 × TAG 24               | 164 RILs    | 95              | SSR                | 24          |    | 882.90                 | Mondal et al., 2012;                             |
| Zhonghua 10 × ICG12625         | 232 F2      | 470             | SSR                | 20          |    | 1,877.30               | Huang et al., 2015;                              |
| Fuchuan Dahuasheng × ICG 6375 | 218 F2:3    | 347             | SSR                | 22          |    | 1,675.60               | Chen, Jiao, et al., 2016;                        |
| Xuhua 13 × Zhonghua 6          | 282 F2:3    | 228             | SSR                | 22          |    | 1,337.70               | Chen, Jiao, et al., 2016;                        |
| Florida- EP™ “113” × Georgia Valencia | 163 F2   | 30              | SSR, SNP           | 1           |    | 157.80                 | Tseng et al., 2016;                              |
| ICGV 00350 × ICGV 97045        | 268 F2      | 1,152           | DArT, DArTseq      | 20          |    | 2,423.12               | Vishwakarma et al., 2016;                        |
| 79266 × D893                  | 151 RILs    | 231             | SSR                | 23          |    | 905.18                 | Li et al., 2017;                                 |
| Yuanza 9102 × Xuzhou 68-4      | 195 RILs    | 743             | SSR                | 22          |    | 1,232.57               | Luo, Ren, et al., 2017;                          |
| ICGV 07368 × ICGV 06420       | 184 F2      | 854             | DArT, SSR          | 20          |    | 3,526.00               | Luo, Xu, et al., 2017;                           |
| ICGV 06420 × SunOleic 95R      | 179 F2      | 1,435           | DArT, DArTseq      | 20          |    | 1,869.00               | Shasidhar et al., 2017;                          |
| Tamrun LO07 × Tx964117         | 90 RILs     | 1,211           | SNP                | 20          |    | –                      | Liang, Baring, Wang, & Septiningsih, 2017;       |
| TMV 2 × TMV 2-NLM             | 432 RILs    | 91              | TE                 | 20          |    | 1,205.66               | Hake et al., 2017;                               |
| Consensus                      | 3 populations | –              | 175               | SSR         | 22          | 885.40                 | Hong et al., 2010;                               |
|                                | 2 populations | –              | 225               | SSR         | 20          | 1,152.90               | Sujay et al 2012                                |
|                                | 3 populations | –              | 293               | SSR         | 20          | 2,840.80               |                                               |

(Continues)
sequencing of 41 groundnut accessions and wild diploid ancestors against the genomes of two groundnut progenitors, that is A. duranensis and A. ipaensis (Pandey, Agarwal, et al., 2017), which was used to identify signatures of selection and tetrasomic recombination in groundnut (Clevenger et al., 2017). For understanding the genetic architecture of domestication-related traits in groundnut, specific-locus amplified fragment sequencing (SLAF-seq) method was employed for large-scale identification of 17,338 high-quality SNPs in the whole groundnut genome, and 1,429 candidate genes for eleven agronomic traits were found using genomewide association studies in 158 peanut accessions (Zhang et al., 2017).

4 | BREEDING

4.1 | Focus traits and breeding methods

Priority traits in groundnut breeding include high pod yield, early maturity, high shelling percentage, high oil, resistance to biotic and abiotic stresses, fresh seed dormancy, confectionery, high oleic acid and dual-purpose types. In the USA and other developed countries, under high input production system, the breeding focus has been maximizing yield, but in recent years, improving quality and flavour, resistance to drought and diseases have become important priorities. In Asia and Africa, the focus has been increasing pod yield with enhanced resistance to biotic and abiotic constraints and high oil content. Conventional breeding approaches such as introduction, selection, mutation and hybridization (pedigree, backcross and single-seed descent, etc.) have been used to develop improved varieties. In the USA, although it was used extensively in the late 1950s to early 1970s, mutation breeding is little used in the present day (Holbrook & Stalker, 2003). In India, mutation breeding is still being used at Bhabha Atomic Research Center (BARC) (Mondal, Badigannavar, Kale, & Murty, 2007).

Genetic resources conserved in gene banks have been important and harbour huge potential for utilization in breeding programmes as sources of variability. Besides, recent advances in genomics have enabled integrating molecular marker-assisted breeding approaches for selected traits, and they hold significant promise for many other traits to enhance the breeding efficiency and increase the rate of genetic gain. Brief highlights of groundnut genetic resources, breeding for specific traits and marker-assisted breeding are provided below. Over the years, several advanced breeding and germplasm lines have been identified and developed for drought, leaf spots, rust, rosette, aflatoxin, rust and quality traits (Table 3). Genotype x environment interaction is widely reported for pod yield and other quantitative traits in groundnut (e.g., Bucheyeki, Shenkalwa, Mapunda, & Matata, 2008; Janila, Manohar, Patne, Variath, & Nigam, 2016; Jogloy, Vorasoot, Akkasaeng, Kemsala, & Patanothai, 2009; Makinde, Ariyo, & Akinbowale, 2013). Hence, multilocation and multisession testing are required to release improved varieties. Farmer participatory variety selection (Ntare et al., 2007) has been an important approach recently in groundnut varieties’ release processes, particularly in South Asia (SA) and sub-Saharan Africa (SSA), to better understand farmers’ trait preferences for varieties and increase farmers’ exposure to new groundnut varieties such that breeding programmes were able to better target varieties to both the ecological and market needs. Table 4 shows some of the released varieties in SA and SSA between 2000 and 2016 for their high yield and other traits including short duration, drought tolerance, rosette resistance and foliar disease resistance.

4.2 | Genetic resources

Genetic resources are important sources of variability for traits of breeding interest and serve as reservoirs of many useful genes for the present and future groundnut improvement programmes. Several groundnut accessions are conserved globally in national and international gene banks including ICRI SAT, the USA, Brazil, India and China (Ntare, Waliyar, Mayeux, & Bissala, 2006; Pandey et al., 2012). Majority of these accessions have been characterized for various mor phoagronomic and biochemical traits using groundnut descriptors (IBPGR and ICRISAT 1992, Jiang & Duan, 2006; Pittman, 1995) where large variation for qualitative and quantitative traits, seed quality traits and resistance to biotic and abiotic stresses was observed (Barkley, Upadhyaya, Liao, & Holbrook, 2016). Diversity studies using molecular markers revealed generally low diversity within the cultivated types (e.g., Halward, Stalker, Larue, & Kochert, 1991; He & Prakash, 1997; Herselman, 2003; Hopkins et al., 1999; Moretzsohn et al., 2004), but moderate-to-high polymorphisms were also reported (e.g., Cuc et al., 2008; Mace, Phong, Upadhyaya, Chandra, & Crouch, 2006; Mace et al., 2007; Oteng-Frimpong, Sriswathi, Ntare, & Dakora, 2015; Roomi et al., 2014).

The use of the accessions from gene banks for crop improvement is less which is attributed to the use of working collections, consisting mostly of elite breeding lines and some improved trait-
| Trait group                      | Trait                                                                 | Number of QTLs identified | Population | Reference                                      |
|---------------------------------|-----------------------------------------------------------------------|---------------------------|------------|-----------------------------------------------|
| Agronomic and yield component   | GH, plant spread, MSH, PH, total biomass, DF, PoM, LNB, haulm weight, | Total* 7 9.19–17.69 5   | Tamrun OL01 × BSS 56 | Selvaraj et al., 2009;                        |
|                                 | shell weight, shelling %, HI, pod number, pod weight, seed number,100-SW, | 106 8.50–26.70 29         | [Fleur 11 × A. ipaënsis × A. duranensis]      |
|                                 | pod beak, pod constriction, pod length, pod width, seed width, seed   | 23 4.80–28.20 17          | Shirasawa et al., 2012;                        |
|                                 | length, FSD                                                           | 25 6.20–30.40 9           | Leal-Bertioli et al., 2015;                    |
|                                 |                                                                       | 31 8.30–26.00 263         | Leal-Bertioli et al., 2016;                    |
|                                 |                                                                       | 24 1.69–18.70 11          | Huang et al., 2015;                            |
|                                 |                                                                       | 18 4.85–20.52 8           | Huang et al., 2016;                            |
|                                 |                                                                       | 22 2.55–7.95 0            | Zhou et al., 2016;                             |
|                                 |                                                                       | 39 1.25–26.11 13          | Chen, Jiao, et al., 2016;                      |
|                                 |                                                                       | 2 22.14–71.21 2           | Vishwakarma et al., 2016;                      |
|                                 |                                                                       | 7 6.12–22.53 2            | Sarvamangala et al., 2011;                     |
|                                 |                                                                       | 27 1.04–42.33 17          | Pandey, Wang, et al., 2014;                    |
|                                 |                                                                       | 191 0.16–40.56 34         | Wang et al., 2015;                             |
|                                 |                                                                       | 11 1.72–20.20 7           | Huang et al., 2015;                            |
|                                 |                                                                       | 48 2.00–17.00 5           | Wilson et al., 2017;                           |
|                                 |                                                                       | 21 8.40–78.60 20          | Shasidhar et al., 2017;                        |
|                                 |                                                                       | 2 15.10 1                 | Hake et al., 2017;                             |
|                                 |                                                                       | 1 11.03 1                 | Selvaraj et al., 2009;                         |
|                                 |                                                                       | 4 1.50–9.10 0             | Sarvamangala et al., 2011;                     |
|                                 |                                                                       | 15 2.53–10.23 5           | Pandey, Wang, et al., 2014;                    |
|                                 |                                                                       | 1 14.36 1                 | Hake et al., 2017;                             |
|                                 |                                                                       | 13 2.00–18.00 2           | Wilson et al., 2017;                           |
|                                 |                                                                       | 8 5.60–22.10 2            | Shasidhar et al., 2017;                        |
|                                 |                                                                       | 6 1.50–10.70 2            | Sarvamangala et al., 2011;                     |
|                                 |                                                                       | 2 – 26.40 1               | Hake et al., 2017;                             |
|                                 |                                                                       | 12 8.50–31.20 8           | Leal-Bertioli et al., 2016;                    |
|                                 |                                                                       | 13 10.40–20.10 13         | Foncêka et al., 2012;                          |
|                                 |                                                                       |                            | (Continues)                                   |

**TABLE 2** Reported QTLs for important traits of breeding interest in groundnut
specific lines (Gowda, Upadhyaya, Sharma, Varshney, & Dwivedi, 2013). It is also costly to screen large collections for specific traits of breeding interest (Holbrook & Stalker, 2003). A subset that represents the genetic diversity facilitates easier access to the genetic resources and enhances their use in crop improvement programmes was required. Hence, core and minicore collections were established in China (Jiang et al., 2008) and USA (Holbrook, Anderson, & Pittman, 1993; Holbrook & Dong, 2005), which have been evaluated for various traits of breeding interest including disease resistance (Anderson, Holbrook, & Culbreath, 1996; Chamberlin, Melouk, & Payton, 2010; Damicone, Holbrook, Smith, Melouk, & Chamberlin, 2010; Jiang et al., 2008; Wang et al., 2011). Similarly, ICRISAT has established a core collection of 1,704 accessions (Upadhyaya, Ortiz, Bramel, & Singh, 2003) and a minicore collection of 184 groundnut accessions (Upadhyaya, Bramel, Ortiz, & Singh, 2002). Besides, a global composite collection consisting of 1,000 accessions was developed, which was further characterized using 21 SSR markers to form a reference set consisting of 300 genetically most diverse accessions (Upadhyaya, Bhattacharjee, et al., 2006). The reference set, core and minicore collections were evaluated and characterized for various traits including drought and disease resistance for use in breeding programmes (Hamidou, Rathore, Waliyar, & Vadez, 2014; Hamidou et al., 2012; Upadhyaya, 2005; Upadhyaya, Dronavalli, Singh, & Dwivedi, 2012; Upadhyaya, Mallikarjunaswamy, Goudar, Kulaiswamy, & Singh, 2005; Upadhyaya, Mukri, Nadaf, & Singh, 2012; Upadhyaya, Reddy, Gowda, & Singh, 2006; Upadhyaya, Dwivedi, Vadez, et al., 2014; Waliyar et al., 2016) and also used for association mapping (Pandey, Upadhyaya, et al., 2017).

### Table 2 (Continued)

| Trait group                  | Trait            | Number of QTLs identified | Population                                      | Reference                      |
|------------------------------|------------------|---------------------------|-------------------------------------------------|--------------------------------|
| Resistance to biotic stress  | Rust resistance  | 12                        | 1-70.55.20                                      | TAG 24 × GPBD 4                |
|                              |                  | 15                        | 2.54-82.96                                      | Sujay et al., 2012;           |
|                              |                  | 13                        | 5.80-59.30                                      | A. ipaënsis (K30076) × A. magna (K30097) | Leal-Bertioli et al., 2015; |
|                              |                  | 6                         | 10.2-70.4                                       | TAG 24 × GPBD 4                |
|                              |                  | 8                         | 42.7-83.6                                       | TAG 24 × GPBD 4                |
|                              | Leaf spot resistance | 5                        | 4.6-53.00                                       | A. duranensis (K7988) × A. stenosperma (V10309) | Leal-Bertioli et al., 2009; |
|                              |                  | 28                        | -                                               | TAG 24 × GPBD 4; TG 26 × GPBD 4 | Sujay et al., 2012; |
|                              |                  | 11                        | 1.70-6.50                                       | TAG 24 × GPBD 4                |
|                              |                  | 50                        | 5.95-27.35                                      | Tifrunner × GT-C20             |
|                              |                  | 20                        | 34.1-19.12                                      | Zhonghua 5 × ICGV 86699       |
|                              |                  | 4                         | 14.1-44.5                                       | TAG 24 × GPBD 4                |
|                              |                  | 42                        | 38.8-16.88                                      | SunOleic 97R × NC94022         | Khera et al., 2016; |
|                              | RKN resistance   | 10                        | -                                               | Tifrunner × TxAG-6             | Burow, Starr, Park, Simpson, & Paterson, 2014; |
|                              |                  | 8                         | 5.70-43.70                                      | A. duranensis × A. stenosperma | Leal-Bertioli et al., 2016; |
|                              | TSWV resistance  | 2                         | 12.90-35.80                                     | SunOleic 97R × NC94022         | Qin et al., 2012; |
|                              |                  | 24                        | 4.40-34.92                                      | Tifrunner × GT-C20             |
|                              |                  | 2                         | 10.02-22.70                                     | Florida- EPTM “113” × Georgia Valencia |
|                              | Thrips resistance | 6                         | 4.36-29.14                                      | SunOleic 97R × NC94022         |
|                              |                  | 11                        | 6.74-14.41                                      | Tifrunner × GT-C20             |
|                              | Bruchid resistance| 3                         | 5.86-19.43                                      | Tifrunner × GT-C20             |
|                              |                  | 44                        | 11.00-82.00                                     | VG 9514 × TAG 24               |

Notes. PVE: percentage phenotypic variance explained; GH: growth habit; MSH: main stem height; PH: plant height; DF: days to flowering; LNB: length and number of branches; PoM: percentage of maturity; HI: harvest index; SW: seed weight; FSD: fresh seed dormancy; T: transpiration (T); TE: transpiration efficiency; LA: leaf area; CI: carbon isotope discrimination ratio; CC: canopy conductance.

*Epistatic QTLs are included for some studies.
from single-event hybridization of diploid wild ancestors and a subsequent lack of allele exchange with the wild species due to cross-incompatibility, has a narrow genetic base with limited variability for some traits, particularly biotic stresses. On the other hand, wild Arachis species are reported to harbour high levels of resistance/tolerance to multiple stresses (Foncéka, Tossim, Rivallan, Vignes, Faye, et al., 2012; Mallikarjuna, Senthilvel, & Hoisington, 2011; Simpson, Burow, Paterson, Starr, & Church, 2003; Simpson & Starr, 2001; Stalker, Tallury, Ozias-Akins, Bertoli, & Leal-Bertioli, 2013; Upadhyaya, Dwivedi, Sharma, et al., 2014) and also offer important variability for agronomic traits including yield (Upadhyaya, Dwivedi, Sharma, et al., 2014). Hence, several lines have been developed through interspecific hybridization to increase the variability for important traits, and some improved varieties were released. Besides, amphiploids and autotetraploids (Mallikarjuna et al., 2011), targeting-induced local lesions in genomes (TILLING) populations (Knoll et al., 2011), multiparent advanced generation intercross (MAGIC) populations (Janila, Variath, et al., 2016) and chromosome segment substitution (CSSL) lines (Foncéka, Tossim, Rivallan, Vignes, et al., 2012; Monyo & Varshney, 2016; Janila, unpublished) have been developed and form important resources of groundnut breeding.

### 4.3 Breeding for specific traits

#### 4.3.1 Drought

With more than 70% of groundnut area being in the semiarid tropics (Pandey, Guo, et al., 2014), drought is a major production constraint.
## Table 4

Improved groundnut varieties released between 2000 and 2016 in SA and SSA

| Region | Country | # of varieties | Release name of varieties | Breeding programme name of varieties | Year of release |
|--------|---------|----------------|---------------------------|--------------------------------------|-----------------|
| SA     | Bangladesh | 2 | BARI Badam-5, BARI Badam-6 | ICGS(E) 55 [ICGV 86072], M-5 | 1997 |
|        |          | 1 | ICGV 89259 | ICGV 89259 | 2004 |
|        |          | 1 | Barichinabadam - 8 | ICGV 94322 | 2006 |
|        |          | 2 | BARI Chinabadam-9, ICGV 96346 | ICGV 96342, ICGV 96346 | 2010 |
|        | India | 2 | SG 99, Pratap Mungrhali - 1 | ICGV 89280, ICGV 92035 | 2004 |
|        |          | 1 | Pratap Mungrhali-2 | ICGV 92195 | 2005 |
|        |          | 2 | Devi, AK 303 | ICGV 91114, AK 303 | 2006 |
|        |          | 8 | ICGV 00348, Mallika, ICR 48, VL Mungrhali 1, ICGV 91114, Vijetha, Ajeya, Avtar | ICGV 00348, ICGV 00440, ICGV 07356, ICGV 86590, ICGV 91114, ICGV 93260, ICGV 93261, ICGV 93468 | 2008 |
|        |          | 2 | ICGV 00350, Co6 | ICGV 00350, ICGV 87846 | 2010 |
|        |          | 3 | ICGV 00298, ALG 06-320, ICGV 99195 | ICGV 00298, ICGV 94118, ICGV 99195 | 2011 |
|        |          | 1 | CTMG 6 | ICGV 05049 | 2012 |
|        |          | 1 | Co7 | ICGV 00351 | 2013 |
|        |          | 2 | KDG 123, Phule Warna | KDG 123, KDG 128 | 2014 |
| SSA   | Ghana | 2 | Gusie-Balin, Kpanieli | ICGV 92099, ICGV 90084 | 2005 |
|        |          | 4 | Oboolo, Obooshi, Otuhia, Yenawosho | ICGV 97049, ICGV 98412, ICGV-SM 88709, ICGV-SM 87057 | 2012 |
|        |          | 2 | ICGV 86065 (ICGS(E) 34), Sameke | ICGV 86065 (ICGS(E) 34), JL 24 (ICG 7827) | 2000 |
|        |          | 3 | Waliyartiga, ICG (FDRS) 4, ICG (FDRS) 10 | ICG 7878, ICG (FDRS) 4, ICG (FDRS) 10 | 2003 |
|        | Mali | 5 | Nieta Tiga, Diakandapé, Baroueli, Bagui-tana, Nisonja | ICGV 86124, Diakandapé, Baroueli, ICGV-IS 96802, ICGV-IS 92525 | 2007 |
|        |          | 2 | ICGV 86024, Yiriwa Tiga | ICGV 86024, ICGV 86015 | 2011 |
|        |          | 2 | ICIAR 19BT, J11 | ICIAR 19BT, J11 | 2015 |
|        | Malawi | 2 | Kakoma, Nsinjiro | JL 24 (ICG 7827), ICGV-SM 90704 | 2000 |
|        |          | 1 | Baka | ICG 12991 | 2001 |
|        |          | 2 | Chitala, Chalimbana 2005 | ICGV-SM 99568, CML851/7 | 2005 |
|        |          | 7 | CG8, CG9, CG10, CG11, CG12, CG13, CG14 | ICGV-SM 08501, ICGV-SM 8503, ICGV-SM 01731, ICGV-SM 01724, ICGV-SM 01514, ICGV-SM 99551, ICGV-SM 99556 | 2014 |
|        | Mozambique | 2 | Mametil, Mamane | ICG 12991, ICGV-SM 90704 | 2002 |
|        |          | 1 | Nyanda | ICGV 93437 | 2004 |
|        |          | 6 | ICGV-SM 99541, ICGV-SM 99568, ICGV-SM 01513, ICGV-SM 01514, CG 7, JL 24 | ICGV-SM 99541, ICGV-SM 99568, ICGV-SM 01513, ICGV-SM 01514, ICGV-SM 83708, JL 24 (ICG 7827) | 2011 |
|        | Niger | 4 | ICGV 86015, ICGV-SM 85045, ICGV 87003, ICGV 87281 | ICGV 86015, ICGV-SM 85045, ICGV 87003, ICGV 87281 | 2006 |
|        |          | 5 | ICG 9346, RRB, Fleur 11, J11, JL 24 | ICG 9346, RRB, Fleur 11, J11, JL 24 (ICG 7827) | 2010 |
|        | Nigeria | 1 | Samnut 24 | ICIAR 19BT | 2011 |

(Continues)
Early season, midseason and end-of-season drought are important forms of drought, but end-of-season (terminal) drought that affects the seed development is more critical (Nigam, Nageswara Rao, & Wright, 2002; Williams, Rao, & Rao, 1985). Over the years, a large number of accessions and lines have been identified as sources of drought resistance (Hamidou et al., 2012; Mayeux, Waliyar, & Ntare, 2003; Monyo & Varshney, 2016; Nigam et al., 2005; Upadhyaya, 2005). Breeding for drought exploits both early maturity and drought resistance/tolerance mechanisms to develop improved varieties. Early maturity enables escape from drought stress conditions (Janila, Nigam, Pandey, Nagesh, & Varshney, 2013; Williams et al., 1985), while resistance/tolerance is usually attributed to water use efficiency, root depth and/or water extraction capacity for high yield. Empirical approach or trait-based approach or a combination of both is used for phenotyping for drought resistance (Janila & Nigam, 2013). The empirical approach involves selection based on pod and grain yield under imposed drought stress conditions. The trait-based approach involves phenotyping for traits such as HI, total amount of water transpired (T), TE and water use efficiency (WUE). Positive correlations were reported between TE and pod yield under water-stressed environments (Devi et al., 2011; Sanogo, 2016). Because WUE and TE are difficult to measure routinely, surrogate traits such as SLA and SCMR are used. Significant correlations have been reported between TE and surrogate traits (Devi et al., 2011; Nageswara Rao et al., 2001).

The evidences about the usefulness of surrogate traits, however, are not consistent in that high SCMR and low SLA may not always lead to higher pod yield. For example, the preponderance of nonadditive effects and poor relationship between surrogate traits and pod yield were observed (Hamidou et al., 2012; Krishnamurthy et al., 2013).
2007; Sanogo, 2016). Janila, Manohar, Rathore, and Nigam (2015) observed low heritability for SCMR and SLA. On the other hand, high correlations of both SCMR and SLA with pod yield and other economic traits such as 100-seed weight were reported (Janila et al., 2015; Songsri et al., 2009; Upadhyaya, 2005; Upadhyaya et al., 2011). High heritability and a lower G × E interaction for the surrogate traits were also reported (Songsri et al., 2009; Upadhyaya et al., 2011). Varshney et al. (2009) reported moderate-to-high heritability for drought-related traits with alleles having moderate additive effects identified. Additive and both additive and nonadditive effects were also reported (Lal, Hariprasanna, Rathnakumar, Gor, & Chikani, 2006; Nigam et al., 2001). A combined use of the empirical and trait-based selection approaches has been suggested under drought stress conditions (Dewi et al., 2011; Janila et al., 2015; Nigam et al., 2005) as it would be advantageous in selecting genotypes which are more efficient water utilizers or partitioners of photosynthates into economic yield.

4.3.2 | Leaf spots

ELS and LLS are caused by Cercospora arachidicola Hori and Cercosporidium personata (Berk & Curt.). Deighton, respectively, are the most common and serious diseases of groundnut, which can cause pod yield losses of over 50% (Mayeux & Ntare, 2001; McDonald, Subrahmanyanam, Gibbons, & Smith, 1985). Field and laboratory screening methods involve sowing genotypes in replicated plots with rows of a highly susceptible cultivar arranged systematically throughout the trial with good disease development ensured through the provision of inoculum (McDonald et al., 1985). A 9-point disease scale is used for measuring reactions separately for the two leaf spots. Earlier germplasm screenings resulted in the identification of promising lines for resistance sources (Subrahmanyanam, Moss, McDonald, Subba Rao, & Rao, 1985), and since then, many additional lines have become available as good sources of resistance (GCP 2011; Ige, Mohammed, & Goni, 2007, Janila, Pandey, Manohar, et al., 2016; Kanyika et al., 2015; Monyo & Varshney, 2016).

4.3.3 | Rust

Groundnut rust, caused by Puccinia arachidis Speg., is an economically important disease that significantly reduces the pod and fodder yield and oil quality. Protocols for screening genotypes at field condition involve the use of infector row technique (Subrahmanyanam et al., 1995). Reviews on groundnut breeding for rust resistance are available (Mondal & Badigannavar, 2015; Subrahmanyanam et al., 1997; Wynne, Beute, & Nigam, 1991). Earlier rust screening efforts identified some advanced rust-resistant lines such as ICG (FDRS) series (Reddy, Nigam, Dwivedi, & Gibbons, 1987). Later, more accesses and advanced lines were identified (GCP 2011; Monyo & Varshney, 2016; Reddy, Nigam, Rao, & Reddy, 2001, Subrahmanyanam et al., 1995; Varshney et al., 2014). Some of these lines combine rust and leaf spot resistance.

4.3.4 | Rosette

Groundnut rosette disease (GRD) caused by the groundnut rosette virus (GRV), groundnut rosette assistor virus (GRAV) and satellite RNA (Janila & Nigam, 2013; Reddy, Nigam, & Reddy, 1995) is a devastating disease. A method for simultaneous detection of the three causal agents has been published (Anitha, Monyo, & Okori, 2014). Sources of resistance were first discovered in cultivars from Burkina Faso and Cote d’Ivoire in 1952 (Ntare, Olorunju, & Hildebrand, 2002; Subrahmanyanam, Hildebrand, Naidu, Reddy, & Singh, 1998). Resistance among these cultivars was effective against both chlorotic and green rosette forms of the disease and was governed by two independent recessive genes (Nigam & Bock, 1990; Olorunju, Kuhn, Demski, Misari, & Ansa, 1992). Breeding through utilizing the cultivars resulted in the development of long-duration Virginia cultivars and early and medium maturing Spanish types (GCP, 2011; Mayeux et al., 2003; Monyo & Varshney, 2016, Ntare et al., 2002).

4.3.5 | Aflatoxin

Aflatoxin contamination induced by Aspergillus flavus and A. parasiticus is a major constraint to the global trade of groundnut. Low-altitude warmer ecologies with low precipitation support high occurrence and distribution of Aflatoxicigenic Aspergilli in soil and high aflatoxin B1 contamination in groundnut (Monyo et al., 2012). Three resistance mechanisms have been focuses of aflatoxin resistance breeding: (a) preharvest natural seed infection, (b) aflatoxin production and (c) in vitro seed colonization (IVSC). Nigam et al. (2009) described a large number of groundnut lines that showed IVSC resistance (15% or fewer seeds colonized) and seed infection resistance (<2% seed infection) including five elite lines recommended for cultivation in SA. In WCA, three varieties were reported for resistance to aflatoxin (Mayeux et al., 2003). More recently, seven accessions with consistent very low aflatoxin accumulation were identified (Waliyar et al., 2016). However, G × E interaction remains a major issue in screening for aflatoxin resistance (Nigam et al., 2009), and generally, little progress has been made in using conventional breeding for enhancing host-plant resistance to aflatoxin contamination (Waliyar et al., 2016). Even if some elite lines were recommended for cultivation in India (Nigam et al., 2009), so far no prominent variety has been officially released with aflatoxin resistance. Two varieties (J 11 and 55-437) released for yield and agronomic performance in WCA are known to have a good level of resistance and serve as standard checks. Recent efforts using biotechnology options have reported a high level of resistance in groundnut by overexpressing antifungal plant defensins MsDef1 and MtDef4.2 and through host-induced gene silencing of aflM and aflP genes from the aflatoxin biosynthetic pathway (Sharma et al., 2018).

4.3.6 | Quality

Oil and oleic acid content and confectionery traits are among the important quality traits. Various physical sensory, chemical and
nutritional factors determine the quality of groundnut for which substantial genetic variability exists (Dwivedi & Nigam, 2005). Near-infrared reflectance spectroscopy (NIRS), a robust and nondestructive method, is gaining popularity for the estimation of oil, protein, carbohydrate and fatty acid contents (Janila & Nigam, 2013). It is also cost-effective compared with wet chemistry. At ICRISAT, a large number of accessions screened had 34%–55% oil content (Dwivedi & Nigam, 2005). Several advanced lines for high oil content have also been recently developed (Janila, Manohar, et al., 2016; Janila unpublished). In the case of oleic acid content, very few lines are officially released, specifically for high O/L ratio (e.g., SunOleic 95R and SunOleic 97R in the USA; PC 223 K8 and PC 223 K9 in South Africa). With regard to confectionery types, large number of varieties have been identified (Mayeux et al., 2003; Monyo & Varshney, 2016).

4.4 Marker-assisted breeding

Genomic tools enhance crop breeding process by increasing the efficiency and speed of precision breeding to develop improved varieties. Diagnostic molecular markers linked with traits of breeding interest (or major effect QTLs) were identified for root-knot nematode (Choi et al., 1999; Chu, Holbrook, Timper, & Ozias-Akins, 2007; Church, Simpson, Burow, Paterson, & Starr, 2000; Garcia, Stalker, Schroeder, & Kochert, 1996; Simpson, 2001), rust (Khedikar et al., 2010; Mondal, Badigannavar, & D’Souza, 2012), rust and LLS (Kolekar et al., 2016; Sujay et al., 2012), nutritional quality traits (Chen, Wang, Barkley, & Pittman, 2010; Chu, Holbrook, & Ozias-Akins, 2009; Sarvamangala et al., 2011; Wilson et al., 2017), TSWV (Tseng, Tillman, Peng, & Wang, 2016) and growth habit (Li et al., 2017). Some of these linked markers have been validated and deployed for marker-assisted selection (MAS) and marker-assisted backcrossing (MABC). In the USA, MAS has been used for pyramiding nematode resistance and high oleic trait (Chu et al., 2011). At ICRISAT, MABC was employed to transfer a major rust resistance QTL from GPBD 4 to three popular varieties (ICGV 91114, JL 24 and TAG 24) resulting in the development of rust resistance lines with 56%–96% increase of pod yield (Varshney et al., 2014). Some of these lines were also found to be resistant to LLS with 39%–79% of higher mean pod yield (Janila, Pandey, Manohar, et al., 2016). Besides, MAS and MABC were used to enhance the oil quality traits in three groundnut varieties (ICGV 06110, ICGV 06142, and ICGV 06420) by transferring FAD2 mutant alleles from SunOleic 95R. A large number of lines with increased oleic acid in the range of 62%–83% were identified (Janila, Pandey, Shasidhar, et al., 2016), which are currently being evaluated for yield (Janila, pers. Comm.). At Dharwad University of Agricultural Sciences in India, MABC was used to improve JL 24 with GPBD 4 as donor parent (Yeri & Bhat, 2016). Similarly, MABC was employed to improve TMV 2 for LLS and rust using GPBD 4 where two backcross lines showed enhanced resistance to LLS and rust along with 71.0% and 62.7% increase of pod yield over TMV 2 (Kolekar et al., 2017). In the case of other important quantitative traits such as drought tolerance and yield components, QTL analyses using biparental populations revealed few major rather several small-effect QTLs. Genomewide association studies for 50 agronomic traits using 300 genotypes from the “reference set” identified a total of 524 highly significant MTAs for 36 traits (Pandey, Upadhaya, et al., 2014) indicating complex genetic control. Breeding approaches such as marker-assisted recurrent selection and genomic selection are the preferred approaches for introgression of a larger number but small-effect QTLs. But such approaches have not been widely used in groundnut.

5 CONCLUSION AND FUTURE PERSPECTIVES

Significant progress has been made in groundnut genetics, genomics and breeding, thus contributing to the increased productivity and production of groundnut globally although the rate of increase varies among regions. It is worth mentioning that the progress has been achieved through strong partnership and collaborations between scientists from national research systems, international research institutes, universities, and private research organizations and service providers. Globally, large numbers of groundnut lines were identified or developed as sources of variability for important traits and many improved varieties were released for target environments by breeding programmes. The last decade has witnessed the rapid development of genomic tools helping to better understand the groundnut genome. MAS and MABC have proved useful for selected traits. Emerging trait mapping approaches are expected to help the search for linked markers for other traits and develop diagnostic markers for breeding applications. The availability of the diploid and tetraploid genome sequences will provide more opportunities to identify the useful genetic variation for breeding at a genome scale, discover the genes of breeding interest and identify additional molecular markers amenable for high-throughput genotyping. High-throughput genotyping technologies are advancing fast with genotyping costs getting cheaper. It will not be far for such technologies to be routinely utilized by many breeding programmes, if not all, for screening segregating populations, purity testing, genetic mapping, targeted resequencing of specific genomic regions and other studies. In summary, groundnut improvement tools are available to exploit and build on past achievements for new discoveries to enhance and accelerate the genetic gain of breeding programmes such that processes for the development and release of improved varieties are speedy, technically efficient and cost-effective.

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