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REVIEW

Designing future peanut: the power of genomics-assisted breeding

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Abstract

Key message **Integrating GAB methods with high-throughput phenotyping, genome editing, and speed breeding hold great potential in designing future smart peanut cultivars to meet market and food supply demands.**

Abstract Cultivated peanut (*Arachis hypogaea* L.), a legume crop greatly valued for its nourishing food, cooking oil, and fodder, is extensively grown worldwide. Despite decades of classical breeding efforts, the actual on-farm yield of peanut remains below its potential productivity due to the complicated interplay of genotype, environment, and management factors, as well as their intricate interactions. Integrating modern genomics tools into crop breeding is necessary to fast-track breeding efficiency and rapid progress. When combined with speed breeding methods, this integration can substantially accelerate the breeding process, leading to faster access of improved varieties to farmers. Availability of high-quality reference genomes for wild diploid progenitors and cultivated peanuts has accelerated the process of gene/quantitative locus discovery, developing markers and genotyping assays as well as a few molecular breeding products with improved resistance and oil quality. The use of new breeding tools, e.g., genomic selection, haplotype-based breeding, speed breeding, high-throughput phenotyping, and genome editing, is probable to boost genetic gains in peanut. Moreover, renewed attention to efficient selection and exploitation of targeted genetic resources is also needed to design high-quality and high-yielding peanut cultivars with main adaptation attributes. In this context, the combination of genomics-assisted breeding (GAB), genome editing, and speed breeding hold great potential in designing future improved peanut cultivars to meet market and food supply demands.

Introduction

Cultivated peanut or groundnut (*Arachis hypogaea* L.), is a highly significant food and oil legume crop grown in > 100 countries worldwide, adapting to a variety of agroecological environments (Zhuang et al. 2019). However, most of the global production is grouped in emerging nations across Asia and Africa. During the 2021/2022 season, global peanut production reached 50.321 million tons, with China being the top producer (https://ipad.fas.usda.gov/cropexplorer/cropview/commodityView.aspx?cropid=2221000). In Asia and Africa, peanut production surpasses that of any other grain legume, including soybean (Zhuang et al. 2019). Peanut is said to have been cultivated approximately 6000 years ago in South America, and subsequently spread widely during the post-Columbian era (Bertioli et al. 2016a; Zhuang et al. 2019). Peanut is known as a "longevity fruit" due to its various health gains, i.e., high levels of heart-healthy oleic and linoleic acid, fiber, folic acid, and certainly digested protein, as well as the presence of resveratrol (Chen et al. 2016b). It plays a vital role in combatting

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malnutrition and safeguarding food safety due to its high content of seed oil (46–58%) and protein (22–32%) (Chen et al. 2016b; Zhuang et al. 2019). Peanut can serve as one of the vital foods in achieving food safety and sustainable development goals mainly "zero hunger" (https://www.fao.org/sustainable-development-goals/en/).

There is a high demand for peanuts and peanut-based products, especially confectionery items, in the global market. Peanuts are a rich source of minerals, vitamins, antioxidants, and various bioactive compounds that offer health benefits. Due to these characteristics, peanuts are promoted as a healthy and nutritious food (Variath and Janila 2017). Peanuts are widely consumed worldwide in various forms, such as cooked seeds, oil, and candy, and hold different meanings in different regions of the world (Variath and Janila 2017). However, peanut production in underdeveloped countries remains low due to numerous production limitations, including biotic and abiotic stressors, ineffective seed distribution techniques, lack of scientific knowledge, economic growth, low-input utilization, and political and social facilities (Varshney et al. 2017). Among these limitations, harmful insects, bacteria, viruses, drought, soil salinity, extreme temperatures, and nutrient imbalance are the most critical biotic and abiotic stresses. Small-scale farmers in underdeveloped countries, who primarily focus on cultivating peanuts due to their viability in their regions, often face many challenges due to limited access to crucial resources and cutting-edge technologies that could significantly impact their productivity level. Affordable sequencing and precise trait discovery tools/methods have strengthened the gene discovery pipeline in peanut, which may become stronger in the coming years (Varshney et al. 2019). Therefore, it is imperative for peanut researchers across the globe to actively incorporate innovative breeding techniques in crop improvement programs, aiming to design superior peanut cultivars characterized by enhanced productivity and stress tolerance that can address the pressing needs of deprived farmers in underdeveloped countries (Pandey et al. 2020b). These improved peanut varieties hold tremendous potential to uplift the socioeconomic conditions of these deprived agriculture communities.

During the past few decades, breeding tools have been successful in improving peanut, resulting in the generation of several varieties that can be cultivated in different agro-ecological regions (Jonnala et al. 2005; Mora-Escobedo et al. 2015; Janila et al. 2016b; Yeri and Bhat 2016; Kolekar et al. 2017; Gangurde et al. 2019; Pandey et al. 2020b). The enhancement in yield productivity varied in different geographical regions, as discussed in some previous work (Jonnala et al. 2005; Mora-Escobedo et al. 2015; Janila et al. 2016b; Yeri and Bhat 2016; Kolekar et al. 2017; Gangurde et al. 2019). Nevertheless, it is imperative to differentiate between the unpredictable yield increase examined across growing regions and the yield improvement succeeded through breeding programs. In the recent past, during the development of stress/disease-smart cultivars/lines, some studies have assessed the actual yield enhancement accomplished in peanut breeding programs (Jonnala et al. 2005; Mora-Escobedo et al. 2015; Janila et al. 2016b; Yeri and Bhat 2016; Kolekar et al. 2017; Liao 2017; Gangurde et al. 2019; Zou et al. 2020). Although climate change is anticipated to be a concern in the future, it has already led to an extensive reduction in the output and quality of peanuts in certain areas. This can be accredited to the augmented incidence of climate change events, especially during crucial phases such as flowering and seed expansion (Akbar et al. 2017; Gangurde et al. 2019). Nevertheless, to hamper the adverse impact of climate change, it is crucial to improve the efficacy of existing breeding methods to ensure a steady increase in peanut yield. Traditional breeding methods have been using phenotyping techniques to identify plants or progenies with required attributes. The conventional breeding strategies include hybridization, selection based on phenotypic traits, and further selection of potential breeding lines via yield assessment trials (Pandey et al. 2012; Janila et al. 2013; Gangurde et al. 2019). Although conventional breeding has been successful, it is a slow and labor-intensive method, taking approximately 10–15 years to design advanced varieties/lines, which includes a multistep route with distinctive timeframes. The duration for designing homozygous lines, testing, and variety release can vary substantially. Normally, the testing phase takes > 4 years, and this interval can vary beyond countries. Designing homozygous lines implies roughly seven crop seasons, which could be nearly 3.5 years in a peanut breeding program with two seasons per year. However, it is imperative to note that traditional breeding methods, while not naturally causing reduced genetic variation, may accidentally lead to reduced genetic diversity between modern cultivars of the same species. It is vital to rationalize that the reduction in genetic variation among modern cultivars of the same species is influenced not exclusively by the breeding method itself but by aspects such as the genetic distance of parent plants used in hybridization and the degree of selective pressure applied throughout breeding. This reduction in genetic variation could possibly make these cultivars more vulnerable to numerous environmental stresses (biotic and abiotic). Genomic breeding provides ample opportunities for integrating multiple genomic tools and technologies such as genomics-assisted breeding (GAB), haplotype-based breeding, gene editing, speed breeding and genomic selection. In case of peanut, multiple examples are now available for deploying GAB leading to molecular breeding products; however, other components of genomic breeding still remain unexploited. Therefore, as we investigate the power of genomic breeding, more specifically GAB as of now in peanut, it is

worth considering whether this approach offers schemes to modernize breeding methods, address possible limitations in genetic diversity, and improve environmental resilience.

Notably, by exploiting innovative genomic tools, GAB can guide peanut breeders to make more learned and accurate choices of parent plants for hybridization, including recognizing favorable alleles and genotypes linked with necessary traits, even if these are contemporary in less-used germplasm. In this way, GAB can contribute to retaining or even increasing genetic variation within the breeding germplasm pool. In recent years, the utilization of GAB has enabled peanut scientists to increase the effectiveness of selecting target traits for future breeding endeavors (Figs. 1 and 2) (Pandey et al. 2012, 2014b, 2020b; Janila et al. 2013, 2016b; Gangurde et al. 2019). Integrating genomic methods with HTP via molecular markers allows GAB to guide breeding attempts in forecasting phenotype from genotype (Figs. 1 and 2). With GAB, it is now possible to integrate numerous significant traits within a single specific variety. Most importantly, it can effectively combine and incorporate desirable characteristics, previously considered as independent entities, into a single genotype. Moreover, GAB assists in utilizing modern genome resources and characterizing allelic variation in advancing germplasm and cultivar advancement over the past decade. However, in order to sustain the progress made with GAB, new approaches must be developed that can quickly and efficiently manipulate allelic variation to create novel diversity that can be incorporated into future peanut designing programs (Varshney et al. 2005, 2020, 2021b). In the future, genomic breeding approaches that focus on optimizing crop genomes by accumulating favorable alleles and eliminating unfavorable alleles will be essential for designing improved future peanut cultivars (Varshney et al. 2005, 2020, 2021b; Pandey et al. 2020b). Therefore, this review presented the recent advancements in utilizing GAB and the integration of cutting-edge genomic tools as part of genomic breeding to design and develop improved future peanut varieties.

Germplasm collection and improvement for future breeding

The limited use of germplasm collections in breeding efforts is primarily attributable to the absence of accurate proof of traits of financial importance, such as yield, quality, tolerance to both biotic and abiotic stresses, and other desirable traits, which frequently exhibit high genotype × environment conversations that demand duplicated multi-locational examinations (Holbrook and Dong 2005; Liao 2017; Zhou et al. 2022b). Complete characterization of the tremendous scale of the germplasm archives is a costly and resource-intensive endeavor, which limits its wider usage in breeding. In order to maximize the utilization of germplasm in crop advancement, the best approach would be to create a small and effective but diverse core collection that signifies the entire collection and trait diversity keeping in mind the current as well as future breeding programs (Liao 2017; Zhou et al. 2022b). This core collection can be significantly assessed, presenting valuable evidence that can be effectively harnessed to manage more effective functioning and management of the entire germplasm collection. By lowering the collection size while retaining diversity, resources can be trained for a more targeted assessment of germplasm,

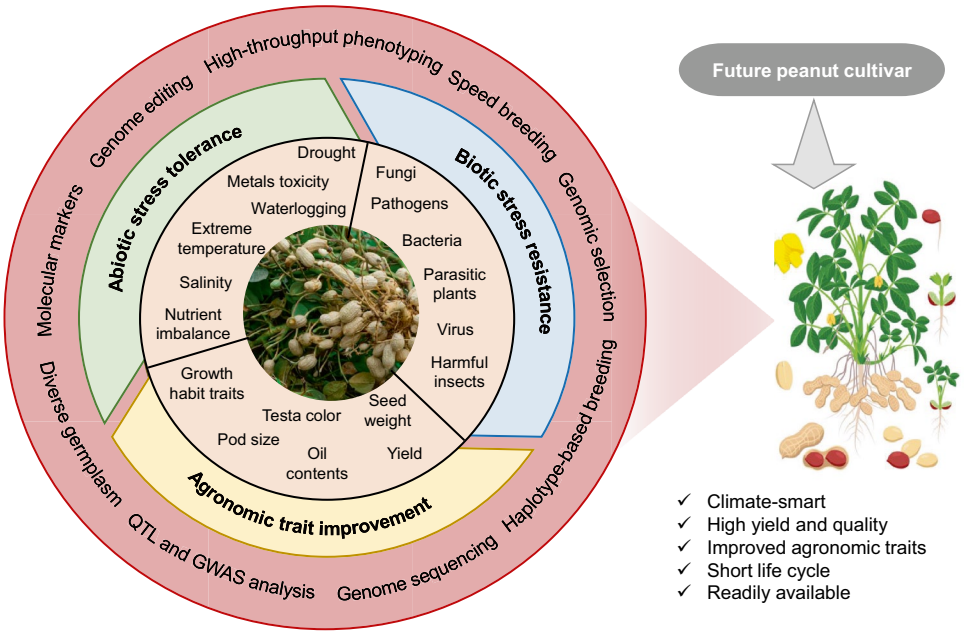

Fig. 1 An overview of integrating genomics-assisted breeding with modern tools to dissect the genetic basis for designing future peanut cultivars. By integrating these tools and methods, peanut breeders can advance their proficiency in recognizing necessary traits and designing new climate change-smart cultivars (such as abiotic stress tolerance and biotic stress resistance) that have improved agronomic traits (such as superior yield and other beneficial properties such as high protein and oil contents, etc.)

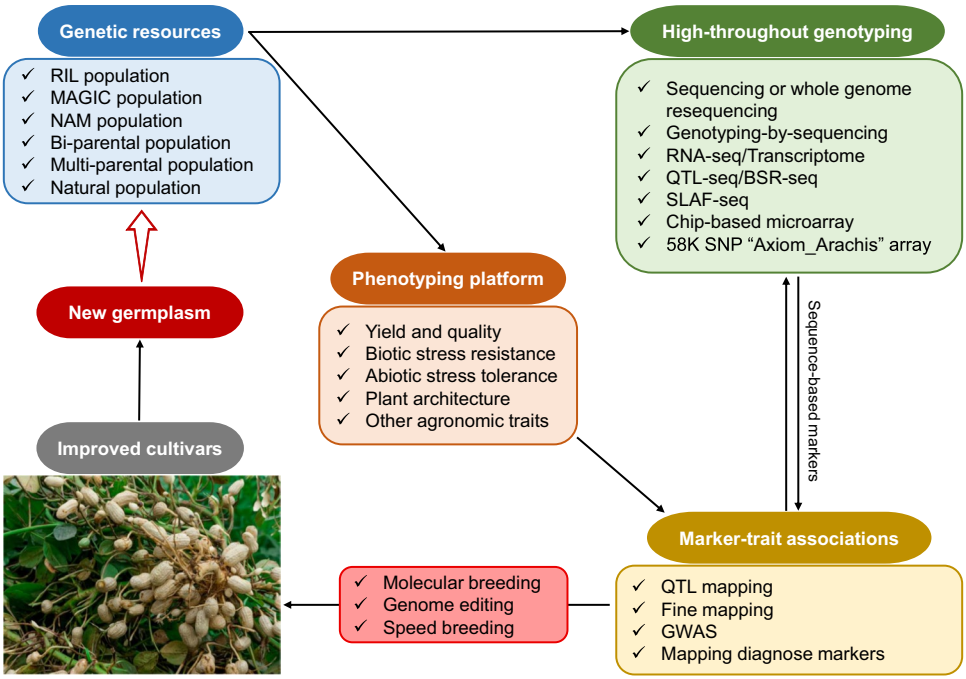

Fig. 2 A proposed flow diagram delineates the GAB process for designing future improved peanut cultivars. GAB-driven rational design approaches can enable the application of stress-smart alleles/genes, help resolve gene systems to manage response to manifold environmental factors (such as biotic and abiotic), and eventually help the designing of breeding systems for the invention of stress-smart and high-yielding cultivars by harmonizing the balance between grain yield and trait improvement. Abbreviations: Bulked segregant RNA-sequencing (BSR-seq); genomics-assisted breeding (GAB); genome-wide association study (GWAS); multi-parent advanced generation inter-cross (MAGIC); nested association mapping (NAM); quantitative trait locus-seq (QTL-seq); quantitative trait loci (QTL); recombinant inbred line (RIL); specific length amplified fragment-sequencing (SLAF-seq)

leading to more effective and operative crop improvement efforts (Holbrook and Dong 2005; Liao 2017). Conservation of conventional landraces is important for the long-term exploitation of geographically developed germplasm resources regardless of the expansion and development of modern peanut cultivars. The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India, the United States Department of Agriculture (USDA) in the USA, Oil Crops Research Institute-Chinese Academy of Agricultural Sciences (OCRI-CAAS) in China, and Brazil are the main repositories of *Arachis* germplasm worldwide. Yet, lesser collections are also found in several countries, such as Argentina, Africa, and others (Hui-Fang et al. 2008; Barkley et al. 2016; Liao 2017). In latest years, researchers have made significant advances in evaluating the genetic divergence contained by *A. hypogaea*, and the credit goes to extensive peanut germplasm characterization attempts (Liao 2017). Notably, the USA, ICRISAT, and Chinese peanut breeding programs have made significant progress in this area since the selection of peanut core- and mini-core collections (Liao 2017). Through the comprehensive characterization of germplasm resources, several elite peanut accessions with needed traits have been selected for designing future research and breeding programs.

For instance, several core- or mini-core collections have been established in peanut to facilitate trait advancement and increased tolerance/resistance to various abiotic/biotic stresses. For instance, 30 accessions associated with drought tolerance (Hamidou et al. 2012), 58 accessions connected with cold stress tolerance (Upadhyaya et al. 2009), 184 accessions associated with abiotic/biotic stress tolerance and agronomic traits (Upadhyaya et al. 2014), 95 accessions associated with Sclerotinia blight resistance (Dura et al. 2020), 231 accessions associated with early/late leaf spot (ELS/LLS) resistance (Shaibu et al. 2020a), 99 accessions (Ding et al. 2022) and 184 accessions (Waliyar et al. 2016) associated with aflatoxin resistance, and 576 core- and 298 mini-core accessions associated with bacterial wilt resistance (Jiang et al. 2013), 298 accessions connected with various agronomic traits (Jiang et al. 2014), 250 accessions linked with six yield-related traits (Zhou et al. 2021), 112 accessions connected with numerous agronomic traits (Shaibu et al. 2020b), 250 accessions associated with fatty acid contents (Zhou et al. 2022a), and 120 accessions associated with seed quality traits (Patel et al. 2022), and many collections are available around the world.

To solve the genetic bottlenecks of constrained gene flow, the improvement/designing of synthetic amphidiploids has

been practiced as an efficient option to expand the cultivated gene pool. Previously, several synthetics have been developed by using different diploid species with high levels of resistance/tolerance to multiple stresses and other agronomic traits. For instance, synthetics obtained from wild peanut species were employed to design chromosome segment substitution line and manipulated to examine plant morphology (Fonceka et al. 2012). A group of scientists from ICRISAT, India, have developed 17 new synthetic amphidiploid and autotetraploid populations to broaden the genetic base, and these innovative synthetics were also associated with resistance to LLS and peanut bud necrosis disease (Mallikarjuna et al. 2012; Shilpa et al. 2013). Two new synthetics (ISATGR 278-18 and ISATGR 5B) were exploited to introduce foliar disease resistance into five elite Indian peanut varieties using the backcross breeding method. Besides disease resistance, these new lines have also displayed diverse adaptations for other significant morphological and agronomic attributes (Kumari et al. 2014).

In another study, Mallikarjuna et al. (2012) developed numerous synthetics (amphidiploids and autotetraploids) using A- and B-genome accessions showing resistance to diverse biotic diseases. These synthetic populations produced introgression lines with hardy resistance to LLS and rust, indicating genetic diversity in key traits. Genotyping of these lines revealed putative novel alleles from diverse wild species, which will be keys for peanut improvement (Mallikarjuna et al. 2012). To introduce LLS resistance into the elite cultivar "ICGS 76," advanced backcrossing employed a synthetic amphidiploid (ISATGR 278-18) known for foliar disease resistance (Kumari et al. 2020). This activity yielded an AB-QTL population of 164 introgression lines and a linkage map with 114 SSRs. Moreover, the analysis detected significant main-effect QTLs for LLS and rust, along with epistatic-QTLs for foliar diseases and agronomic traits. Notably, resistance from the wild species (i.e., *A. batizocoi*) has proven possibilities in peanut improvement (Kumari et al. 2020). The designing of a fertile, cross-compatible synthetic amphidiploid (TxAG-6) proposed a novel way forward to introduce wild alleles for disease and pest resistance into commercial peanut cultivars (Denwar et al. 2021). Assessment of 27 interspecific lines developed from an advanced backcross population in Ghana uncovered thriving introgression of ELS resistance. Notably, some lines displayed decreased leaf spot symptoms and high pod yields, demonstrating the prospective to overcome yield loss naturally correlated with resistance. Nonetheless, the multigenic nature of resistance led to some awareness, highlighting the necessity for future QTL analysis to discover and merge resistance alleles while reducing linkage drag (Denwar et al. 2021). Altogether, the above-discussed examples suggest that these lines can assist as donors in future peanut breeding programs intended to design better-quality cultivars with necessary agronomic traits such as improved resistance/tolerance to biotic/abiotic factors and an expanded genetic base.

Based on above-discussion, it can be concluded that the use of core- and mini-core collection and the development of synthetic amphidiploid approaches together with advanced methods have enabled the uniform characterization and assessment of peanut germplasm to be significantly and intensively carried out in recent years. These attempts have significantly aided varietal advancement in peanut, proceeding in enhanced production. Additionally, the application of genomic techniques in germplasm characterization and trait innovation has fast-tracked these advancements. As a result, the discovery and choice of appropriate accessions or germplasms correlated with particular traits can be effectively employed in the future peanut breeding programs for designing improved cultivars.

Genome sequencing and molecular marker technologies

Improvements in peanut genome sequencing projects

Arabidopsis thaliana was the very first model plant whose entire genome was sequenced in 2000, marking a significant milestone in plant genomics research. After that, technological advancements have made it feasible to sequence the genomes of thousands of plant species (https://www.ncbi.nlm.nih.gov/genome/browse#!/overview/). Plant species are selected for genome sequencing based on specific criteria such as their economic importance, small genome size, diploid nature, availability of genetic and physical maps, transcriptomes, and other genomic tools, and presence of a huge research community (Michael and Jackson 2013; Bertioli et al. 2016b). In 2002, rice (*Oryza sativa* L.) was the first crop to be sequenced completely, making available the reference genome (Goff et al. 2002). Despite the achievement and improvements in sequencing tools, it undertook 14 years to sequence the complex peanut genome due to the small research community, lack of funding support and also the large and complex polyploid genome. Nonetheless, the peanut research community deployed the modern sequencing and genome assembly tools for developing high quality reference genomes, which is now fast-tracking the process of varietal development in order to contribute toward achieving global food security.

The US Peanut Genome Initiative (PGI) was revealed in 2004, and later expanded to the International Peanut Genome Initiative (IPGI) to coordinate global efforts in genome research for peanut. In 2010, the Peanut Genome Consortium (PGC) introduced a peanut genome sequencing project and published the genome sequences of two

diploid peanut [*A. duranensis* (~ 1.21 Gb) and *A. ipaensis* (~ 1.51 Gb)] progenitors in 2016 (Bertioli et al. 2016a). On the other hand, IPGI and PGC have been directing and managing revolutions in peanut genome exploration and breeding. The allotetraploid wild peanut (*A. monticola*) genome assembly (~ 2.62 Gb) was made available in 2018 (Yin et al. 2018), providing valuable information for peanut research community.

The recent improvements in genomics and sequencing technologies faster the publication of whole-genome sequences of three cultivated peanuts (*A. hypogea*) in 2019, including Shitouqi (~ 2.54 Gb) (Zhuang et al. 2019), Fuhuasheng (~2.64 Gb) (Chen et al. 2019a), and Tifrunner (~ 2.54 Gb) (Bertioli et al. 2019). Three-dimensional chromatin organization of cultivated peanut was released in 2021 (Zhang et al. 2021b). Genome sequencing of diploid and tetraploid peanuts provides valuable information on domesticated genes, future breeding targets for improvement and genome evolution. It also offers a valuable means for genome-wide marker discovery and re-sequencing. In this regard, innovations in peanut omics have initiated an investigation of population genomics in the current fast-forward breeding era (Bhat et al. 2021b). These omics explorations have illuminated genome features, origin, domestication, and the complicated genotype–phenotype alliances, aiding to a broad understanding (Bhat et al. 2021b). For instance, Samoluk et al. (2022) stipulated the most widespread look of the repeatome underlying forces that led to the genome variation of *Arachis* species. This study concluded that contrasting alterations in the richness of satellite DNA and long-terminal repeat retroelements are the key players involved in the difference in genome size and heterochromatin quantity in *Arachis* diploids (Samoluk et al. 2022). Another recent study examined genomic differences between cultivated peanut subspecies (ssp. *hypogaea* and ssp. *fastigiata*) using genes, repeat elements, and transposable element analysis (Bhat et al. 2023), considering their importance in gene-based ground-breaking breeding methods and superior evolutionary assess in the size, structure and function of the host genomes leading to species diversity. This study exploited a reference genome, exposing insights into gene distribution, density, and structure. Particularly, allelic alterations were monitored in genes and transposable elements, with effects for the genetic variation of peanut subspecies (Bhat et al. 2023).

Nevertheless, the current single reference genome (mainly for cultivated peanut) is insufficient to comprehend the vast genetic variations in the crop germplasm collections that include its landraces and wild-relatives (Khan et al. 2020a; Pandey et al. 2020b; Bohra et al. 2022a, b; Raza et al. 2023b, c). With the ongoing advances in sequencing technologies, the peanut community can now move forward with the sequencing of multiple peanut genomes (e.g., pan-genome and super-pangenome) that could enable intense investigations on genetic divergence and allelic alteration controlling important traits and also accelerate the genetics and genomics breeding efforts for designing future peanut cultivars.

Genomic resources help to identify novel gene families in peanut

The availability of reference peanut genome sequencing promotes the comprehensive utilization of different genomic resources to identify and characterize novel gene families in peanut (Bertioli et al. 2019; Zhuang et al. 2019; Chen et al. 2019a). Recently, different gene families have been reported to play vital roles in peanut growth and development, and stress tolerance. For instance, Song et al. (2016) discovered 77 and 75 WRKY proteins from *A. duranensis* and *A. ipaënsis*, respectively, and some of the genes were up-regulated against salicylic acid and jasmonic acid treatments (Song et al. 2016). After having the sequence of cultivated varieties, Zhao et al. (2020) identified 158 *AhWRKY* and Yan et al. (2022) identified 174 *AhWRKY* genes in *A. hypogea*, using two different genome versions. Both studies have discovered some novel genes that significantly respond to drought stress and *Ralstonia solanacearum* infection (Zhao et al. 2020; Yan et al. 2022). Gao et al. (2017) discovered 132 and 129 bHLH proteins from *A. duranensis* and *A. ipaensis*, respectively, and established that most of the genes were found to be involved in pod development in peanut. Another study reported a total of 650 *FAR1* genes from four *Arachis* species and its closely related species like Glycine max (Lu et al. 2022). Among these, *A. hypogea* was found to have a maximum number (i.e., 246) of *AhFAR1* genes, and expression analysis suggested their key role in pod development (Lu et al. 2022).

Mou et al. (2022) identified 72 *LOX* genes in *A. hypogea* and the overexpression of one gene "*AhLOX29*" in *Arabidopsis* improved the drought stress tolerance by regulating physio-biochemical traits. Huang et al. (2022) discovered 126 *AhLEA* genes and most of them were significantly up-regulated against diverse abiotic stresses. A recent study identified 29 and 30 *ARF* genes from *A. duranensis* and *A. ipaensis*, respectively (Tang et al. 2022a). Of these, *Arahy.7DXUOK* gene was found to be a prospective target of miR160. Furthermore, the overexpression of miR160 reduced the expression level of *Arahy.7DXUOK* gene and thus improved salinity tolerance in miR160OX transgenic plants (Tang et al. 2022a). Raza et al. (2022b) discovered 166 *AhAPX* genes in cultivated peanut and suggested their vital role against different hormones and abiotic stresses, and tissue development. Liu et al. (2022b) identified 162 *AhSAUR* genes in *A. hypogea* and the functional analysis of *AhSAUR3* suggested its negative role against drought stress tolerance. Wu et al. (2023) reported 178 *AhPP2C* genes and

the expression analysis showed that most of the *AhPP2C* genes respond to salinity stress. A recent study discovered 43 *AhUbiA* genes in *A. hypogea* and expression analysis suggested their key role in ABA signaling and cold tolerance (Yang et al. 2023b). In recent studies, the same group of authors reported 84 *AhGLPs* (Yang et al. 2023c) and 116 *AhOMT* genes (Cai et al. 2023) in *A. hypogea* and expression analysis suggested their key role in tissue development and stress tolerance, i.e., temperature, water, and hormones (Yang et al. 2023c). Sharif et al. (2023) identified 17 *AhAPYs* genes in *A. hypogea* and the functional characterization of *AhAPY2-1P* advocated that this promotor can be employed to drive the resistance-associated genes to boost the protective power of the pericarp (Sharif et al. 2023).

Likewise, Wang et al. (2023) detected 46 *AhHsf* genes in peanut, and most of the genes were induced by salinity and drought stress. At the same time, the overexpression of *AhHsf20* gene enhances the salinity tolerance in transgenic *Arabidopsis* plants (Wang et al. 2023). A recent study identified 29 *AhNRAMPs* genes in *A. hypogea* and revealed their role in cadmium tolerance (Yan et al. 2023). Zhang et al. (2023a) discovered 52 *AhPLCP* genes in *A. hypogea* and evaluated their expression mainly under cold stress. Meanwhile, the functional validation of *AhRD21B* extensively improved cold tolerance in transgenic *Arabidopsis* plants (Zhang et al. 2023a). These outcomes not only subsidize our insight into the novel role of genes but also postulate valuable data for disease resistance, stress tolerance, and growth and development regulation in peanut. In the future, these novel genes could be functionally verified using overexpression or gene editing techniques to fully uncover their function in designing future improved peanut cultivars.

Progresses in molecular markers development for genetic linkage mapping

The combination of plant breeding, genetics, and/or genomics can lead to increased productivity and improvements in traits, and resistance/tolerance to biotic/abiotic stresses in peanut (Pandey et al. 2020b). In comparison to other major legume crops, peanut has made slow advancements in acquiring genomic resources (Pandey et al. 2020b; Bohra et al. 2022b). Recent innovations have led to the improvement of genomic resources, like molecular markers (including simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) and genetic maps for diploid and tetraploid peanuts (Pandey et al. 2014b; Zhao et al. 2016; Ozias-Akins et al. 2017; Choudhary et al. 2019; Zhuang et al. 2019). Before 2016, some recent publications have reviewed the progress made with the application of marker-assisted breeding (MAB) in peanut (Pandey et al. 2014b; Ozias-Akins et al. 2017). Since the sequencing of diploid and tetraploid peanuts, momentous advancement has been made in evolving several thousand markers, genetic maps, and QTL mapping for molecular breeding of peanut for agronomically significant traits, and resistance/tolerance to biotic/abiotic stresses. Genome sequencing not only boosts our knowledge of genome structure and gene functions, but also facilitates the discovery of various genome-wide SSR sites that can have considerable purposes in genetics and breeding.

The diploid genomes of *A. duranensis* (A genome) and *A. ipaensis* (B genome), led by the IPGI, were used to discover SSRs, resulting in the discovery of 135,529 and 199,957 SSRs, respectively (Zhao et al. 2017). Comparative analysis of the diploid genomes of *A. duranensis* and *A. ipaensis* discovered 515,223 InDels (269,973 insertions and 245,250 deletions) by comparing the two genomes (Vishwakarma et al. 2017). The reference genome sequence can also enable the discovery of SNPs, which are the utmost prevalent type of genetic variation throughout the genome.

After 2016, several molecular markers correlated with numerous traits have been identified using the available genomic resources (Table 1). For instance, miniature inverted-repeat transposable elements (MITEs) are non-autonomous elements and usually of < 600 bp in length (Shirasawa et al. 2012a). In peanut research, the utilization of AhMITE1 markers has seen extensive growth, with their count approaching 4000 (Shirasawa et al. 2012a, b; Gayathri et al. 2018). Although quite a novel type of DNA molecular markers, AhMITE1 markers hold excellent promise, even though their utilization has not been widespread. Particularly, AhMITE1 markers have shown substantial potential, showing effective effects in diverse domains such as finding true hybrids, genetic mapping, and studying evolution and genetic variation (Hake and Bhat 2017; Hake et al. 2017; Gayathri et al. 2018).

Newly developed SSR markers were employed to genotype cultivated peanut germplasm and breeding materials, showing the power of the 6455 novel SSRs and 11,902 SNPs identified markers (Peng et al. 2016). Three studies have effectively applied QTL-seq approach to discover SNP markers connected with disease resistance in peanut. Zhao et al. (2016) first identified SNP and SSR markers located within two adjacent QTLs controlling bacterial wilt resistance using SSR joint with resistance-related SNP markers created by BSA-RAD sequencing. Cui et al. (2020) identified SNP markers linked with two QTL regions that control stem rot resistance. While Pandey et al. (2017c) identified allele-specific diagnostic markers for rust- and LLS-resistance based on whole-genome resequencing (WGR). In a study by Kim et al. (2017), WGR produced high-throughput SNPs for two peanut cultivars. A total of 1,954,267 SNPs for *A. duranensis* (A) and 353,490 for *A. ipaensis* (B) were detected, with nearly 90% of the SNPs being homozygous for *A. duranensis* and 43% for *A. ipaensis*. These numerous

Table 1 A comprehensive list of high-density genetic linkage maps developed in peanuts to identify genomic regions, molecular markers, and QTLs associated with different traits

Populations	Genotyping assay	Number of mapping individuals	Number of mapped markers	Map distance (cM)	Number of QTLs (or genes)	Associated trait(s)	References
Stress/disease tolerance/resistance							
RIL (Tifrunner × GT-C20)	WGR	91	8869 SNPs	3120	35 main-effect QTLs	Disease resistance	Agarwal et al. (2018)
RIL (TAG 24 × GPBD 4)	ddRAD-seq and WGR	266	171 SNPs, 89 transposons, and 193 SSRs	1510.1	2 QTL regions for late leaf spot and 1 region for rust resistance; 4 and 6 genes for late leaf spot and rust resistance, respectively	Late leaf spot and rust disease	Shirasawa et al. (2018)
RIL (TG37A × NRCG-CS85)	GBS	270	585 SNPs	2430	44 major epistatic QTLs	Stem rot resistance	Dodia et al. (2019)
RIL (SunOleic 97R × NC94022	WGR	140	11,106 SNPs (5816 bins)	2004	3 QTLs	Tomato spotted wilt virus	Agarwal et al. (2019)
F_9 RIL (Yuanza 9102 × Xuzhou 68–4)	QTL-seq	195	164,522 SNPs	38.14	1 major QTL	Bacterial wilt resistance	Luo et al. (2019b)
RIL (TAG 24 × GPBD 4)	BSA-seq, SLAF-seq, QTL-seq and RNA-seq	25	7183 and 5019 SNPs	2990.54 and 2468.61	216 and 171 candidate genes for each disease, respectively	Leaf rust and late leaf spot resistance	Zhuang et al. (2019)
F_{4-6} RIL (Zhonghua 10 × ICG 12625)	SSRs	140	1175 SSRs and 42 transposon markers	2038.75	12 QTLs	Aflatoxin resistance	Yu et al. (2019)
F_{10} RIL (Xinhuixiaoli × Yueyou 92)	SLAF-seq	314	5022 SNPs	2231.25	2 major QTLs	Aflatoxin resistance	Khan et al. (2020b)
F_{12} RIL (Zheng8903 × Yuhua4)	SNPs and KASP	212	3634 bin markers	1817.91	8 QTLs	Web blotch resistance	Liu et al. (2020a)
$F_{6:7}$ RIL (NC 3033 × Tifrunner)	58 K SNP array	156	1451 SNPs and 73 SSRs	3381.96	33 additive QTLs	Stem rot resistance	Luo et al. (2020b)
RIL (TAG 24 × ICGV 86031)	58 K SNP "Axiom_*Arachis*" array	309	1028 SNPs and 177 SSRs	2598.3	19 major main-effect QTLs	Drought and iron deficiency tolerance	Pandey et al. (2021)
F_8 RIL (Zhonghua 16 × J 11)	WGR and SNPs/InDels	2802	233,365 SNPs/InDels	1573.85	6 novel QTLs	Aflatoxin resistance	Jiang et al. (2021)
F_{5-6} RIL (JL-24 × NRCGCS-85)	SSRs	108	1980 SSRs	977.42	2 major QTLs	Bud necrosis resistance	Jasani et al. (2021)
$F_{7:9}$ RIL (JS17304-7-B × JS1806)	48 K "Axiom_*Arachis*" SNP array	103	1819 SNPs	2531.81	2 consistent QTLs	Smut resistance	de Blas et al. (2021)

Table 1 (continued)

Populations	Genotyping assay	Number of mapping individuals	Number of mapped markers	Map distance (cM)	Number of QTLs (or genes)	Associated trait(s)	References
Chinese mini-mini core collection	RAD-seq	99	38,237 SNPs and 6207 InDels	–	GWAS revealed 16 SNPs/InDels associated resistance	Aflatoxin resistance	Ding et al. (2022)
$F_{19–23}$ RIL (TMV 2 × TMV 2-NLM)	SMA	432	553 SNPs, 8 SSRs and 139 AhTEs	2438.2	3 main-effect QTLs for PYPP and 9 for SDW_70	Drought tolerance	Ghosh et al. (2022)
$F_{19–20}$ RIL (TMV 2 × TMV 2-NLM)	SMA	432	553 SNPs, 8 SSRs and 139 AhTEs	2438.2	11 main-effect QTLs for VCR and 12 for SCMR	Iron deficiency chlorosis tolerance	Tayade et al. (2022)
$F_{8:10}$ RIL (Yuanza9102 × wt09-0023)	KASP markers and dRAD sequencing	521	5120 SNPs	3179	4 major QTLs	Bacterial wilt resistance	Qi et al. (2022)
F_{13} RIL (Yueyou 92 × Xinhuixiaoli)	QTL-seq	581	381,642 SNPs and 98,918 InDels	1627.4	Two major QTLs and eight NBS-LRR genes	Bacterial wilt resistance	Zhang et al. (2023b)
MAGIC lines	Affymetrix 48 K SNP "Axiom_*Arachis*" array	600	15,708 SNPs	–-	11 QTLs and 62 MTAs	Late leaf spot resistance	Wankhade et al. (2023)
$F_{7–9}$ RIL (Zhonghua 16 × J 11)	SNPs/InDels	200	233,365 SNPs/InDels	1573.85	11 QTLs for aflatoxin resistance and six QTLs for hundred-seed weight	Aflatoxin resistance and yield traits	Jin et al. (2023)
$F_{7–9}$ RIL (Xuhua13 × Zhonghua6)	QTL-seq, WGR and RNA-seq	186	2183 SNPs	2063.55	4 major QTLs and QTL *qAFTRA07.1* was fine-mapped	Aflatoxin resistance	Yu et al. (2023)
F_8 RIL (DF12 × Huayu 44)	WGR	807	447,528 SNPs (2494 bins)	6.01 cM (46.74 cM—61.75 cM)	1 major QTL and 15 candidate genes	Cold tolerance	Zhang et al. (2023d)
$F_{7:8}$ RIL (JL 24 × 55–437)	GBS	248	478 SNPs	1961.39	45 major main-effect QTLs and different genes for 21 traits	Heat tolerance	Sharma et al. (2023b)
Agronomic traits							
$F_{6:10}$ RIL (79266 × D893)	SSRs	151	231 SSRs	905.18	11 QTLs for MSH and 16 for LBH	MSH and LBL	Li et al. (2017)
F_2 RILs (ICGV 07368 × ICGV 06420) for oil, and (06420 × SunOleic 95R) for fatty acid contents	DArT and DArT\seq	184 and 179	854 and 1435	3526 and 1869	8 QTLs for oil and 21 for fatty acid contents	Oil and fatty acid contents	Shasidhar et al. (2017)

Table 1 (continued)

Populations	Genotyping assay	Number of mapping individuals	Number of mapped markers	Map distance (cM)	Number of QTLs (or genes)	Associated trait(s)	References
$F_{2:11}$ RIL (Huayu28 × P76)	SLAF-seq and SSRs	146	2334 (68 SSRs and 2266 SNPs)	2586.37	2 main QTLs	Oleic acid and linoleic acid contents	Hu et al. (2018)
F_2 RIL (Yueyou 92 × Xinhuixiaoli)	BSA-seq, SLAF-seq, QTL-seq and RNA-seq	267	7183 and 5019 SNPs	2990.54 and 2468.61	7 major QTLs and 19 genes for seed size; and 202 candidate genes for testa color	Testa color and six seed size traits	Zhuang et al. (2019)
$F_{8–10}$ RIL (Zhonghua 10 × ICG 12625)	SSRs	140	1399 SSRs	2279.10	59 additive QTLs	Saturated fatty acid contents	Liu et al. (2019)
F_8 RIL (Jihua 5 × M130)	SLAF-seq	188	2808 SNPs	1308.20	39 QTLs	Growth habit traits	Li et al. (2019)
RIL (Silihong × Jinonghei 3)	SSRs	248	226 SSRs	1511.32	7 QTLs	Multi-seed pod	Wang et al. (2019)
RIL (Fuchuan Dahuasheng × ICG6375)	SSRs	188	161 SSRs	1557.48	28 consensus and 14 single QTLs	Seed number per pod	Chen et al. (2019b)
RIL (Tifrunner × NC 3033)	Axiom_*Arachis* SNP array and SSRs	156	1998 SNPs and 100 SSRs	3382.0	49 QTLs	Seed and pod traits	Chavarro et al. (2020)
Two NAM RILs populations	58 K SNP "Axiom_*Arachis*" array	581 for NAM_Tifrunner and 496 for NAM_Florida-07	3874 SNPs for NAM_Tifrunner and 2860 SNPs for NAM_Florida-07	2585.9 for NAM_Tifrunner and 2393.4 for NAM_Florida-07	19 QTLs in NAM_Tifrunner, and 23 QTLs in NAM_Florida-07	Seed and pod weights	Gangurde et al. (2020)
$F_{2:11}$ RIL (Silihong × Jinonghei 3)	SLAF-seq	248	2996 SNPs and 330 SSRs	1822.83	19 QTLs	Initial flowering date	Liang et al. (2020)
RIL (Xuhua 13 × Zhonghua 6)	ddRAD-seq	186	8064 SNPs	2465.62	7 major QTLs	Oil content	Liu et al. (2020b)
F_{11} RIL (Silihong × Jinonghei 3)	SLAF-seq	248	2996 SNPs and 330 SSRs	1822.83	15 significant QTLs	CDFFD	Wang et al. (2020)
$F_{14\text{-}19}$ RIL (TMV 2 × TMV 2-NLM)	GBS, AhTE, and SSRs	432	713 SNPs, 143 AhTEs, and 9 SSRs	2438.2	47 main-effect QTLs	Yield and oil quality traits	Jadhav et al. (2021)
$F_{7:9}$ RIL (Hanoch × Harari)	47 K "Axiom *Arachis*_SNP" array	260	1833 SNPs	1773.5	30 QTLs	Time to maturation	Kunta et al. (2021)
F_8 RIL (Zhonghua16 × sd-H1)	QTL-seq and WGR	242	541,282 SNPs	–	17 QTLs	Seed weight	Wang et al. (2022b)
$F_{7:9}$ RIL (Runner × Virginia)	Arachis SNP-array	243	2744 SNPs	950.2	6 significant QTLs	Maturity trait	Kunta et al. (2022)
RIL (Tifrunner × GT-C20)	58 K SNP "Axiom_*Arachis*" array	164	1147 SNPs	1679.72	2 major QTLs	Seed dormancy	Wang et al. (2022a)
$F_{7:8}$ RIL (ICGV 02266 × ICGV 97045)	5 K mid-density genotyping assay	160	325 SNPs	2335.3	5 major QTLs	Fresh seed dormancy	Bomireddy et al. (2022)

Table 1 (continued)

Populations	Genotyping assay	Number of mapping individuals	Number of mapped markers	Map distance (cM)	Number of QTLs (or genes)	Associated trait(s)	References
$F_{2:9}$–$F_{2:11}$ RIL (YZ9102 and wt09-0023)	DNA sequencing	521	5120 SNPs	3179	24 QTLs	Fresh seed germination	Zhang et al. (2022b)
$F_{2:4}$ RIL (YZ9102 × ZH12 and ZH2)	BSA-seq	491	412,874 SNPs/InDels	59.27	*AhRt2* gene on chromosome 12	Red testa	Zhang et al. (2022a)
RIL (Huayu36 × 6–13)	KASP	181	3829 SNPs and 37 SSRs	1266.87	11 additive QTLs	Pod number per plant	Zhang et al. (2023c)
$F_{9:11}$ RIL (JH5 × KX01-6)	Affymetrix genotyping array	192	2840 SNPs	3,706.382	14 significant QTLs	Oil content	Yang et al. (2023d)
$F_{9–10}$ RIL (Zhonghua 10 × ICG 12625)	QTL-seq and WGR	140	382,569 SNPs and 48,182 InDels (2700 bins)	1469.6	12 QTLs and 19 candidate genes	Sucrose content	Li et al. (2023)
RIL (ICGV 00440 × ICGV 06040)	5 K high-density SNP assay	218	5078 SNPs	1536.33	5 and 4 major main-effect QTLs for Fe and Zn contents, respectively	Iron and zinc content	Parmar et al. (2023)
RIL (Yuanza9102 × wt09-0023)	RAD-seq	521	5120 SNPs	3179	2 major QTLs	Growth habit traits	Fang et al. (2023)
F_2 RIL (79266 × D893)	WGR, BSA-seq, and KASP markers	1020 individuals and 151 lines	174 SNPs	905.18	1 major QTL and 3 haplotypes	Pod size	Yang et al. (2023a)
RIL (Chico × ICGV 02251)	58 K high-density SNP array	352	4199 SNPs	2708.36	6 QTLs for shelling percentage and seven QTLs for 100-seed weight	Seed weight and shelling percentage	Gangurde et al. (2023)

Arachis hypogaea transposable element (AhTE); bulked-segregant analysis sequencing (BSA-seq); concentration degree of floret flowering date (CDFFD); double-digest restriction-site-associated DNA sequencing (ddRAD-seq); genotyping by target sequencing (GBTS); Kompetitive Allele-Specific PCR (KASP); lateral branch length (LBL); markers-trait associations (MTAs); marker-assisted backcrossing (MABC); main stem height (MSH); pod yield per plant (PYPP); restriction-site-associated DNA sequencing (dRAD-seq); recombinant inbred line (RIL); single nucleotide (SSRs); single marker analysis (SMA); single nucleotide polymorphisms (SNPs); specific leaf area at 70 DAS (SLA_70); SPAD chlorophyll meter reading (SCMR); specific-locus amplified fragment sequencing (SLAF-seq); visual chlorotic rating (VCR); whole-genome resequencing (WGR). The dash (–) means no data available in the article

markers can assist as a worthy genetic resource for MAB programs and germplasm investigation to design improved peanut cultivars (Kim et al. 2017). Recently, Bhat et al. (2022) identified 4,309,724 SNPs from WGR data of 178 accessions. Of which, 46,087 had the maximum polymorphic information content. Moreover, among the numerous chromosomal settings, intergenic and intronic regions held more SNPs than the exonic regions. In short, these structural and functional landscapes of the SNPs will be of massive significance for their effectiveness in genetic and genomic studies in peanut.

The deployment of reference genomes and sequencing-based trait mapping approach started by using QTL-seq approach for identifying genes for resistance to rust and LLS followed by diagnostic marker development (Pandey et al. 2017c). These reference genomes were further analyzed, leading to the discovery of 135,529 SSRs from the A genome and 199,957 from the B genome (Zhao et al. 2017). Using these markers, two physical maps were created for each genome, and disease resistance QTLs (*qF2TSWV5* for tomato spotted wilt virus and *qF2LS6* for leaf spot virus) were mapped on a specific region (8.135 Mb) of chromosome A04 of the A genome. From this region, 719 novel SSRs were obtained, which can aid in fine mapping of these QTLs (Zhao et al. 2017). Additionally, this region contains 652 genes, including 49 defense-related genes, such as *NB-ARC* genes, *LRR* receptor-like genes, and WRKY TFs. In short, this study supplies a valuable resource for peanut genetic map construction, QTL mapping, and molecular breeding (Zhao et al. 2017). Another genome-wide analysis discovered a total of 8,329,496 SSRs, which were allotted in subgenome A (3,772,653), B (4,414,961), and nine scaffolds (141,882) (Lu et al. 2019), but we believe these should be evaluated and identified in future works. In addition, 1276 public SSRs were incorporated with the freshly designed SSRs. Furthermore, the freshly designed SSRs were combined with 1276 public SSRs loci. This study also detected a previously recognized leaf spot QTL (*qLLS_T13_A05_7*), which was located in a 1.448-Mb region on chromosome A05. Within this region, a total of 819 freshly established SSRs and 108 candidate genes were identified. These freshly designed and public SSRs offer a useful resource for trait genetic analysis and molecular breeding plans in cultivated peanut (Lu et al. 2019).

Using a density map with 7183 SNP markers, fine-mapping was performed for a single dominant gene (*Ahwrky13*) associated with red testa on a region of 0.905 cM on chromosome 3 (Zhuang et al. 2019). A recent study anticipated 512,900 SSRs from 2556.9-Mb genomic sequences of four peanut genotypes (Ma et al. 2020). Approximately 60% of these SSRs were single-locus SSRs, which are limited in recognizing the alleles of the A and B subgenomes of peanut. This study discovered two markers related to purple testa color and 27 markers near *FAD2* genes that can be benefited for breeding new varieties with purple testa and high-oleic acid content. These genomic SSRs will be handy for diversity assessment, genetic mapping, and functional genomics investigations in peanut (Ma et al. 2020). Another study constructed a peanut genetic map using a RIL population of 151 individuals, and 231 SSRs and identified 11 and 16 QTLs associated with main stem height and the first lateral branch length of peanut, respectively (Li et al. 2017). These findings offer valuable evidence for the fine mapping of QTLs and breeding optimal plant-types in cultivated peanut (Li et al. 2017).

By finer QTL mapping and BSA together with BSR analysis using RIL population, a candidate region was identified on chromosome 07 (0.87–1.95 Mb in contigs 000199F) and chromosome 12 (4.41–5.91 Mb in 000164F), which include 99 (such as ABC transporters, oligopeptide transporter 5 (OPT5), histidine kinase 2 (AHK2), amino acid permease 3 and transcriptional regulator STERILE APETALA-SAP), and 97 (such as auxin transcription factors-ARF2 and CYP78A6) candidate genes, respectively, associated with seed size (Zhuang et al. 2019). This study also noticed that one SNP and one InDel marker discriminate the promoter region of CYP78A6 between large and small-seeded parents. In both regions, a total of 248 significant SNPs were identified (Zhuang et al. 2019). This QTL mapping helped to discover a total of seven QTL regions associated with five seed size-related traits (Zhuang et al. 2019). A RIL population was created by crossing a cultivar called "Huayu36" with a germplasm line called "6–13", which had different seed weight, size, and shape. A high-density genetic map was developed using SLAF-seq and SSR markers, including a map distance of 1266.87 cM (Zhang et al. 2019). This new map helped to identify 27 QTLs on chromosome 8 for various seed-associated traits, which will be useful for additional functional examination of yield-associated traits in peanut (Zhang et al. 2019). In another study, a high-density genetic linkage map of cultivated peanut was improved using a combination of SLAF-seq and SSR methods to discover QTLs guiding the concentration degree of floret flowering date (Wang et al. 2020). The map comprised of 3326 genetic markers (including 2996 SNPs and 330 SSRs) allocated across 20 linkage groups, covering a total length of 1822.83 cM. This high-resolution and accurate map will enable more QTL discoveries associated with agronomic- and quality-connected attributes in cultivated peanut (Wang et al. 2020). By combining GWAS and BSA-seq, Li et al. (2022) discovered 12,342 high-quality SNPs, and found 90 significant SNPs delivered on 15 chromosomes linked with various peanut plant traits such as lateral branch angle, main stem height, lateral branch height, extent radius, and the index of plant type (Li et al. 2022). This study also discovered 597 candidate genes involved in biological processes,

phytohormone signaling, plant growth and expansion. BSA-seq combined with SLAF-seq was utilized to discover a genomic region on B05 connected with lateral branch angle, with four candidate genes implicated in peanut growth. These findings can be useful in MAB for peanut growth habits (Li et al. 2022).

Pandey et al. (2021) developed a high-density genetic map with 1205 loci using the 58 K SNP "Axiom_*Arachis*" array in the RILs population (TAG 24 × ICGV 86031). QTL analysis for 20 drought tolerance and two iron deficiency tolerance-related traits was accomplished, revealing numerous QTLs and genes on the recently constructed genetic map. These genes are implied to be involved in plant growth, development of seed and pod, and photosynthesis under stress conditions (such as drought or iron deficiency) in peanut (Pandey et al. 2021). In a recent study, Ghosh et al. (2022) identified the genomic regions associated with drought stress tolerance in peanut using a RIL population (TMV 2 × TMV 2-NLM). This study assessed the population over six seasons at two locations in India, i.e., Dharwad (non-stress conditions), and Tirupati (water-stress conditions) (Ghosh et al. 2022). Using 700 SNPs linkage map, QTLs and candidate genes accompanying drought stress tolerance were recognized in peanut. These candidate genes possess high potential in advancing the field of genetic research and also the linked markers can be employed to design drought tolerance peanut (Ghosh et al. 2022). Likewise, Agarwal et al. (2018) developed a high-density genetic map using SNP markers derived from WGR methods. The map comprised of 8869 SNPs circulated across 20 linkage groups and can enable disease resistance QTL exploration and candidate gene discovery in peanut (Agarwal et al. 2018). Based on the above-discussed examples, it can be inferred that peanut has a wealth of SNP molecular markers available for use in diverse genetic and molecular breeding applications. The improvement of genomic resources, i.e., molecular markers, genetic maps, QTLs identification, and MAB has assisted advancement in overcoming genetic constraints and has the promise to fast-track genetic improvement in peanut.

Marker-assisted breeding for peanut improvement

MAB (including QTL mapping and GWAS analysis) is a useful tool for trait discovery in peanut, as it can obtain historical recombination episodes and allelic variety not exhibited in structured populations. MAB data also provide support to further explore other genomics resources. For instance, technological innovations in sequencing and high-throughput genotyping methods (such as GBS, SSRs, QTL-seq, SLAF-seq, ddRAD-seq, RAD-seq, and BSA-seq) have greatly accelerated trait-finding efforts, enabling high-resolution mapping and quicker candidate gene detection in peanut (Table 1) (Pandey et al. 2014b, 2020b; Ozias-Akins et al. 2017; Zhuang et al. 2019; Zhang et al. 2023b). The reduced cost of sequencing and accessibility of high-quality reference genomes has presented marker- and sequence-based trait mapping as more reasonable and time-effective.

In recent years, MAB has also contributed to the design and release of improved varieties. The commercialization of marker-assisted backcrossing (MABC) lines with fungal foliar disease resistance in India marks an important milestone in peanut breeding. For instance, a rust resistance major QTL was introgressed using MABC in three popular Indian peanut cultivars, which resulted in 200 promising introgression lines with improved rust resistance and superior yield (Varshney et al. 2014). In another study, 82 introgression lines were developed through MABC and 387 lines through marker-assisted selection (MAS), combining DNA markers accompanied with higher oleic acid content (Janila et al. 2016a). High oleic acid alleles from SunOleic 95R were fruitfully introgressed into ICGV 05141 using MAS, resulting in recombinant lines with improved oleic acid content, oil quality, pod yield, and necessary pod/seed traits. These lines economically help Indian farmers and meet the market's breeding demand for high oleic peanuts (Bera et al. 2018). Likewise, (Deshmukh et al. 2020) utilized MAS to introgress high oleic content, resistance to LLS and rust qualities into the popular peanut cultivar (Kadiri 6). Sixteen homozygous plants were recognized with anticipated qualities in BC_1F_2, of which three lines demonstrated > 80% oleic acid, high resistance to LLS and rust, and promising pod and kernel structures, making them hopeful candidates for commercial release in India (Deshmukh et al. 2020). The MABC strategy was used by Kolekar et al. (2017) to generate a peanut line resistant to LLS, which can be used as a genetic resources in peanut improvement. They found and introduced LLS resistance genes into the peanut genome using molecular markers. The MABC line that resulted from this breeding protocol, developed by a series of backcrosses and directed by MAS, has a remarkable level of resistance to LLS (Kolekar et al. 2017). Similarly, Yeri and Bhat (2016) developed LLS-resistant peanut lines with MABC. These lines were further evaluated and released for commercial use, significantly contributing to combating a critical issue in peanut crops. This invention can potentially lower the need for chemical treatments, enhancing crop quality and production, further contributing to the profitability of peanut farming in India. These outcomes highlight the real efforts of GAB in designing improved cultivars, which are readily available to the farmers. As discussed in the below sections, several examples have shown the potential of these methods for fast-tracking MAB-assisted peanut breeding and some latest examples are also organized in Table 1.

Insights from QTLs and GWAS analysis

The identification of multiple QTLs that control significant quantitative traits in peanut is crucial for MAB (Pandey et al. 2014b; Ozias-Akins et al. 2017; Choudhary et al. 2019). Classical linkage mapping is a trustworthy approach to examine the genetic basis of these traits, while genome-wide mapping in huge populations can assist the cloning of target genes in peanut. The accessibility of high-density SNPs has allowed the use of GWAS, a natural population-based method that beats the restrictions of traditional linkage mapping. Combining phenotypic and genotypic data using GWAS delivers valuable visions into the complex genetic architecture of significant traits (Varshney et al. 2005, 2020, 2021b). Prior to the sequencing of diploid and tetraploid peanuts, limited progress was achieved in GWAS and QTL mapping for numerous traits and stress tolerance, as reviewed in some previous publications (Pandey et al. 2014b; Ozias-Akins et al. 2017; Choudhary et al. 2019; Bera et al. 2022). However, after 2016 and 2019, peanut genetics and genomics investigation has accelerated to guide future peanut breeding programs. Despite this progress, abiotic and biotic stresses continue to influence peanut production and agronomic traits, highlighting the ought to discover QTLs or genomic regions that can design future peanut cultivars under stress conditions. In this context, several studies have reported many QTLs/regions associated with different abiotic/biotic stresses and agronomically important traits.

Abiotic stress

Climate change imposes several abiotic stresses (such as drought, nutrient imbalance, temperature, soil salinity, etc.) that significantly impact crop productivity, including peanut (Raza et al. 2021, 2022a, 2023e, d, f, a; Varshney et al. 2021a; Zandalinas et al. 2021; Rivero et al. 2022; Benitez-Alfonso et al. 2023; Varshney and Bohra 2023). For instance, widespread phenotyping data from multiple locations and seasons were used for QTL analysis of drought- and iron deficiency tolerance-connected attributes in peanut (Pandey et al. 2021). This genome-wide analysis recognized 19 major QTLs, explaining up to 33.9% of the PVE. Numerous imperative candidate genes were also discovered in these QTL regions, possibly involved in plant growth, seed and pod development, and photosynthesis under stress conditions. These discoveries could be employed to design molecular markers for MAB to boost peanut yield under drought and iron-deficient soil conditions following validation (Pandey et al. 2021).

In a recent study, Ghosh et al. (2022) utilized a RIL population to discover genomic regions allied with drought stress tolerance in peanut. They discovered three major QTLs for pod yield per plant, with a PVE of 10.5%, and nine QTLs for specific dry weight at 70 days after sowing, with the highest PVE of 18.4%. Some of these QTLs showed epistatic interactions and were stable across different locations. This study also detected candidate genes with SNPs and *AhMITE1* insertions in the major QTL regions, including a rare non-synonymous SNP at Ah02_1558700 within the gene *ArahyW1P0U6* controlling pod yield per plant. These outcomes offer potential targets for genetic mutation and the improvement of linked markers to advance drought stress tolerance in peanut (Ghosh et al. 2022). Previously, 52 QTLs correlated with nine yield-related traits were discovered using a combination of phenotyping and genotyping data under well-watered and water-stress conditions at two locations in West Africa. Nonetheless, these QTLs had low PVE, with values of less than 12% (Faye et al. 2015).

Pattanashetti et al. (2020) identified 32 QTLs for iron deficiency chlorosis tolerance in peanut using an RIL population. The QTLs had low PVE for yield-related traits, but two major QTLs for visual chlorosis rating at 60 and 90 days were detected. The validated QTLs/markers could be used for MAB in peanut (Pattanashetti et al. 2020). In another recent study, 11 and 12 main-effect QTLs were spotted for visual chlorotic rating and SPAD chlorophyll meter reading, respectively (Tayade et al. 2022). Three QTLs were major for visual chlorotic rating and two were major for SPAD chlorophyll meter reading. A SNP marker was identified for visual chlorotic rating sited in an influential protein-binding gene (*Arahy.QA0C1*). The study discovered new QTLs and validated QTLs for iron deficiency chlorosis tolerance, delivering beneficial genomic resources for MAB (Tayade et al. 2022).

Sun et al. (2023) used BSA-seq to identify genomic regions and SNPs linked with low temperature tolerance in high oleic acid peanut. They identified a 2.29 Mb interval on chromosome A05 that restrained 122 genes associated to abiotic stress and plant-pathogen interaction, delivering comprehension into the molecular mechanisms of low temperature tolerance and potential for future MAB (Sun et al. 2023). Zou et al. (2020) conducted GWAS analysis using the 58 K SNP Axiom_*Arachis* array to identify SNPs associated with salinity tolerance and radical root length in peanut. They found three putative SNPs located on chromosomes Aradu.A03, Araip.B01, and Araip.B05 that were significantly related to the salinity tolerance and radical root length (Zou et al. 2020). More studies on different abiotic stresses in peanut are expected to be conducted in the future to design the climate-smart future peanut cultivars.

Biotic stress

Like abiotic stress, various biotic stresses also negatively impact peanut growth and production (Gangurde et al. 2019; Huang et al. 2023; Lokya et al. 2023). Using RAD-seq along

with SSRs and linked SNPs, Zhao et al. (2016) identified two major QTLs (*qBW-1* consistent in F2 and F8 generation and *qBW-2* in F2) for bacterial wilt resistance in cultivated peanut and found all linked SNP makers for *qBW-1* region located at the chromosome B02 of *A. ipaensis*, provided basic foundations for functional studies to enhance disease resistance in peanut (Zhao et al. 2016). Further studies by linkage mapping with SSRs or SNPs in other crosses of different resistance origins or resources obtained similar mapping regions on chromosome 12 (or B02) (Wang et al. 2018; Luo et al. 2019b, 2020a; Qi et al. 2022). Using QTL-seq led to design of closely linked KASP markers within R genes, which can be used for resistance varieties enhancement by MAB (Luo et al. 2019b, 2020a; Qi et al. 2022; Zhang et al. 2023b). This work has led to functionally characterizing key genes that can be used as precision breeding for bacterial wilt resistance in cultivated peanut. Agarwal et al. (2018) used WGR to identify 35 main-effect QTLs for disease resistance in peanut, including two QTLs for early leaf spot, two for LLS, and one for Tomato spotted wilt virus. They also detected QTL regions having disease-resistance genes (such as R-genes) and transcription factors. The authors developed KASP markers for these QTLs and validated them in a population that can contribute to design the GAB-mediated disease resistant peanut cultivars (Agarwal et al. 2018). In another study, Agmon et al. (2022) performed QTL mapping for stem rot resistance in peanut, and identified 20 significant QTLs in four locations. The B05 QTL was the strongest, with a PVE of 11.6–21.7%. Interestingly, this QTL was found to be colocalized with a major locus for branching habit, indicating that plant architecture can induce the disease rate of *Sclerotium rolfsii* in the peanut field (Agmon et al. 2022).

Aflatoxins are highly lethal mycotoxins delivered by *Aspergillus* fungi in peanuts. DNA markers related with aflatoxin production can aid in designing resistant peanut cultivars via molecular breeding methods. In this context, Yu et al. (2019) recognized four major- and six minor-QTLs associated with aflatoxin resistance using a genetic linkage map created by SSRs. However, due to the map's low resolution, related candidate genes could not be identified. To overcome this constraint, in the next study, Yu et al. (2020) conducted a GWAS analysis on 99 peanut accessions using RAD-seq and identified 60 SNP markers linked with aflatoxin resistance, explaining 16.87–31.70% of PVE. Of these, two SNPs, SNP02686 and SNP19994, had the highest PVE of 31.70 and 28.91%, respectively (Yu et al. 2020). These resistant accessions and SNPs may facilitate peanut breeding for resistant to aflatoxin. In another study, authors utilized the SLAF-seq method to create high-density genetic linkage maps and discover QTLs associated with aflatoxin resistance in peanut (Khan et al. 2020b). Two consistent QTLs (*qRAF-3-1* and *qRAF-14-1*) were identified on chromosomes A03 and B04, respectively, with *qRAF-3-1* having more than 19% PVE. The mapped QTLs were positioned inside a physical gap of 1.44 and 2.22 Mbp, possessing several candidate genes, including *RPP13*, *lox*, *WRKY*, and *cytochrome P450 71B34*. These QTLs and/or candidate genes will enable marker improvement and validation for exploitation in MAB programs to design aflatoxin-resistant peanut cultivars (Khan et al. 2020b).

A GWAS study using Affymetrix version 2.0 SNP array identified 46 QTLs associated with resistance to ELS and LLS in peanuts (Zhang et al. 2020). Among these, four and two major QTLs were identified for ELS and LLS resistance, respectively, and two genomic regions on chromosome B09 provided resistance to both diseases. Moreover, 74 non-redundant resistance genes were discovered, with 12 candidate genes in noteworthy genomic regions. The identified QTLs and candidate genes will aid in the breeding of resistant peanut cultivars (Zhang et al. 2020). GBS-based sequencing method was used to develop three dense genetic maps and identify genomic regions and candidate genes for rust and LLS resistance in TAG 24 × GPBD 4 (Pandey et al. 2017a) as well as for stem rot disease resistance in peanut (Dodia et al. 2019). By QTLseq based on STQ reference genome unexpectedly found that the rust and LLS resistances derived from wild peanut A03 had now been transferred onto chromosome 13 in cultivated peanut as result of mutual chromosomes translocation, indicating cultivated peanut genome was able to provide accurate traits mapping and genes discovery (Zhuang et al. 2019). Using GBS method, Dodia et al. (2019) identified 44 major epistatic QTLs for resistance to stem rot disease in peanut. They found a QTL on B04 comprising 170 genes. Another study by Han et al. (2018) also utilized GBS to identify major QTLs for resistance to LLS and ELS in peanut. They identified a major QTL on B05 anchored by two *NBS-LRR* resistance genes and two QTLs on A03 and B04 correlated with resistance genes for ELS. Sequences within the identified intervals could aid in discovering resistance genes and executing MAB for designing disease-resistant peanut (Han et al. 2018). In summary, the categorized genomic regions and candidate genes will enable marker development for designing disease-resistant peanut varieties using GAB.

Agronomic traits

Several QTL mapping studies have spotted substantial locus associated with different agronomic and quality traits in cultivated peanut (Table 1). For instance, SLAF-seq was used to discover 27 QTLs related to 100-seed weight, length, width, and length-to-width ratio, on 8 chromosomes with LOD values of 3.16–31.55 and PVE ranging from 0.74 to 83.23% (Zhang et al. 2019). Interestingly, two constant QTL regions were found on chromosomes 2 and 16, with gene content

providing significant knowledge for designing modern peanut cultivars with improved seed size by molecular breeding (Zhang et al. 2019). Pandey et al. (2014c) performed GWAS using 300 peanut genotypes and detected nine loci linked with seed length, three with seed width, and five with 100 seed weight. On the other hand, Huang et al. (2015) carried out QTL mapping for these traits in an F_2 population and also successfully identified genetic regions explaining PVE from 1.69 to 17.88%. Additionally, another study utilizing two $F_{2:3}$ populations distinguished 10 QTLs for seed length and 7 for seed width, with the PVE up to 20.80 and 14.43%, respectively (Chen et al. 2016a). These studies deliver useful evidence for peanut breeding programs to design innovative cultivars with advanced seed traits.

Chen et al. (2017) performed QTL mapping and meta-analysis using an RIL population and found 83 QTLs associated with pod- and seed-related traits. While Li et al. (2022) conducted a combined analysis of GWAS and BSA-seq to discover candidate genes related to lateral branch angle in peanut. They found three candidate genes associated with F-box family proteins (*Araip.E64SW, Araip.YG1LK,* and *Araip.JJ6RA*) and one target gene linked to PPP family protein (*Araip.YU281*) that are essential for plant growth and development. These genes could be used as molecular breeding targets in MAB to improve peanut growth habits (Li et al. 2022). Another study used GWAS to analyze 11 agronomically important traits in 158 peanut accessions and identified 1429 genes in a 200 K genomic region related to domestication (Zhang et al. 2017).

In another study, QTL-seq approach discovered five genomic regions for seed weight, and these regions were found to have 182 SNPs in genic and intergenic regions (Gangurde et al. 2022). Of these, 11 non-synonymous SNPs in the genomic regions had ten candidate genes containing *Ulp proteases* and *BIG SEED locus* genes. Moreover, KASP markers for 14 SNPs were cultivated, among which four markers (snpAH0031, snpAH0033, snpAH0037, and snpAH0038) were effectively validated, contributing to breeding large-seeded peanut varieties (Gangurde et al. 2022). In a study, Luo et al. (2019a) used the QTL-seq approach to enhance shelling percentage in cultivated peanut. This study discovered two overlapping genomic regions (2.75 Mb on A09 and 1.1 Mb on B02) linked with shelling percentage. Nine candidate genes affected by SNPs were identified, heading to the advancement of KASP markers. These outcomes pose valuable insights for gene cloning and the utilization of diagnostic markers, assisting the designing of superior peanut varieties with increased shelling percentage (Luo et al. 2019a). Using the BSA-seq and QTL mapping methods, Pan et al. (2022) fine-mapped a candidate gene (*AhLBA1*) on 136.65 kb physical region on chromosome 15, controlling lateral branch angel. This study will promote an explanation of the genetic mechanism of lateral branch angels in peanut and assist MAS in future breeding programs (Pan et al. 2022).

Wang et al. (2020) used a combination of SLAF-seq and SSRs methods to identify 15 QTLs connected with concentration degree of floret flowering date, including a major QTL found on chromosome 6 (Wang et al. 2020). Huang et al. (2015) discovered 12 QTLs for eight diverse quality-related traits using SSR markers. While Hake et al. (2017) detected a major effect QTL for days to 50% flowering on linkage group A03. Khedikar and coauthors identified three minor-effect QTLs associated with days to flowering and 62 main-effect QTLs for morphological and yield-associated traits (Khedikar et al. 2018). Recently, Sun et al. (2022) used WGR to create a high-density linkage map and identified 110 QTLs for peanut quality traits. One major QTL (*qA05.1*) on chromosome A05 was detected in multiple environments and was found to affect oil, protein, and six fatty acids. Two SNPs in the genomic region of *qA05.1* may be useful for MAB (Sun et al. 2022). Previously, another group of authors discovered two major QTLs on chromosomes A02 and A10, and 20. These QTLs were found to be associated with oil content and fatty acid organizations on other chromosomes using DArT markers in two F2 populations (Shasidhar et al. 2017). These findings are providing beneficial information for fast-tracking peanut breeding and trait improvement.

A study using ddRAD-seq, mapped a major and stable QTL (*qOCA08.1*) to a genomic region possessing two annotated genes that affect oil biosynthesis (Liu et al. 2020b). Another study by Zhang et al. (2018) performed GWAS by using 268 lines and 120 markers to discover genetic markers connected with key agronomic traits, i.e., protein, oleic acid, and linoleic acid Zhang et al. (2018). A total of 2559 genes implicated in fatty acid metabolism and lipid storage were identified through genomic analysis of peanut (Chen et al. 2019a). These findings indicate that further study of major and stable QTLs could lead to gene discovery for peanut breeding. Additionally, strictly linked molecular markers and genes correlated with yield-related traits and oil content could be valuable in MAB for peanut improvement.

The above-discussed studies demonstrate the successful use of various sequencing-based methods for trait mapping in peanut, leading to the finding of significant genomic regions, candidate genes, and molecular markers related to required traits such as yield, quality, stress tolerance and disease resistance. In short, these new sources can be used for MAB to fast-track the breeding procedure and design improved peanut cultivars with desired traits.

Genomic selection: a modern molecular breeding method to fast-track peanut breeding program

Genomic selection (GS) is a modern molecular breeding method that promises to improve complex traits with greater accuracy and precision in less time (Crossa et al. 2017; Xu et al. 2020; Anilkumar et al. 2022). In GS, precise multilocation phenotyping data and optimum genotyping density are essential to designing training and testing populations for adjusting genomic prediction by different GS models. The benefit of GS is the decrease of the selection cycle and avoidance of broad phenotyping across the collection of greater lines based on the estimate of genomic-estimated breeding values (GEBV) (Fig. 3) (Crossa et al. 2017; Xu et al. 2020; Anilkumar et al. 2022). Nevertheless, estimate accuracy in GS is influenced by numerous factors, including training population size and constitution/structure, accurate and superiority phenotyping, marker density, and attribute heritability (Xu et al. 2020; Anilkumar et al. 2022). In contrary to QTLs and GWAS, GS utilizes all DNA markers for genomic-enabled estimation of the implementation of the candidates for selection, targeting to estimate breeding and/or genetic values (Crossa et al. 2017).

In peanut research, GS breeding is a rapidly progressing field, driven by advances in genomics. A study investigated genotyping data on 2356 DArT markers and six seasons of phenotyping data on the ICRISAT mini-core collection for days to flowering, seed weight, and pod yield (Pandey et al. 2014a, 2015). Higher prediction precisions were perceived with connected markers than with total markers in the whole mini-core collection. Conversely, this was not seen when a lesser set of lines were counted as the training population. Regardless of the training and validation set size, there was a positive association between high trait heritability and estimate accuracy. To facilitate GS breeding, a high-density genotyping assay was developed and validated using the 58 K Axiom_*Arachis* SNP array (Pandey et al. 2017b; Clevenger et al. 2017). This assay has helped to identify 13,355 genome-wide polymorphic SNPs for performing GS analysis in peanuts (Chaudhari et al. 2019). This study also phenotyped a training population of 340 elite peanut lines for 11 agronomic, seven quality, and six foliar disease resistance traits (such as LLS and rust resistance) at four locations (Chaudhari et al. 2019). The resulting phenotypic and genomic data can be managed to design GS estimate models for future breeding efforts (Chaudhari et al. 2019). A training population of 340 elite peanut lines was genotyped using a 58 K "Axiom_*Arachis*" SNP array and phenotyped for key agronomic attributes across three Indian locations (Pandey et al. 2020a). The comparative analysis uncovered that naïve interaction models and naïve and informed interaction GS models successfully improved prediction accuracy, counting the complex genotype × environment interaction in peanut. This evaluation gave valuable insights into the possible application of GS breeding, specifically for untested genotypes and overlooked environments (Pandey et al. 2020a).

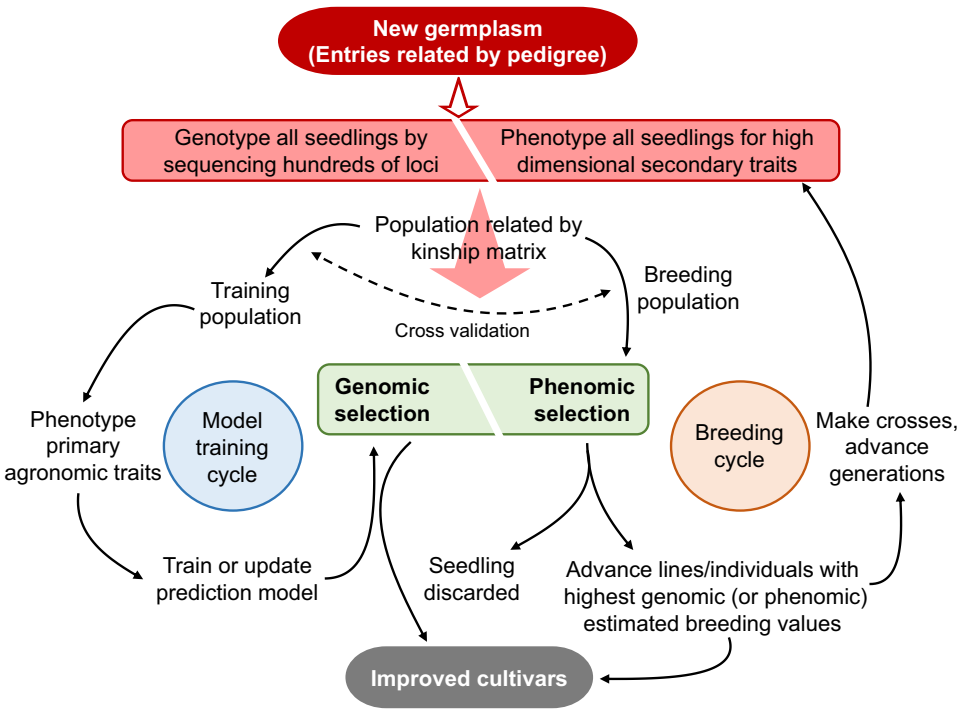

Fig. 3 Simplified design for genomic and phenomic selection process (Van Tassel et al. 2022). Novel forms of phenotypic data, such as high-dimensional secondary traits, have prompted the expansion of phenomics-based methods in breeding programs. These methods are similar to genomic selection, but rely on phenomic estimated breeding values rather than genomic data, assisting economical and competent advancement of diverse germplasm. Phenomics-based methodologies may show effectiveness in peanut crop with limited genomic resources. Productive application of phenomics could help peanut breeders accomplish their goals by deepening selection, adjusting accuracy, and decreasing the time needed for breeding cycles

In a recent study, the infusion of exotic germplasm via a multistage breeding method improves the sustained development of polygenic traits. This can create a pre-breeding strategy with response mechanisms to adjust recurrent GS in peanut breeding programs (Breider et al. 2022). In short, this multistage breeding method can upgrade long-term genetic gain for polygenic traits and potentially participate in future food security.

In current years, the genomics era has viewed a paradigm shift in modern breeding approaches with the appearance of allele mining (Varshney et al. 2021b; Tripodi et al. 2023). This pioneering approach implies the systematic evaluation and deployment of genetic diversity existing within a species, providing a treasure trove of untapped genetic potential (Varshney et al. 2018, 2021b; Sharwood et al. 2022; Tripodi et al. 2023). By tapping into the treasure of genetic diversity, breeders gain access to a pool of unique alleles, permitting the designing of new, improved cultivars with enhanced yield, resilience to stresses, and nutritional satisfaction (Sharwood et al. 2022; Tripodi et al. 2023). In this GAB era, the importance of allele mining cannot be inflated, as it supplies a central tool in forming the future of peanut improvement. For instance, a recent study examined the genome-wide DNA methylation pattern, and the results showed that CHG regions had the maximum (30,537,376) DNA methylation after CpG (30,356,066) and CHH (15,993,361) through 11 genotypes (Bhat et al. 2020). Sub-genome B displayed superior DNA methylation sites (46,294,063) compared to the sub-genome A (30,415,166). The genes illustrating changed methylation and expression were recognized between the parent (TMV2) and its EMS-derived mutant (TMV2-NLM). Notably, foliar disease-resistant genotypes confirmed substantial distinction DNA methylation at 766 sites corresponding to 25 genes. In short, this study specified the alteration in the DNA methylation design among the different genotypes and its impact on gene expression (Bhat et al. 2020), which could be utilized during future breeding design.

Recently, Liu et al. (2022a) used genetic diversity and genomic scan analysis to discover selective loci for GS breeding in peanut. They obtained large-scale SNPs from WGR of 203 cultivated peanut accessions and discovered selective sweeps underlying QTL and genes associated with seed size, plant architecture, and disease resistance. Two genes implied in seed weight and length regulation were also recognized via GWAS testing with functional investigation. Overall, this study provides new genetic information for innovative peanut breeding (Liu et al. 2022a). In another study, Ravelombola et al. (2022) identified SNPs correlated with sting nematode resistance in cultivated peanut and reviewed the precision of GS in calculating resistance. Using 13,306 filtered SNPs and phenotyping for sting nematode resistance, the authors discovered numerous SNPs connected with resistance using distinct regression models. GS precision was higher when using SNPs from GWAS. Notably, this is the first study on SNPs correlated with resistance and GS for sting nematode resistance in peanuts. This study specifies essential information to design a molecular breeding strategy to choose for sting nematode resistance in peanuts during GAB/MAB breeding (Ravelombola et al. 2022). In the near future, more of such efforts are required to fully explore the potential of GS that can help to fast-track and design future peanut breeding programs.

In modern agriculture, the haplotype-based breeding (HBB) approach has emerged as a potential approach for accelerating the generation of crop varieties with improved traits (Bhat et al. 2021a). HBB approach, centered on haplotypes, holds significant promise for enhancing peanut hybrid breeding efforts. Its key benefit is the careful selection of parent plants based on the existence of superior and diversified haplotypes (Bhat et al. 2021a). A key challenge for breeders is cultivating climate-smart crop varieties with increased yield potential, particularly in global climate change (Zandalinas et al. 2021; Rivero et al. 2022). Promoting the utilization of haplotypes in GS is championed as a potential approach to enhance the precision and effectiveness of trait prediction and offer more precise and efficient crop improvement. This is because extensive haplotype maps enable more accurate identification and utilization of genomic regions associated with specific traits prominently in populations characterized by prominent linkage disequilibrium structures (Varshney et al. 2005, 2021b; Bhat et al. 2021a). Additionally, the use of haplotypes streamlines the process of trait prediction in populations with strong LD structures. HBB speeds up traditional breeding operations by making picking individuals with desired haplotypes easier. As a result, the time necessary to produce superior crop variety is reduced (Won et al. 2020; Bhat et al. 2021a; Zhang et al. 2021a). Haplotypes has allowed for higher accuracy in trait selection, resulting in crop varieties with more uniformity and predictability in trait expression (Houston et al. 2020; Bhat et al. 2021a; Varshney et al. 2021b).

For instance, a significant QTL for seed weight in peanut was fine-mapped using haplotype-based association analysis in this work (Chu et al. 2020). This study showed how HBB has been utilized in peanut to enhance trait improvement. The researchers were able to gain a more accurate grasp of the genetic basis of this crucial feature by concentrating on haplotypes (Chu et al. 2020). Recently, Liu et al. (2022a) identified different haplotypes associated with seed traits in cultivated peanuts. The authors carried out transgenic experimentations in *Arabidopsis* to confirm the function of the candidate gene (i.e., *AhFAX1*). In comparison to WT plants, both overexpression lines, *AhFAX1* with haplotype G (*35S:AhFAX1hapG*) and *AhFAX1* with haplotype A (*35S:AhFAX1hapA*), had greater seed size and seed weights

in transgenic *Arabidopsis* (Liu et al. 2022a), suggesting the key role of these haplotypes in seed trait improvement in peanut. In a recent study, diverse RILs and peanut varieties were employed to examine the major haplotype of a candidate gene (i.e., *PSW1*) associated with pod size in peanut (Zhao et al. 2023). The authors showed that a natural allele (i.e., $PSW1^{HapII}$) conversed higher expression patter of *PSW1* and a robust kinship of *PSW1* for its co-receptor (*AhBAK1*) to up-regulate *PSW1*-based pathways, suggesting the contribution of haplotype II ($PSW1^{HapII}$) in regulating pod size and potential for peanut advancement. This outcome features the relationship among natural deviation in *PSW1* and phenotypic variety, explaining a modern way for variety advancement in several crop species (Zhao et al. 2023). The continuous efforts in haplotype breeding highlight its potential to transform agricultural development. In conclusion, HBB, within the context of GS, focuses on genetic data and precise trait mapping and offers the potential to produce crop varieties that are superior in both yield and adaptability to shifting environmental conditions, thus playing a pivotal role in enhancing global food security.

High-throughput phenotyping: a bridge between genotype and phenotype

Functional exploration of plant genomes has progressed to a high-throughput point, but modern plant breeding still faces a major challenge in plant high-throughput phenotyping (HTP). Conventional phenotyping is insufficient to estimate complex quantitative traits accurately (Araus et al. 2018; Großkinsky et al. 2015; Yang et al. 2020; Van Tassel et al. 2022). Consequently, plant HTP based on non-destructive phenotyping and high-capacity data recording and processing demands to be recognized for plant phenomics (Fig. 3) (Van Tassel et al. 2022). Technological developments in computing, robotics, light detection and ranging, and unmanned aerial vehicle remote sensing have assisted rapid advancement in plant HTP (Großkinsky et al. 2015; Araus et al. 2018; Yang et al. 2020; Hall et al. 2022). However, plant HTP still lags far behind the power to characterize whole genomes. Even though physiological components are vital in forecasting gene-to-phenotype associations for crop innovations. Notably, most presently used HTP only ultimately assess physiological activities despite being indicated as "high-throughput plant physiology" (Furbank and Tester 2011).

Despite technological advancements in recent decades, there has been little progress in achieving genetic gains in major crops (Li et al. 2018; Voss-Fels et al. 2019; Varshney et al. 2020). This has created an urgent need to expand breeding efficiency. The efficiency of phenotyping is seen as a major limitation to genetic development in breeding programs (Araus and Cairns 2014; Tardieu et al. 2017; Araus et al. 2018), predominantly in the field of plant HTP, which is a bottleneck in conventional breeding, MAB, or GS (Desta and Ortiz 2014; Crossa et al. 2017). Quality plant phenotyping is also necessary for evaluating the findings of genetic modifications. This observation has prompted national, regional, and international programs to advance plant phenotyping resources. The development of more reliable, accurate, and inexpensive plant HTP will aid in forecasting the performance of peanut genotypes under complex field conditions and can guide future peanut breeding directions.

To associate markers with traits, it is crucial to develop and evaluate peanut RIL populations using molecular genotyping. A structured 16 RIL population was previously established, and a selected list of populations and traits was designed for beginning high-resolution phenotyping in peanut (Holbrook et al. 2013). In-depth HTP and genotypes can lead to the identification of several key markers that can guide future peanut breeding (Holbrook et al. 2013). Through the pool of complementary phenotypic data from plant morphology and disease resistance to pod and seed traits, Chu et al. (2018) identified up to 79,000 SNPs among the parental genotypes of the NAM population, which were further genotyped using Affymetrix SNP arrays to assemble high-density genetic maps (Chu et al. 2018). Genetic mapping will assist the invention of genomic regions, manipulating phenotypic differences between peanut lines (Chu et al. 2018). In a recent study, Pandey et al. (2019) used a monoclonal antibody-based ELISA protocol to measure five major allergens in an extremely different peanut germplasm pool. The conclusions showed a wide phenotypic deviation for all five allergens studied, covering the avenue for using hypoallergenic peanut genotypes in breeding and genomics investigations. Furthermore, these hypoallergenic genotypes are presented for cultivation and industry, opening up new prospects to fight peanut allergies globally (Pandey et al. 2019).

To summarize, using diverse peanut germplasm estimated in multiple locations and with accurate phenotyping data is valuable for marker detection and crop breeding. Re-sequencing whole germplasm pools can also assist in discovering diversity sets for numerous applications in peanut exploration and genetic improvement. In addition, GS can be used as a substitution for phenotype-based selection for quicker and more cost-effective breeding (Fig. 3) (Desta and Ortiz 2014; Crossa et al. 2017; Van Tassel et al. 2022). The challenge is to design low-cost and available data management techniques that can bridge the gap between genotype and phenotype (gene to field). With the advancement of HTP, peanut breeders can benefit from the new and advanced cultivars via GAB/MAB.

Nonetheless, it is vital to differentiate between the uses of HTP in QTL/gene finding and its practice for making selection choices in breeding programs. While HTP may not continually supply favorably accurate information due to model-based expectations, it can yet play a vital role in adjusting selection practices by supporting breeders in decision-making. The value of HTP remains in its power to direct which individuals in a population should continue to the next generation, which can efficiently reduce the population size while retaining genetic gains.

Genome editing for advancing future peanut cultivars

The precise and efficient CRISPR/Cas9-based gene-editing tools have become a promising complementary for plant breeding to generate proposed traits. This high-throughput technology offers a highly precise and efficient tool that holds immense promise as a complementary approach to generate desired traits in crops, enabling researchers to manipulate specific genes and introduce targeted modifications in a controlled manner (Tariq et al. 2023; Tuncel et al. 2023; Zaman et al. 2023b). With adaptable gene-editing methods established, this technology has been employed in a variety of plant species for crop improvement, including maize, orange, potato, rice, sorghum, tobacco, tomato, rapeseed, and wheat (Yin et al. 2017; Moradpour and Abdulah 2020; McCarty et al. 2020; Zhu et al. 2020; Liu et al. 2023; Tariq et al. 2023; Tuncel et al. 2023; Wang and Doudna 2023; Yaqoob et al. 2023; Zaman et al. 2023a). One relevance of CRISPR/Cas9 is to alter a gene via the loss-of-function mutation by informing small indels that affect in frame-shift mutations or untimely stop codons. Interrupting genes is effective for gene function assessment and trait amendment, specifically for engineering quantitative features. Though it can be more challenging to engineer qualitative traits with interference; hence, accurate base editing may deliver an effective path to amend such traits (Yin et al. 2017; Moradpour and Abdulah 2020; McCarty et al. 2020; Zhu et al. 2020; Liu et al. 2023; Tariq et al. 2023; Tuncel et al. 2023; Wang and Doudna 2023; Yaqoob et al. 2023; Zaman et al. 2023b). The CRISPR/Cas tool has stipulated a new breeding method for producing genetic adaptability in plants, compelling it to complement classical breeding tremendously. Nevertheless, its application to peanuts is still limited.

Recently, CRISPR/Cas9 technology has been applied to peanut research for targeted gene modification. For instance, the fatty acid desaturase 2 (*FAD2*) gene, which controls oleic acid content in peanut seeds, was effectively mutated utilizing the CRISPR/Cas9 technique in a proof-of-concept study (Yuan et al. 2019). The resultant mutants have high oleic acid content in peanut seeds with high nutritional and profitable values. Even though the efficiency of the CRISPR system in peanuts needs improvement, this study confirmed that the method can produce mutations at the same hotspots as real mutations (Yuan et al. 2019). Another study by Shu et al. (2020) used the CRISPR/Cas9 system in peanut hairy root transformation system to investigate the role of *NFR* genes involved in nitrogen fixation. The authors positively designed knock-out mutants of *AhNFR1* and *AhNFR5* genes, exhibiting the effectiveness of CRISPR for targeted mutation in cultivated peanut. By using CRISPR/Cas9 system to target peanut *AhNFR* genes in the hairy root transformation system, for the first time the authors confirmed the role of *AhNFR5* genes in nodule development in cultivated peanut (Shu et al. 2020).

In a recent study by Neelakandan et al. (2022b), two diverse constructs were designed to induce insertion/deletion mutations in targeted genes for loss-of-function studies in peanut. The efficiency of these constructs was confirmed using the hairy root transformation system, and both constructs demonstrated insertions and deletions as types of edits. The construct with the enlarged plus gRNA terminator exhibited extraordinary editing efficacy compared to the regular scaffold for monoallelic and biallelic mutations. This tool could theoretically be used to enhance peanut lines for the gain of peanut breeders, growers, and trade (Neelakandan et al. 2022b). In another study, the same group of authors used CRISPR/Cas9-mediated gene-editing to alter *cis*-regulatory elements in the 5′ UTR and intron of *FAD2* genes to possibly produce seeds with improved oleic acid content deprived of disturbing the fatty acid arrangement in other plant tissues (Neelakandan et al. 2022a). These outcomes confirmed the power of CRISPR/Cas9-based methods to attain high-frequency focused edits in controlling sequences for the production of new transcriptional alleles, leading to adjustment of gene expression and functional genomic investigations in peanut (Neelakandan et al. 2022a). In another study, the CRISPR/Cas9 system was exploited to design two sgRNAs to edit the two homologs of *AhFatB* gene (*Arahy.4E7QKU* and *Arahy.L4EP3N*) in peanut (Tang et al. 2022b). The authors discovered a variety of mutations, and mutations in the *Arahy.4E7QKU* homolog demonstrated lower palmitic acid and higher oleic acid phenotypes. The achieved peanut mutants with transformed saturated fatty acid contents have the power to enhance peanut oil excellence for human health. These reports explain the promise of CRISPR/Cas9 gene-editing technology for enhancing peanut quality and nutrition.

The use of CRISPR/Cas9 in improving disease resistance, abiotic stress tolerance, and other agronomic- and yield-associated attributes in peanut has not been reported. This can be accredited to the challenges linked with peanut genetic transformation and the complexity of the peanut

genome. The polyploidy of the peanut genome poses challenges in designing specific gRNAs for targeted/desired genome editing. Peanut researchers need to discover diverse approaches to overcome these challenges, including enlightening protocols for genetic transformation and tissue culture in peanut, as well as evolving new delivery methods, such as the use of nanoparticles or virus-like particles. With persistent research and improvement of new methods and tools, it is assumed that these bottlenecks can be overcome to harness the potential of CRISPR/Cas9 in peanut genome editing. CRISPR system could also be used to introduce helpful traits from peanut wild relatives to cultivated peanut to design future smart cultivars.

Furthermore, GAB can be augmented with CRISPR/Cas9 genome editing to improve peanut production. This implies recognizing key genes correlated with desirable traits using genomic information and using gene editing to alter these genes. By doing so, the time and assets needed to design new peanut varieties with increased traits can be decreased. CRISPR/Cas system has the potential to design peanut cultivars that are better adapted to changing environmental conditions, more resistant to biotic diseases, and have higher yields and nutritional value.

Contribution of speed breeding for developing rapid generations

Conventional crop breeding is time-consuming and resource-intensive owing to the lengthy seed-to-seed cycle. Speed breeding, which uses procedures such as photoperiod extension and temperature control to expedite plant growth and development, has appeared as a promising tool for fast-tracking the breeding process (Watson et al. 2018; Chiurugwi et al. 2019; Wanga et al. 2021; Samantara et al. 2022; Pandey et al. 2022; Sharma et al. 2023a). Speed breeding has been successful in major crops like wheat, barley, pigeonpea, chickpea, rapeseed, pea (Christopher et al. 2015; Hickey et al. 2017; Watson et al. 2018, 2019; Alahmad et al. 2018; Saxena et al. 2019; Chiurugwi et al. 2019; Cazzola et al. 2020; Fikre et al. 2021), as well as orphan crops such as peanut (Chiurugwi et al. 2019). Speed breeding can facilitate the production of crosses, mapping populations, and assessment of agronomically important attributes of interest.

Speed breeding has the potential to substantially decrease the time mandatory to develop new peanut cultivars with anticipated traits. By using controlled environments with optimal conditions, multiple generations of peanut can be generated in a single year (O'Connor et al. 2013; Chiurugwi et al. 2019). This can fast-track the growth of new cultivars with higher yield, better quality, and resistance/tolerance to biotic/abiotic stresses. For example, speed breeding decreased the generation speed of full-season maturity cultivars from 145 to 89 days. It can also accelerate the inbreeding of F_2, F_3, and F_4 generations to less than 12 months, and theoretically decrease the time to release first cross to industrial release from 10–15 years to 6–7 years (O'Connor et al. 2013). However, to take full vantage of this, more resources and possessions may be needed to accept elite lines from speed breeding to appear in the next phase of the breeding or research cycle, which can be achieved within one month for peanut (O'Connor et al. 2013) by modernizing the assessment and selection methods, e.g., effective selection methods, fast data analysis, and policymaking protocols to instantly recognize and proceed the elite lines. Furthermore, effective organization and distribution of resources, such as devoted services and workers, can guarantee a uniform and accelerated transition within the stipulated time.

Combining speed breeding with GAB and genome editing can advance peanut breeding effectiveness (Pandey et al. 2022). GAB identifies genes linked to desirable traits, such as yield, disease resistance, and stress tolerance. Genome editing can then modify these genes completely. Speed breeding can confirm genome editing results in a quicker time frame, resulting in more competent and targeted breeding. Overall, the coupling of GAB, HTP, genome editing, and speed breeding holds great promise for fast-tracking the breeding of peanut. This innovative approach to peanut breeding can lead to the designing of new cultivars with higher yields, improved quality, and enhanced resistance/tolerance to biotic/abiotic stresses. The impact on global food security could be noteworthy by offering farmers with new means to boost peanut productivity under harsh environmental conditions.

Concluding remarks and future outlooks

To achieve sustainable food development in a changing climate, it is crucial to improve the proficiency of peanut breeding for higher-yield and stress tolerance. Innovative breeding designs, along with appropriate genomic technologies, will modernize breeding programs. Plant genome information has facilitated many NGS methods for allele mining and candidate gene discovery. High-throughput trait-related markers development, economical genotyping procedures, and precise HTP programs enable the fast utilization of GAB. Although recently renovated genetic and genomic approaches can boost conventional breeding and assessment activities, but cannot replace conventional breeding. In the future, the vast utilization of MAB and GS (alone or in integration with other approaches) will further enhance peanut breeding efforts at the genomics level.

While GAB has a significant prospective, there are still numerous challenges that hinder its speedy application, such

as climate volatility, yield phases, linking genotype to phenotype, and the need for advanced plant HTP approaches. Nevertheless, groundbreaking tools and expertise have been influential in advancing our interpretation of genome structure and function, delivering the genetic foundations of key attribute designs. Despite climate change, we predict sustained advancement in the speed of genetic gains in peanut breeding globally as our ability to assess and manipulate quantitative attribute adaptation in elite varieties raises. Though, reaching anticipated phenotypic appearances and enhanced plant performance by targeted management of a substantial quantity of QTLs also requires a whole system biology technique, where peanut breeders prerequisite to sensibly arrange attributes for a quantified target pool of milieus. Additionally, the challenge of HTP is to be focused on advancing the genetic gain in peanut breeding. To reach this goal, equal importance should be targeted on interpreting trait architectures in grouping with GS that does not essentially depend on the science of target attributes. The power of GAB will be executed during the progress of the approaches of manipulating crop genome data for sustainable crop advancement, which expects repeated revolutions in modern breeding techniques developing from new learning and advanced tools.

The challenge for higher yield, enriched nutritional value, and developed resilience/tolerance to biotic/abiotic stresses in peanuts demands the integration of diverse methods such as NGS, MAB, QTLs, GS, HTP, speed breeding, and genome editing. To enable the discovery and utilization of mysterious trait alteration attributable to a variety of minor QTLs, competent breeding approaches are required. Consequently, modern breeding techniques, such as GS, which use genome-wide marker data, are becoming progressively appropriate for constant population advancement and increasing the speed of genetic gain. Furthermore, the optimization and acceptance of methods that fast-track the group yield by controlling the plant growth conditions is also important in peanut breeding. Advances in genome editing have also substantially boosted the power for fast and precise amendments of plant genomes. To design future peanut cultivars, we believe that a combination of GAB methods such as GS, speed breeding, HTP, and genome editing can be employed to fast-track the designing of new cultivars in a shorter period. Also, targeted gene-editing or introgression breeding can assist in retrieving domesticated characteristics while maintaining helpful exceptional traits via de novo domestication.

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Declarations

Conflict of interest No conflict of interest was declared.

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