REVIEW ARTICLE

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

Haile Desmae[1](http://orcid.org/0000-0003-2612-9315) | **Pasupuleti Janila²** | **Patrick Okori3** | **Manish K. Pandey²** | **Babu N. Motagi⁴** | **Emmanuel Monyo[5](http://orcid.org/0000-0002-5248-4735)** | **Omari Mponda⁶** | **David Okello⁷** | **Dramane Sako⁸** | **Candidus Echeckwu⁹** | **Richard Oteng-Frimpong¹⁰** | **Amos Miningou¹¹** | **Chris Ojiewo⁵** | **Rajeev K. Varshney²**

1 International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Bamako, Mali

2 ICRISAT, Patancheru, India

3 ICRISAT, Lilongwe, Malawi

4 ICRISAT, Kano, Nigeria

5 ICRISAT, Nairobi, Kenya

6 Division of Research and Development (DRD), Tanzania Agricultural Research Institute (TARI) - Naliendele, Mtwara, Tanzania

7 National Agricultural Research Organization (NARO), Entebbe, Uganda

⁸Institut d'Economie Rurale (IER), Bamako, Mali

⁹Institute of Agricultural Research (IAR), Zaria, Nigeria

10Savanah Agricultural Research Institute (SARI), Tamale, Ghana

11Institut National d'Environnement et de Recherches Agricoles (INERA), Ouagadougou, Burkina Faso

Correspondence

Haile Desmae, International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Bamako, Mali. Email: [h.desmae@cgiar.org](mailto:)

Funding information Bill and Melinda Gates Foundation, Grant/ Award Number: OPP 1114827

Communicated by: Bradley Morris

Abstract

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

KEYWORDS

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

1 | **INTRODUCTION**

Groundnut (*Arachis hypogaea* L.), also known as peanut, is a member of genus *Arachis* and family *Leguminosae* (Krapovickas & Gregory,

1994). It is believed to have originated in the southern Bolivia to northern Argentina region of South America. The genus *Arachis* contains 80 species, and most of them are diploid (2*n* = 2x = 20) with only two allotetraploids. The cultivated groundnut is allotetraploid

--- --------------------------------------- This is an open access article under the terms of the [Creative Commons Attribution](http://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. © 2018 The Authors Plant Breeding Published by Blackwell Verlag GmbH

(AABB, 2*n* = 4x = 40), which is believed to be the result of hybridization between two wild species, *Arachis duranensis* (AA‐genome, 2*n* = 2x = 20) named as "A‐genome ancestor" and *Arachis ipaensis* (BB‐genome, 2*n* = 2x = 20) named as "B‐genome ancestor" and subsequent chromosome doubling. Based on the patterns of reproductive and vegetative branching and on the pod morphology, **426** WILEY- **AND AND PANE ET AL.**

the cultivated species is divided into two cultivated subspecies that is *A. hypogaea* subsp. *hypogaea* and *A. hypogaea* subsp. *fastigiata*. The subspecies are further divided into botanical varieties. The subsp. *hypogaea* is divided into *hypogaea* (virginia) and hirsuta, while the subsp. *fastigiata* is divided into *fastigiata* (valencia), *vulgaris* (Spanish), *peruviana* and *aequatoriana* (Krapovickas & Gregory, 1994).

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

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

2 | **GENETICS**

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

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

negative correlations between protein content and oil content and between oleic acid and linoleic acid were reported (Sarvamangala et al., 2011).

3 | **GENOMICS**

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

Genetic maps were constructed to understand the groundnut genome structure and organization and to identify QTLs for traits of breeding interest. Different marker systems such as RFLP (Halward, Stalker, & Kochert, 1993), RAPD (Garcia, Stalker, Schroeder, Lyerly, & Kocher, 2005), AFLP (Herselman, Thwaites, Kimmins, & Seal, 2004), SSR (Moretzsohn, Barbosa, Alves‐Freitas, Teixeira, & Leal‐Bertioli, 2009), SNP (Bertioli et al., 2014) and DArT (Shasidhar et al.,

DESMAE ET AL. **ALL PROPERTY AREA** ET ALL ALL PROPERTY AND RESIDENCE THE UPPER CONTRACT AND RESIDENCE THE UPPER CONTRACT AND ALL PROPERTY AND RESIDENCE THE UPPER CONTRACT AND RESIDENCE THE UPPER CONTRACT AND RESIDENCE THE U

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

Another significant advance in groundnut genomics has been the release of the draft genome sequences of the 1.1 Gb genome size for A‐genome progenitor (*A. duranensis,* accession V14167) and 1.38 Gb for B‐genome progenitor (*A. ipaensis,* accession K30076) (Bertioli et al., 2016). In addition, the draft genome sequence of another A‐genome progenitor accession (*A. duranensis,* accession [PI475845](http://www.ncbi.nlm.nih.gov/nuccore/PI475845)) was generated with 1.07 Gb genome size which provided greater insights into the genome architecture and genes related to important traits such as geocarpy, oil biosynthesis and allergens (Chen, Li, et al., 2016). In the case of cultivated tetraploid genotype, a high-quality genome assembly of 'Tifrunner', an important US variety with good market and growth characteristics and resistance to several diseases, was released in December 2017 ([https://peanutba](https://peanutbase.org/peanut_genome) [se.org/peanut_genome\)](https://peanutbase.org/peanut_genome). The draft genome sequences have enabled large‐scale genomewide discovery of 515,223 indels (Vishwakarma et al., 2017) and SSRs including 105,003 SSRs in the A‐genome (Chen, Li, et al., 2016), 135,529 SSRs in the A‐genome (Zhao et al., 2017), 199,957 SSRs in the B‐genome (Zhao et al., 2017), 84,383 in the A‐genome (Luo, Ren, et al., 2017) and 120,056 in the B‐genome (Luo, Ren, et al., 2017). Further, a high‐throughput genotyping platform, an Axiom_Arachis SNP array with 58K genomewide SNPs, was developed from the analysis of DNA resequencing and RNA

TABLE 1 Genetic maps for diploid and tetraploid *Arachis* species

(Continues)

TABLE 1 (Continued)

Note. TE: transposon elements; RGC: resistance gene candidate; RGA: resistance gene analogue.

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

4 | **BREEDING**

4.1 | **Focus traits and breeding methods**

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

Genetic resources conserved in gene banks have been important and harbour huge potential for utilization in breeding programmes as sources of variability. Besides, recent advances in genomics have enabled integrating molecular marker‐assisted breeding approaches for selected traits, and they hold significant promise for many other traits to enhance the breeding efficiency and increase the rate of genetic gain. Brief highlights of groundnut genetic resources, breeding for specific traits and marker‐assisted breeding are provided below. Over the years, several advanced breeding and germplasm lines have been identified and developed for drought, leaf spots,

rust, rosette, aflatoxin, rust and quality traits (Table 3). Genotype \times environment interaction is widely reported for pod yield and other quantitative traits in groundnut (e.g., Bucheyeki, Shenkalwa, Mapunda, & Matata, 2008; Janila, Manohar, Patne, Variath, & Nigam, 2016; Jogloy, Vorasoot, Akkasaeng, Kesmala, & Patanothai, 2009; Makinde, Ariyo, & Akinbowale, 2013). Hence, multilocation and multiseason testing are required to release improved varieties. Farmer participatory variety selection (Ntare et al., 2007) has been an important approach recently in groundnut varieties' release processes, particularly in South Asia (SA) and sub‐Saharan Africa (SSA), to better understand farmers' trait preferences for varieties and increase farmers' exposure to new groundnut varieties such that breeding programmes were able to better target varieties to both the ecological and market needs. Table 4 shows some of the released varieties in SA and SSA between 2000 and 2016 for their high yield and other traits including short duration, drought tolerance, rosette resistance and foliar disease resistance.

4.2 | **Genetic resources**

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

The use of the accessions from gene banks for crop improvement is less which is attributed to the use of working collections, consisting mostly of elite breeding lines and some improved trait‐ DESMAE ET AL. **431**

TABLE 2 Reported QTLs for important traits of breeding interest in groundnut

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

specific lines (Gowda, Upadhyaya, Sharma, Varshney, & Dwivedi, 2013). It is also costly to screen large collections for specific traits of breeding interest (Holbrook & Stalker, 2003). A subset that represents the genetic diversity facilitates easier access to the genetic resources and enhances their use in crop improvement programmes was required. Hence, core and minicore collections were established in China (Jiang et al., 2008) and USA (Holbrook, Anderson, & Pittman, 1993; Holbrook & Dong, 2005), which have been evaluated for various traits of breeding interest including disease resistance (Anderson, Holbrook, & Culbreath, 1996; Chamberlin, Melouk, & Payton, 2010; Damicone, Holbrook, Smith, Melouk, & Chamberlin, 2010; Jiang et al., 2008; Wang et al., 2011). Similarly, ICRISAT has established a core collection of 1,704 accessions (Upadhyaya, Ortiz, Bramel, & Singh, 2003) and a minicore collection of 184 groundnut accessions (Upadhyaya, Bramel, Ortiz, & Singh, 2002). Besides, a global

composite collection consisting of 1,000 accessions was developed, which was further characterized using 21 SSR markers to form a reference set consisting of 300 genetically most diverse accessions (Upadhyaya, Bhattacharjee, et al., 2006). The reference set, core and minicore collections were evaluated and characterized for various traits including drought and disease resistance for use in breeding programmes (Hamidou, Rathore, Waliyar, & Vadez, 2014; Hamidou et al., 2012; Upadhyaya, 2005; Upadhyaya, Dronavalli, Singh, & Dwivedi, 2012; Upadhyaya, MallikarjunaSwamy, Goudar, Kullaiswamy, & Singh, 2005; Upadhyaya, Mukri, Nadaf, & Singh, 2012; Upadhyaya, Reddy, Gowda, & Singh, 2006; Upadhyaya, Dwivedi, Vadez, et al., 2014; Waliyar et al., 2016) and also used for association mapping (Pandey, Upadhyaya, et al., 2014).

In addition to accessions of the cultivated groundnut, gene banks hold several wild accessions. Cultivated groundnut, being originated

DESMAE ET AL. | **433**

TABLE 3 Some sources of variability identified/developed for traits of breeding interest in groundnut

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

4.3 | **Breeding for specific traits**

4.3.1 | **Drought**

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

TABLE 4 Improved groundnut varieties released between 2000 and 2016 in SA and SSA

(Continues)

TABLE 4 (Continued)

DESMAE ET AL. **435**
All Seconds and Secon

Note. ^aThese are derivatives of a cross involving ICGV-SM 83708 (CG7) and ICGV-SM 90704 (Monyo & Varshney, 2016). ^bThe varieties were released based on their performance for one or more of important traits including high yield, drought resistance, foliar disease resistance, rosette resistance, etc.

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

The evidences about the usefulness of surrogate traits, however, are not consistent in that high SCMR and low SLA may not always lead to higher pod yield. For example, the preponderance of nonadditive effects and poor relationship between surrogate traits and pod yield were observed (Hamidou et al., 2012; Krishnamurthy et al.,

2007; Sanogo, 2016). Janila, Manohar, Rathore, and Nigam (2015) observed low heritability for SCMR and SLA. On the other hand, high correlations of both SCMR and SLA with pod yield and other economic traits such as 100‐seed weight were reported (Janila et al., 2015; Songsri et al., 2009; Upadhyaya, 2005; Upadhyaya et al., 2011). High heritability and a lower $G \times E$ interaction for the surrogate traits were also reported (Songsri et al., 2009; Upadhyaya et al., 2011). Varshney et al. (2009) reported moderate‐to‐high heritability for drought-related traits with alleles having moderate additive effects identified. Additive and both additive and nonadditive effects were also reported (Lal, Hariprasanna, Rathnakumar, Gor, & Chikani, 2006; Nigam et al., 2001). A combined use of the empirical and trait‐based selection approaches has been suggested under drought stress conditions (Devi et al., 2011; Janila et al., 2015; Nigam et al., 2005) as it would be advantageous in selecting genotypes which are more efficient water utilizers or partitioners of photosynthates into economic yield.

4.3.2 | **Leaf spots**

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

4.3.3 | **Rust**

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

4.3.4 | **Rosette**

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

4.3.5 | **Aflatoxin**

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

4.3.6 | **Quality**

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

4.4 | **Marker‐assisted breeding**

Genomic tools enhance crop breeding process by increasing the efficiency and speed of precision breeding to develop improved varieties. Diagnostic molecular markers linked with traits of breeding interest (or major effect QTLs) were identified for root-knot nematode (Choi et al., 1999; Chu, Holbrook, Timper, & Ozias‐Akins, 2007; Church, Simpson, Burow, Paterson, & Starr, 2000; Garcia, Stalker, Schroeder, & Kochert, 1996; Simpson, 2001), rust (Khedikar et al., 2010; Mondal, Badigannavar, & D'Souza, 2012), rust and LLS (Kolekar et al., 2016; Sujay et al., 2012), nutritional quality traits (Chen, Wang, Barkley, & Pittman, 2010; Chu, Holbrook, & Ozias‐ Akins, 2009; Sarvamangala et al., 2011; Wilson et al., 2017), TSWV (Tseng, Tillman, Peng, & Wang, 2016) and growth habit (Li et al., 2017). Some of these linked markers have been validated and deployed for marker‐assisted selection (MAS) and marker‐assisted backcrossing (MABC). In the USA, MAS has been used for pyramiding nematode resistance and high oleic trait (Chu et al., 2011). At ICRISAT, MABC was employed to transfer a major rust resistance QTL from GPBD 4 to three popular varieties (ICGV 91114, JL 24 and TAG 24) resulting in the development of rust resistance lines with 56%–96% increase of pod yield (Varshney et al., 2014). Some of these lines were also found to be resistant to LLS with 39%– 79% of higher mean pod yield (Janila, Pandey, Manohar, et al., 2016). Besides, MAS and MABC were used to enhance the oil quality traits in three groundnut varieties (ICGV 06110, ICGV 06142, and ICGV 06420) by transferring FAD2 mutant alleles from SunOleic 95R. A large number of lines with increased oleic acid in the range of 62%–83% were identified (Janila, Pandey, Shasidhar, et al., 2016), which are currently being evaluated for yield (Janila, pers. Comm.). At Dharwad University of Agricultural Sciences in India, MABC was used to improve JL 24 with GPBD 4 as donor parent (Yeri & Bhat, 2016). Similarly, MABC was employed to improve TMV 2 for LLS and rust using GPBD 4 where two backcross lines showed enhanced resistance to LLS and rust along with 71.0% and 62.7% increase of pod yield over TMV 2 (Kolekar et al., 2017). In the case of other important quantitative traits such as drought

 \mathbb{L} DESMAE ET AL. \blacksquare $\$

tolerance and yield components, QTL analyses using biparental populations revealed few major rather several small‐effect QTLs. Genomewide association studies for 50 agronomic traits using 300 genotypes from the "reference set" identified a total of 524 highly significant MTAs for 36 traits (Pandey, Upadhyaya, et al., 2014) indicating complex genetic control. Breeding approaches such as marker‐assisted recurrent selection and genomic selection are the preferred approaches for introgression of a larger number but smalleffect QTLs. But such approaches have not been widely used in groundnut.

5 | **CONCLUSION AND FUTURE PERSPECTIVES**

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

ACKNOWLEDGMENTS

The authors are thankful to Bill & Melinda Gates Foundation (BMGF) for the financial support under TL III project: Opportunity/Contract ID OPP1114827. The BMGF financial support has significantly contributed to groundnut research and development globally and in Asia and Africa particularly, through tropical legume (TL) projects.

438 | DESMAE ET AL. | DESMAE ET AL. | DESMAE ET AL.

AUTHOR CONTRIBUTIONS

Haile Desmae wrote the first draft and incorporated all inputs from the coauthors and editors. Manish K Pandey, Emmanuel Monyo and Rajeev K Varshney revised the first draft and made suggestions for improving the manuscript. Pasupuleti Janila, Babu N Motagi, Patrick Okori, Omari Mponda, David Okello, Dramane Sako, Candidus Echeckwu, Richard Oteng‐Frimpong, Amos Miningou and Chris Ojiewo provided country‐specific data and information regarding groundnut improvement and accordingly revised the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Haile Desmae http://orcid.org/0000-0003-2612-9315 *Pasupuleti Janila* https://orcid.org/0000-0003-2583-9630 *Babu N. Motagi* http://orcid.org/0000-0001-6113-0667 *Emmanuel Monyo* http://orcid.org/0000-0002-5248-4735 *Richard Oteng-Frimpong* http://orcid.org/0000-0001-6083-1461 *Chris Ojiewo* http://orcid.org/0000-0002-2885-9381 *Rajeev K. Varshney* http://orcid.org/0000-0002-4562-9131

REFERENCES

- Alves, D. M. T., Pereira, R. W., Leal-Bertioli, S. C. M., Moretzsohn, M. C., Guimarães, P. M., & Bertioli, D. J. (2008). Development and use of single nucleotide polymorphism markers for candidate resistance genes in wild peanuts (*Arachis* spp). *Genetics and Molecular Research*, *7*, 631–642.<https://doi.org/10.4238/vol7-3gmr453>
- Anderson, W. F., Holbrook, C. C., & Culbreath, A. K. (1996). Screening the peanut core collection for resistance to tomato spotted wilt virus. *Peanut Science*, *23*, 57–61. [https://doi.org/10.3146/i0095-3679-23-](https://doi.org/10.3146/i0095-3679-23-1-11) [1-11](https://doi.org/10.3146/i0095-3679-23-1-11)
- Anim-Somuah, H., Henson, S., Humphrey, J., & Robinson, E. (2013) *Strengthening agri-food value chains for nutrition: Mapping value chains for nutrient-dense foods in ghana*. IDS EVIDENCE REPORT No 2, Reducing Hunger and Undernutrition.
- Anitha, S., Monyo, E. S., & Okori, P. (2014). Simultaneous detection of groundnut rosette assistor virus (GRAV), groundnut rosette virus (GRV), and satellite RNA (SatRNA) in groundnut using multiplex RT‐ PCR. *Archives of Virology*, *159*, 3059–3062. [https://doi.org/10.1007/](https://doi.org/10.1007/s00705-014-2139-7) [s00705-014-2139-7](https://doi.org/10.1007/s00705-014-2139-7)
- Aruna, R., & Nigam, S. N. (2009). Inheritance of fatty acid content and related quality traits in groundnut, *Arachis hypogaea* L. *Journal of Oilseeds Research*, *26*, 10–17.
- Asibuo, J. Y., Akromah, R., Safo-Kantanka, O., Adu-Dapaah, H. K., Ohemeng-Dapaah, S., & Agyeman, A. (2008). Inheritance of fresh seed dormancy in groundnut. *African Journal of Biotechnology*, *7*, 421–424.
- Barkley, N. A., Upadhyaya, H. D., Liao, B., & Holbrook, C. C. (2016). Global resources of genetic diversity in peanut. In H. T. Stalker, & R. F. Wilson (Eds.), *Peanuts: Genetics, processing, and utilization* (pp. 67– 109). London, UK: Academic Press and AOCS Press. [https://doi.org/](https://doi.org/10.1016/B978-1-63067-038-2.00003-4) [10.1016/B978-1-63067-038-2.00003-4](https://doi.org/10.1016/B978-1-63067-038-2.00003-4)
- Bertioli, D. J., Cannon, S. B., Froenicke, L., Huang, G., Farmer, A. D., Cannon, E. K. S., … Ozias-Akins, P. (2016). The genome sequences of

Arachis duranensis and *Arachis ipaensis*, the diploid ancestors of cultivated peanut. *Nature Genetics*, *48*, 438–446. [https://doi.org/10.](https://doi.org/10.1038/ng.3517) [1038/ng.3517](https://doi.org/10.1038/ng.3517)

- Bertioli, D. J., Ozias-Akins, P., Chu, Y., Dantas, K. M., Santos, S. P., Gouvea, E., … Moretzsohn, M. C. (2014). The use of SNP markers for linkage mapping in diploid and tetraploid peanuts. *G3 (Bethesda)*, *4*, 89–96.<https://doi.org/10.1534/g3.113.007617>
- Bucheyeki, T. L., Shenkalwa, E. M., Mapunda, T. X., & Matata, L. W. (2008). On‐farm evaluation of promising groundnut varieties for adaptation and adoption in Tanzania. *African Journal of Agricultural Research*, *3*, 531–536.
- Burow, M. D., Simpson, C. E., Starr, J. L., & Paterson, A. H. (2001). Transmission genetics of chromatin from a synthetic amphiploid in cultivated peanut (*A. hypogaea* L.): Broadening the gene pool of a monophyletic polyploid species. *Genetics*, *159*, 823–837.
- Burow, M. D., Starr, J. L., Park, C. H., Simpson, C. E., & Paterson, A. H. (2014). Introgression of homeologous quantitative trait loci (QTLs) for resistance to the root‐knot nematode [*Meloidogyne arenaria* (Neal) Chitwood] in an advanced backcross‐QTL population of peanut (*Arachis hypogaea* L.). *Molecular Breeding*, *34*, 393–406. [https://doi.org/](https://doi.org/10.1007/s11032-014-0042-2) [10.1007/s11032-014-0042-2](https://doi.org/10.1007/s11032-014-0042-2)
- Chamberlin, K. D. C., Melouk, H. A., & Payton, M. E. (2010). Evaluation of the US peanut mini core collection using a molecular marker for resistance to Sclerotinia minor Jagger. *Euphytica*, *172*, 109–115. <https://doi.org/10.1007/s10681-009-0065-7>
- Chen, W., Jiao, Y., Cheng, L., Huang, L., Liao, B., Tang, M., … Jiang, H. (2016). Quantitative trait locus analysis for pod‐ and kernel‐related traits in the cultivated peanut (*Arachis hypogaea* L.). *BMC Genetics*, *17*, 25.<https://doi.org/10.1186/s12863-016-0337-x>
- Chen, X., Li, H., Pandey, M. K., Yang, Q., Wang, X., Garg, V., … Yud, S. (2016). Draft genome of the peanut A‐genome progenitor (*Arachis duranensis*) provides insights into geocarpy, oil biosynthesis, and allergens. *PNAS*, *113*, 6785–6790. [https://doi.org/10.1073/pnas.](https://doi.org/10.1073/pnas.1600899113) [1600899113](https://doi.org/10.1073/pnas.1600899113)
- Chen, Z., Wang, M. L., Barkley, N. A., & Pittman, R. N. (2010). A simple allele‐specific PCR‐assay for detecting FAD2 alleles in both A and B genomes of the cultivated peanut for high‐oleate trait selection. *Plant Molecular Biology Reporter*, *28*, 542–548. [https://doi.org/10.1007/](https://doi.org/10.1007/s11105-010-0181-5) [s11105-010-0181-5](https://doi.org/10.1007/s11105-010-0181-5)
- Choi, K., Burow, M. D., Church, G., Burow, G., Paterson, A. H., Simpson, C. E., & Starr, J. L. (1999). Genetics and mechanism of resistance to *Meloidogyne arenaria* in peanut germplasm. *Journal of Nematology*, *31*, 283–290.
- Chopra, R., Burow, G., Farmer, A., Mudge, J., Simpson, C. E., Wilkins, T. A., … Burow, M. D. (2015). Next generation transcriptome sequencing, SNP discovery and validation in four market classes of peanut *Arachis hypogaea* L.. *Molecular Genetics and Genomics*, *290*, 1169– 1180.<https://doi.org/10.1007/s00438-014-0976-4>
- Chu, Y., Holbrook, C. C., & Ozias-Akins, P. (2009). Two alleles of ahFAD2B control the high oleic acid trait in cultivated peanut. *Crop Science*, *49*, 2029–2036.<https://doi.org/10.2135/cropsci2009.01.0021>
- Chu, Y., Holbrook, C. C., Timper, P., & Ozias-Akins, P. (2007). Development of a PCR‐based molecular marker to select for nematode resistance in peanut. *Crop Science*, *47*, 841–845. [https://doi.org/10.2135/](https://doi.org/10.2135/cropsci2006.07.0474) [cropsci2006.07.0474](https://doi.org/10.2135/cropsci2006.07.0474)
- Chu, Y., Wu, C. L., Holbrook, C. C., Tillman, B., Person, G., & Ozias-Akins, P. (2011). Marker assisted selection to pyramid nematode resistance and high oleic trait in peanut. *Plant Genome*, *4*, 110–117. [https://doi.](https://doi.org/10.3835/plantgenome2011.01.0001) [org/10.3835/plantgenome2011.01.0001](https://doi.org/10.3835/plantgenome2011.01.0001)
- Church, G. T., Simpson, C. E., Burow, M. D., Paterson, A. H., & Starr, J. L. (2000). Use of RFLP markers for identification of individuals homozygous for resistance to *Meloidogyne arenaria* in peanut. *Nematology*, *2*, 575–580.<https://doi.org/10.1163/156854100509367>
- Clevenger, J., Chu, Y., Chavarro, C., Agarwal, G., Bertioli, D. J., Leal-Bertioli, S. C. M., … Ozias-Akins, P. (2017). Genome‐wide SNP

Genotyping Resolves Signatures of Selection and Tetrasomic Recombination in Peanut. *Molecular Plant*, *10*, 309–322. [https://doi.org/10.](https://doi.org/10.1016/j.molp.2016.11.015) [1016/j.molp.2016.11.015](https://doi.org/10.1016/j.molp.2016.11.015)

- Cuc, L. M., Mace, E. S., Crouch, J., Quang, V. D., Long, T. D., & Varshney, R. K. (2008). Isolation and characterization of novel microsatellite markers and their application for diversity assessment in cultivated groundnut (*Arachis hypogaea*). *BMC Plant Biology*, *8*, 55. [https://doi.](https://doi.org/10.1186/1471-2229-8-55) [org/10.1186/1471-2229-8-55](https://doi.org/10.1186/1471-2229-8-55)
- Damicone, J. P., Holbrook, C. C. Jr, Smith, D. L., Melouk, H. A., & Chamberlin, K. D. (2010). Reaction of the core collection of peanut germplasm to Sclerotinia blight and pepper spot. *Peanut Science*, *37*, 1–11. <https://doi.org/10.3146/PS09-001.1>
- Devi, M. J., Bhatnagar-Mathur, P., Sharma, K. K., Serraj, R., Anwar, S. Y., & Vadez, V. (2011). Relationships between transpiration efficiency and its surrogate traits in the rd29A:DREB1A transgenic lines of groundnut. *J. Agronomy & Crop Science*, *197*, 272–283. [https://doi.](https://doi.org/10.1111/j.1439-037X.2011.00464.x) [org/10.1111/j.1439-037X.2011.00464.x](https://doi.org/10.1111/j.1439-037X.2011.00464.x)
- Dwivedi, S. L., & Nigam, S. N. (2005). Confectionery groundnuts: Issues and opportunities to promote export and food uses in India. *Journal of Oilseeds Research*, *22*, 1–4.
- Dwivedi, S. L., Nigam, S. N., Chandra, S., & Ramraj, V. M. (1998). Combining ability of biomass and harvest index under short‐ and long‐day conditions in groundnut. *Annals of Applied Biology*, *133*, 237–244. <https://doi.org/10.1111/j.1744-7348.1998.tb05824.x>
- Dwivedi, S. L., Pande, S., Rao, J. N., & Nigam, S. N. (2002). Components of resistance to late leaf spot and rust among interspecific derivatives and their significance in a foliar disease resistance breeding in groundnut (*Arachis hypogaea* L.). *Euphytica*, *125*, 81–88. [https://doi.](https://doi.org/10.1023/A:1015707301659) [org/10.1023/A:1015707301659](https://doi.org/10.1023/A:1015707301659)
- FAOSTAT (2017). *FAOSATAT, statistical data base*. Rome: Food and Agricultural Organizations of the United Nations. Visited on 29/05/2017.
- Foncéka, D., Tossim, H.-A., Rivallan, R., Faye, I., Sall, M. N., Ndoye, O., … Rami, J.-F. (2009). Genetic mapping of wild introgressions into cultivated peanut: A way toward enlarging the genetic basis of a recent allotetraploid. *BMC Plant Biology*, *9*, 103. [https://doi.org/10.1186/](https://doi.org/10.1186/1471-2229-9-103) [1471-2229-9-103](https://doi.org/10.1186/1471-2229-9-103)
- Foncéka, D., Tossim, H.-A., Rivallan, R., Vignes, H., Faye, I., Ndoye, O., … Rami, J.-F. (2012). Fostered and left behind alleles in peanut: Interspecific QTL mapping reveals footprints of domestication and useful natural variation for breeding. *BMC Plant Biology*, *12*, 26. [https://doi.](https://doi.org/10.1186/1471-2229-12-26) [org/10.1186/1471-2229-12-26](https://doi.org/10.1186/1471-2229-12-26)
- Foncéka, D., Tossim, H. A., Rivallan, R., Vignes, H., Lacut, E., de Bellis, F., … Rami, J. F. (2012). Construction of chromosome segment substitution lines in peanut (*Arachis hypogaea* L.) Using a wild synthetic and QTL mapping for plant morphology. *PLoS One*, *7*(11), e48642. <https://doi.org/10.1371/journal.pone.0048642>
- Gaikpa, D. S., Akromah, R., Asibuo, J. Y., Appiah-Kubi, Z., & Nyadanu, D. (2015). Evaluation of yield and yield components of groundnut genotypes under Cercospora leaf spots disease pressure. *International Journal of Agronomy and Agricultural Research*, *7*, 66–75.
- GAIN (2010). *Revitalization of the groundnut sector in West Africa (Gambia, Guinea Bissau and Senegal)*. Global Agricultural Information Network (GAIN). Retrieved from [http://gain.fas.usda.gov/Recent%20GAIN%](http://gain.fas.usda.gov/Recent%20GAIN%20Publications/Revitalization%20of%20the%20Groundnut%20sector%20in%20West%20Africa_Dakar_Senegal_12-3-2010.pdf) [20Publications/Revitalization%20of%20the%20Groundnut%20sector](http://gain.fas.usda.gov/Recent%20GAIN%20Publications/Revitalization%20of%20the%20Groundnut%20sector%20in%20West%20Africa_Dakar_Senegal_12-3-2010.pdf) [%20in%20West%20Africa_Dakar_Senegal_12-3-2010.pdf](http://gain.fas.usda.gov/Recent%20GAIN%20Publications/Revitalization%20of%20the%20Groundnut%20sector%20in%20West%20Africa_Dakar_Senegal_12-3-2010.pdf). Accessed 18 Nov. 2016.
- Gangadhara, K., & Nadaf, H. L. (2016). Inheritance of high oleic acid content in new sources of groundnut (*Arachis hypogaea* L.). *Agricultural Science Digest*, *36*, 299–302.
- Garcia, G. M., Stalker, H. T., Schroeder, C., & Kochert, G. (1996). Identification of RAPD, SCAR and RFLP markers tightly linked to nematode resistance genes introgressed from *Arachis cardenasii* into *Arachis hypogaea*. *Genome*, *39*, 836–845.<https://doi.org/10.1139/g96-106>
- Garcia, G. M., Stalker, H. T., Schroeder, E., Lyerly, J. H., & Kocher, G. (2005). A RAPD‐based linkage map of peanut based on a backcross

population between the two diploid species *Arachis stenosperma* and *A. cardenasii*. *Peanut Science*, *32*, 1–8. [https://doi.org/10.3146/0095-](https://doi.org/10.3146/0095-3679(2005)32%5b1:ARLMOP%5d2.0.CO;2) [3679\(2005\)32\[1:ARLMOP\]2.0.CO;2](https://doi.org/10.3146/0095-3679(2005)32%5b1:ARLMOP%5d2.0.CO;2)

- Gautami, B., Foncéka, D., Pandey, M. K., Morezsohn, M. C., Sujay, V., Qin, H., … Varshney, R. K. (2012). An international reference consensus genetic map with 897 marker loci based on 11 mapping populations for tetraploid groundnut (*Arachis hypogaea* L.). *PLoS One*, *7*, e41213.<https://doi.org/10.1371/journal.pone.0041213>
- Gautami, B., Pandey, M. K., Vadez, V., Nigam, S. N., Ratnakumar, P., Krishnamurthy, L., .., Varshney, R. K. (2012). OTL analysis and consensus genetic map for drought tolerance traits based on three RIL populations of cultivated groundnut (*Arachis hypogaea* L.). *Molecular Breeding*, *32*, 757–772.<https://doi.org/10.1007/s11032-011-9660-0>
- GCP (2011). *CGIAR generation challenge programme. 2011 Project updates (incorporating projects completed in 2010 and 2009)*. Texcoco, Mexico: Generation Challenge Programme.
- Gowda, C. L. L., Upadhyaya, H. D., Sharma, S., Varshney, R. K., & Dwivedi, S. L. (2013). Exploiting genomic resources for efficient conservation and utilization of chickpea, groundnut, and pigeonpea collections for crop improvement. *The Plant Genome*, *6*, 1–11. [https://doi.org/10.](https://doi.org/10.3835/plantgenome2013.05.0016) [3835/plantgenome2013.05.0016](https://doi.org/10.3835/plantgenome2013.05.0016)
- Guo, Y., Khanal, S., Tang, S., Bowers, J. E., Heesacker, A. F., Khalilian, N., … Knapp, S. J. (2012). Comparative mapping in intraspecific populations uncovers a high degree of macrosynteny between A‐ and B‐ genome diploid species of peanut. *BMC Genomics*, *13*, 608. [https://d](https://doi.org/10.1186/1471-2164-13-608) [oi.org/10.1186/1471-2164-13-608](https://doi.org/10.1186/1471-2164-13-608)
- Hake, A. A., Shirasawa, K., Yadawad, A., Sukruth, M., Patil, M., Nayak, S. N., … Bha, R. S. (2017). Mapping of important taxonomic and productivity traits using genic and non‐genic transposable element markers in peanut (*Arachis hypogaea* L.). *PLoS One*, *12*(10), e0186113. <https://doi.org/10.1371/journal.pone.0186113>
- Halward, T. M., Stalker, H. T., & Kochert, G. (1993). Development of an RFLP linkage map in diploid peanut species. *TAG. Theoretical and Applied Genetics.*, *87*, 379–384.<https://doi.org/10.1007/BF01184927>
- Halward, T. M., Stalker, H. T., Larue, E. A., & Kochert, G. (1991). Genetic variation detectable with molecular markers among unadapted germ‐ plasm resources of cultivated peanut and related wild species. *Genome*, *34*, 1013–1020.<https://doi.org/10.1139/g91-156>
- Hamidou, F., Rathore, A., Waliyar, F., & Vadez, V. (2014). Although drought intensity increases aflatoxin contamination, drought tolerance does not lead to less aflatoxin contamination. *Field Crops Research*, *156*, 103–110.<https://doi.org/10.1016/j.fcr.2013.10.019>
- Hamidou, F., Ratnakumar, P., Halilou, O., Mponda, O., Kapewa, T., Monyo, E., … Vadez, V. (2012). Selection of intermittent drought tolerant lines across years and locations in the reference collection of groundnut (*Arachis hypogaea* L.). *Field Crops Research*, *126*, 189–199. <https://doi.org/10.1016/j.fcr.2011.10.009>
- He, G., & Prakash, C. S. (1997). Identification of polymorphic DNA markers in cultivated peanut (*Arachis hypogaea* L.). *Euphytica*, *97*, 143– 149.<https://doi.org/10.1023/A:1002949813052>
- Herselman, L. (2003). Genetic variation among Southern African cultivated peanut (*A. hypogaea* L.) genotypes as revealed by AFLP analysis. *Euphytica*, *133*, 319–327.<https://doi.org/10.1023/A:1025769212187>
- Herselman, L., Thwaites, R., Kimmins, F. M., & Seal, S. E. (2004). Identification and mapping of AFLP markers linked to peanut (*Arachis hypogaea* L.) resistance to the aphid vector of groundnut rosette disease. *TAG. Theoretical and Applied Genetics.*, *109*, 1426–1433. [https://doi.](https://doi.org/10.1007/s00122-004-1756-z) [org/10.1007/s00122-004-1756-z](https://doi.org/10.1007/s00122-004-1756-z)
- Holbrook, C. C., Anderson, W. F., & Pittman, R. N. (1993). Selection of a core collection from the U. S. germplasm collection of peanut. *Crop Science*, *33*, 859–861. [https://doi.org/10.2135/cropsci1993.](https://doi.org/10.2135/cropsci1993.0011183X003300040044x) [0011183X003300040044x](https://doi.org/10.2135/cropsci1993.0011183X003300040044x)
- Holbrook, C. C., & Dong, W. (2005). Development and evaluation of a mini core collection for the U.S. Peanut Germplasm Collection. *Crop Science*, *45*, 1540–1544.<https://doi.org/10.2135/cropsci2004.0368>
- **440 WILEY- AND PLANE ET AL.** PLANE Breeding
- Holbrook, C. C., & Stalker, H. T. (2003). Peanut breeding and genetic resources. In J. Janick (Ed.), *Plant breeding reviews*, Vol. *22*. NY: John Wiley & Sons Inc. ISBN 0-471-21541-4 © 2003.
- Hong, Y., Chen, X., Liang, X., Liu, H., Zhou, G., Li, S., … Guo, B. (2010). A SSR-based composite genetic linkage map for the cultivated peanut (*Arachis hypogaea* L.) genome. *BMC Plant Biology*, *10*, 17. [https://doi.](https://doi.org/10.1186/1471-2229-10-17) [org/10.1186/1471-2229-10-17](https://doi.org/10.1186/1471-2229-10-17)
- Hong, Y., Liang, X., Chen, X., Liu, H., Zhou, G., Li, S., & Wen, S. (2008). Construction of genetic linkage map based on SSR markers in peanut (*Arachis hypogaea* L.). *Agricultural Sciences in China*, *7*, 915–921. [https://doi.org/10.1016/S1671-2927\(08\)60130-3](https://doi.org/10.1016/S1671-2927(08)60130-3)
- Hong, Y., Pandey, M. K., Liu, Y., Chen, X., Liu, H., Varshney, R. K., … Huan, S. (2015). Identification and evaluation of single‐nucleotide polymorphisms in allotetraploid peanut (*Arachis hypogaea* L.) based on amplicon sequencing combined with high resolution melting (HRM) analysis. *Frontiers in Plant Science*, *6*, 1068. [https://doi.org/10.3389/](https://doi.org/10.3389/fpls.2015.01068) [fpls.2015.01068](https://doi.org/10.3389/fpls.2015.01068)
- Hopkins, M. S., Casa, A. M., Wang, T., Mitchell, S. E., Dean, R. E., Kochert, G. D., & Kresovich, S. (1999). Discovery and characterization of polymorphic simple sequence repeats (SSRs) in cultivated peanut (*Arachis hypogaea* L.). *Crop Science*, *39*, 1243–1247. [https://doi.org/](https://doi.org/10.2135/cropsci1999.0011183X003900040047x) [10.2135/cropsci1999.0011183X003900040047x](https://doi.org/10.2135/cropsci1999.0011183X003900040047x)
- Huang, L., He, H., Chen, W., Ren, X., Chen, Y., Zhou, X., … Jiang, H. (2015). Quantitative trait locus analysis of agronomic and quality‐ related traits in cultivated peanut (Arachis hypogaea L.). *TAG. Theoretical and Applied Genetics.*, *128*, 1103–1115. [https://doi.org/10.1007/](https://doi.org/10.1007/s00122-015-2493-1) [s00122-015-2493-1](https://doi.org/10.1007/s00122-015-2493-1)
- Huang, L., Ren, X., Wu, B., Li, X., Chen, W., Zhou, X., … Jiang, H. (2016). Development and deployment of a high-density linkage map identified quantitative trait loci for plant height in peanut (*Arachis hypogaea* L.). *Scientific Reports*, *6*, 39478.<https://doi.org/10.1038/srep39478>
- IBPGR and ICRISAT (1992). *Descriptors for groundnut*. International Board Plant Genetic Resources, Rome, Italy, and Intern. Crops Res. Inst. for the Semi-Arid Tropics, Patancheru, A. P., India.
- Izge, A. U., Mohammed, Z. H., & Goni, A. (2007). Levels of variability in groundnut (*Arachis hypogaea* L.) to cercospora leafspot disease ‐ implications for selection. *African Journal of Agricultural Research*, *2*, 182–186.
- Jakkeral, S. A., Nadaf, H. L., Gowda, M. V. C., & Bhat, R. S. (2013). Inheritance of rust resistance in cultivated groundnut (*Arachis hypogaea* L.). *Indian Journal of Genetics and Plant Breeding*, *73*, 450–453. [https://d](https://doi.org/10.5958/j.0975-6906.73.4.069) [oi.org/10.5958/j.0975-6906.73.4.069](https://doi.org/10.5958/j.0975-6906.73.4.069)
- Janila, P., Manohar, S. S., Patne, N., Variath, M. T., & Nigam, S. N. (2016). Genotype \times environment interactions for oil content in peanut and stable high‐oil‐yielding sources. *Crop Science*, *56*, 01–10.
- Janila, P., Manohar, S. S., Rathore, A., & Nigam, S. N. (2015). Inheritance of SPAD chlorophyll meter reading and specific leaf area in four crosses of groundnut (*Arachis hypogaea* L.). *Indian Journal of Genetics*, *75*, 408–412.
- Janila, P., & Nigam, S. N. (2013). Phenotyping for groundnut (*Arachis hypogaea* L.) improvement. In S. K. Panguluri & A. A. Kumar (eds.), *Phenotyping for plant breeding: Applications of phenotyping methods for crop improvement*, Springer Science Business Media New York: Springer. https://doi.org/10.1007/978-1-4614-8320-5_5
- Janila, P., Nigam, S. N., Pandey, M. K., Nagesh, P., & Varshney, R. K. (2013). Groundnut improvement: Use of genetic and genomic tools. *Plant Science*, *4*, 1–12.
- Janila, P., Pandey, M. K., Manohar, S. S., Variath, M. T., Nallathambi, P., Nadaf, H. L., ... Varshney, R. K. (2016). Foliar fungal disease-resistant introgression lines of groundnut (*Arachis hypogaea* L.) record higher pod and haulm yield in multilocation testing. *Plant Breeding*, *135*, 355–366.
- Janila, P., Pandey, M. K., Shasidhar, Y., Variath, M. T., Sriswathi, M., Khera, P., … Varshney, R. K. (2016). Molecular breeding for introgression of fatty acid desaturase mutant alleles (ahFAD2A and ahFAD2B)

enhances oil quality in high and low oil containing peanut genotypes. *Plant Science*, *242*, 203–213. [https://doi.org/10.1016/j.plantsci.2015.](https://doi.org/10.1016/j.plantsci.2015.08.013) [08.013](https://doi.org/10.1016/j.plantsci.2015.08.013)

- Janila, P., Ramaiah, V., Rathore, A., Upakula, A., Reddy, R. K., Waliyar, F., & Nigam, S. N. (2013). Genetic analysis of resistance to late leaf spot in interspecific groundnuts. *Euphytica*, *193*, 13–25.
- Janila, P., Variath, M. T., Pandey, M. K., Desmae, H., Motagi, B. N., Okori, P., … Varshney, R. K. (2016). Genomic tools in groundnut breeding program: Status and perspectives. *Frontiers in Plant Science*, *7*, 289. <https://doi.org/10.3389/fpls.2016.00289>
- Jiang, H. F., & Duan, N. X. (2006). *Descriptors and data standard for peanut (Arachis spp.)*. Beijing: China Agricultural Press. ISBN: 7-109- 10911-9.
- Jiang, H. F., Ren, X. P., Liao, B. S., Huang, J. Q., Lei, Y., Chen, B. Y., … Upadhyaya, H. D. (2008). Peanut core collection established in china and compared with ICRISAT mini core collection. *Acta Agronomica Sinica*, *34*, 25–30.
- Jogloy, P. S., Vorasoot, N., Akkasaeng, C., Kesmala, T., & Patanothai, A. (2009). Variability in yield responses of peanut (*Arachis hypogaea* L.) genotypes under early season drought. *Asian Journal of Plant Sciences*, *8*, 254–264.<https://doi.org/10.3923/ajps.2009.254.264>
- John, K., Reddy, P. R., Reddy, P. H., Sudhakar, P., & Reddy, N. P. E. (2011). Genetic variability for morphological, physiological, yield and yield traits in F2 populations of groundnut (A*rachis hypogaea* L). *International Journal of Applied Biology and Pharmaceutical Technology*, *2*, 463–469.
- John, K., Vasanthi, R. P., Sireesha, K., & Krishna, T. G. (2013). Genetic variability studies in different advanced breeding genotypes of Spanish bunch groundnut (*Arachis hypogeae*). *International Journal of Applied Biology and Pharmaceutical Technology*, *4*, 185–187.
- Kanyika, B. T. N., Lungu, D., Mweetwa, A., Kaimoyo, E., Njung'e, V. M., Monyo, E. S., … de Villiers, S. M. (2015). Identification of groundnut (*Arachis hypogaea* L.) SSR markers suitable for multiple resistance traits QTL mapping in African germplasm. *Electronic Journal of Biotechnology*, *18*, 61–67.<https://doi.org/10.1016/j.ejbt.2014.10.004>
- Khedikar, Y. P., Gowda, M. V. C., Sarvamangala, C., Patgar, K. V., Upadhyaya, H. D., & Varshney, R. K. (2010). A QTL study on late leaf spot and rust revealed one major QTL for molecular breeding for rust resistance in groundnut (*Arachis hypogaea* L.). *TAG. Theoretical and Applied Genetics.*, *121*, 971–984. [https://doi.org/10.1007/s00122-](https://doi.org/10.1007/s00122-010-1366-x) [010-1366-x](https://doi.org/10.1007/s00122-010-1366-x)
- Khedikar, Y., Pandey, M. K., Sujay, V., Singh, S., Nayak, S. N., Klein-Gebbinck, H. W., … Bhat, R. S. (2018). Identification of main effect and epistatic quantitative trait loci for morphological and yield‐related traits in peanut (*Arachis hypogaea* L.). *Molecular Breeding*, *38*, 1–12.
- Khera, P., Pandey, M. K., Wang, H., Feng, S., Qiao, L., Culbreath, A. K., … Guo, B. (2016). Mapping quantitative trait loci of resistance to tomato spotted wilt virus and leaf spots in a recombinant inbred line population of peanut (Arachis hypogaea L.) from SunOleic 97R and NC94022. *PLoS One*, *11*(7), e0158452. [https://doi.org/10.1371/jour](https://doi.org/10.1371/journal.pone.0158452) [nal.pone.0158452](https://doi.org/10.1371/journal.pone.0158452)
- Khera, P., Upadhyaya, H. D., Pandey, M. K., Roorkiwal, M., Sriswathi, M., Janila, P., … Varshney, R. K. (2013). Single nucleotide polymorphism– based genetic diversity in the reference set of peanut (Arachis spp.) by developing and applying cost‐effective kompetitive allele specific polymerase chain reaction genotyping assays. *Plant Genome*, *6*, 1–11.
- Knauft, D. A., & Wynne, J. C. (1995). Peanut breeding and genetics. *Advances in Agronomy*, *55*, 393–445. [https://doi.org/10.1016/S0065-](https://doi.org/10.1016/S0065-2113(08)60544-1) [2113\(08\)60544-1](https://doi.org/10.1016/S0065-2113(08)60544-1)
- Knoll, J. E., Ramos, M. L., Zeng, Y., Holbrook, C. C., Chow, M., Chen, S., … Ozias-Akins, P. (2011). TILLING for allergen reduction and improvement of quality traits in peanut (*Arachis hypogaea* L.). *BMC Plant Biology*, *11*, 81.<https://doi.org/10.1186/1471-2229-11-81>
- Kolekar, R. M., Sujay, V., Shirasawa, K., Sukruth, M., Khedikar, Y. P., Gowda, M. V. C., … Bhat, R. S. (2016). QTL mapping for late leaf

spot and rust resistance using an improved genetic map and extensive phenotypic data on a recombinant inbred line population in peanut (*Arachis hypogaea* L.). *Euphytica*, *209*, 147–156. [https://doi.org/](https://doi.org/10.1007/s10681-016-1651-0) [10.1007/s10681-016-1651-0](https://doi.org/10.1007/s10681-016-1651-0)

- Kolekar, R. M., Sukruth, M., Shirasawa, K., Nadaf, H. L., Motagi, B. N., Lingaraju, S., … Bhat, R. S. (2017). Marker‐assisted backcrossing to develop foliar disease‐ resistant genotypes in TMV 2 variety of peanut (*Arachis hypogaea* L.). *Plant Breeding*, *136*, 948–953. [https://doi.](https://doi.org/10.1111/pbr.12549) [org/10.1111/pbr.12549](https://doi.org/10.1111/pbr.12549)
- Krapovickas, A., & Gregory, W. C. (1994). Taxonomıa del genero Arachis (Leguminosae). *Bonplandia*, *8*, 1–186.
- Krishnamurthy, L., Vadez, V., Devi, M. J., Serraj, R., Nigam, S. N., Sheshshayee, M. S., … Aruna, R. (2007). Variation in transpiration efficiency and its related traits in a groundnut. *Field Crops Research.*, *103*, 189–197.<https://doi.org/10.1016/j.fcr.2007.06.009>
- Lal, C., Hariprasanna, K., Rathnakumar, A. L., Gor, H. K., & Chikani, B. M. (2006). Gene action for surrogate traits of water‐use efficiency and harvest index in peanut (*Arachis hypogaea*). *Annals of Applied Biology*, *148*, 165–172.<https://doi.org/10.1111/j.1744-7348.2006.00047.x>
- Leal‐Bertioli, S. C. M., Cavalcante, U., Gouvea, E. G., Ballén Taborda, C., Shirasawa, K., Guimarães, P. M., … Moretzsohn, M. C. (2015). Identification of QTLs for rust resistance in the peanut wild species *Arachis magna* and the development of KASP markers for marker assisted selection. *G3 (Bethesda)*, *5*, 1403–1413. [https://doi.org/10.1534/g3.](https://doi.org/10.1534/g3.115.018796) [115.018796](https://doi.org/10.1534/g3.115.018796)
- Leal-Bertioli, S. C. M., José, A. C., Alves-Freitas, D. M., Moretzsohn, M. C., Guimarães, P. M., Nielen, S., … Bertioli, D. J. (2009). Identification of candidate genome regions controlling disease resistance in *Arachis*. *BMC Plant Biology*, *9*, 112.<https://doi.org/10.1186/1471-2229-9-112>
- Leal-Bertioli, S. C. M., Moretzsohn, M. C., Roberts, P. A., Ballén-Taborda, C., Borba, T. C., Valdisser, P. A., … Bertioli, D. J. (2016). Genetic mapping of resistance to meloidogyne arenaria in arachis stenosperma: A new source of nematode resistance for peanut. *G3 (Bethesda)*, *6*, 377–390.<https://doi.org/10.1534/g3.115.023044>
- Li, Y., Li, L., Zhang, X., Zhang, K., Ma, D., Liu, J., … Wan, Y. (2017). QTL mapping and marker analysis of main stem height and the first lateral branch length in peanut (*Arachis hypogaea* L.). *Euphytica*, *213*, 57. <https://doi.org/10.1007/s10681-017-1847-y>
- Liang, Y., Baring, M., Wang, S., & Septiningsih, E. M. (2017). *Mapping QTLs for leaf spot resistance in peanut using SNP-based next-generation sequencing markers*. Abstract Poster Number 106169. Monday, October 23, 2017, Tampa Convention Center, East Exhibit Hall. In: Managing Global Resources for a Secure Future. 2017 Annual Meeting | Oct. 22-25 | Tampa, FL
- Luo, H., Ren, X., Li, Z., Xu, Z., Li, X., Huang, L., … Jiang, H. (2017). Co‐ localization of major quantitative trait loci for pod size and weight to a 3.7 cM interval on chromosome A05 in cultivated peanut (*Arachis hypogaea* L.). *BMC Genomics*, *18*, 58. [https://doi.org/10.1186/](https://doi.org/10.1186/s12864-016-3456-x) [s12864-016-3456-x](https://doi.org/10.1186/s12864-016-3456-x)
- Luo, H., Xu, Z., Li, Z., Li, X., Lv, J., Ren, X., … Jiang, H. (2017). Development of SSR markers and identification of major quantitative trait loci controlling shelling percentage in cultivated peanut (*Arachis hypogaea* L.). *TAG. Theoretical and Applied Genetics.*, *130*, 1635–1648. [https://d](https://doi.org/10.1007/s00122-017-2915-3) [oi.org/10.1007/s00122-017-2915-3](https://doi.org/10.1007/s00122-017-2915-3)
- Mace, E. S., Phong, D. T., Upadhyaya, H. D., Chandra, S., & Crouch, J. H. (2006). SSR analysis of cultivated groundnut (*Arachis hypogaea* L.) germplasm resistant to rust and late leaf spot diseases. *Euphytica*, *152*, 317–330.<https://doi.org/10.1007/s10681-006-9218-0>
- Mace, E. S., Yuejin, W., Boshou, L., Upadhyaya, H., Chandra, S., & Crouch, J. H. (2007). Simple sequence repeat (SSR)‐based diversity analysis of groundnut (*Arachis hypogaea* L.) germplasm resistant to bacterial wilt. *Plant Genetic Resources*, *5*, 27–36. [https://doi.org/10.1017/](https://doi.org/10.1017/S1479262107390916) [S1479262107390916](https://doi.org/10.1017/S1479262107390916)
- Makinde, S. C. O., Ariyo, O. J., & Akinbowale, R. I. (2013). Assessment of groundnut performance in different environments using Additive

Main effects and Multiplicative Interaction (AMMI) model. *Canadian Journal of Plant Breeding*, *1*, 60–66.

- Mallikarjuna, N., Senthilvel, S., & Hoisington, D. (2011). Development of new sources of tetraploid Arachis to broaden the genetic base of cultivated groundnut (*Arachis hypogaea* L.). *Genetic Resources and Crop Evolution*, *58*, 889–907.<https://doi.org/10.1007/s10722-010-9627-8>
- Mayeux, A. H., & Ntare, R. B. (2001). Accessions with resistance to foliar diseases, *A*. *flavus*/*Aflatoxin* contamination and rosette disease. *Groundnut Germplasm Catalogue*, *2*, 23.
- Mayeux, A.H., Waliyar, F., & Ntare, B. R. (2003). *Groundnut varieties recommended by the Groundnut Germplasm Project (GGP) for West and Central Africa (in En, Fr.)*. ICRISAT, Patancheru 502 324, Andhra Pradesh, India. 80 pp.
- McDonald, D., Subrahmanyam, P., Gibbons, R. W., & Smith, D. H. (1985). *Early and late leaf spots of groundnut*. Information Bulletin no. 21. ICRISAT, Patancheru 502 324, Andhra Pradesh, India.
- Mondal, S., & Badigannavar, A. M. (2015). Peanut rust (Puccinia arachidis Speg.) disease: Its background and recent accomplishments towards disease resistance breeding. *Protoplasma*, *252*(6), [https://doi.org/10.](https://doi.org/10.1007/s00709-015-0783-8) [1007/s00709-015-0783-8](https://doi.org/10.1007/s00709-015-0783-8)
- Mondal, S., Badigannavar, A. M., & D'Souza, S. F. (2012). Development of genic molecular markers linked to a rust resistance gene in cultivated groundnut (*Arachis hypogaea* L.). *Euphytica*, *188*, 163–173. [https://d](https://doi.org/10.1007/s10681-011-0619-3) [oi.org/10.1007/s10681-011-0619-3](https://doi.org/10.1007/s10681-011-0619-3)
- Mondal, S., Badigannavar, A. M., Kale, D. M., & Murty, G. S. S. (2007). Induction of genetic variability in a disease‐resistant groundnut breeding line. *BARC Newsletter*, *185*, 237–246.
- Mondal, S., Hadapad, A. B., Hande, P. A., & Badigannavar, A. M. (2014). Identification of quantitative trait loci for bruchid (*Caryedon serratus* Olivier) resistance components in cultivated groundnut (*Arachis hypogaea* L.). *Molecular Breeding*, *33*, 961–973. [https://doi.org/10.1007/](https://doi.org/10.1007/s11032-013-0011-1) [s11032-013-0011-1](https://doi.org/10.1007/s11032-013-0011-1)
- Monyo, E. S., Njoroge, S. M. C., Coe, R., Osiru, M., Madinda, F., Waliyar, F., … Anitha, S. (2012). Occurrence and distribution of aflatoxin contamination in groundnuts (arachis hypogaea) and population densities of aflatoxigenic aspergilli. *Crop Protection*, *42*, 149–155. [https://doi.](https://doi.org/10.1016/j.cropro.2012.07.004) [org/10.1016/j.cropro.2012.07.004](https://doi.org/10.1016/j.cropro.2012.07.004)
- Monyo, E. S., & Varshney, R. K. (Eds.), (2016). *Seven seasons of learning and engaging smallholder farmers in the drought-prone areas of sub-Saharan Africa and South Asia through Tropical Legumes, 2007–2014*. Patancheru 502 324, Telangana, India: International Crops Research Institute for the Semi-Arid Tropics. ISBN 978-92-9066-568-7. 236 pp.
- Moretzsohn, M. C., Barbosa, A. V., Alves-Freitas, D. M., Teixeira, C., & Leal-Bertioli, S. C. (2009). A linkage map for the B‐genome of *Arachis* (Fabaceae) and its synteny to the A‐genome. *BMC Plant Biology*, *9*, 40.<https://doi.org/10.1186/1471-2229-9-40>
- Moretzsohn, M. C., Hopkins, M. S., Mitchell, S. E., Kresovich, S., Valls, J. F. M., & Ferreira, M. E. (2004). Genetic diversity of peanut (*Arachis hypogaea* L.) and its wild relatives based on the analysis of hypervariable regions of the genome. *BMC Plant Biology*, *4*, 11. [https://doi.](https://doi.org/10.1186/1471-2229-4-11) [org/10.1186/1471-2229-4-11](https://doi.org/10.1186/1471-2229-4-11)
- Moretzsohn, M. C., Leoi, L., Proite, K., Guimarães, P. M., Leal-Bertioli, S. C. M., Gimenes, M. A., … Bertioli, D. J. (2005). A microsatellite‐based, gene‐rich linkage map for the AA genome of *Arachis* (*Fabaceae*). *TAG. Theoretical and Applied Genetics.*, *111*, 1060–1071. [https://doi.org/10.](https://doi.org/10.1007/s00122-005-0028-x) [1007/s00122-005-0028-x](https://doi.org/10.1007/s00122-005-0028-x)
- Nageswara Rao, R. C., Talwar, H. S., & Wright, G. C. (2001). Rapid assessment of specific leaf area and leaf N in peanut (*Arachis hypogaea* L.) using chlorophyll meter. *Journal of Agronomy and Crop Science*, *189*, 175–182.<https://doi.org/10.1046/j.1439-037X.2001.00472.x>
- Nagy, E. D., Guo, Y., Tang, S., Bowers, J. E., Okashah, R. A., Taylor, C. A., … Knapp, S. J. (2012). A high‐density genetic map of *Arachis duranensis*, a diploid ancestor of cultivated peanut. *BMC Genomics*, *13*, 469. <https://doi.org/10.1186/1471-2164-13-469>
- Ndjeunga, J., Ibro, A., Cisse, Y., Ben, A., Miko, I., Moutari, A., … Echekwu, C. A. (2010). *Characterizing village economies in major groundnut producing countries in West Africa: Cases of Mali* (p. 89). Niger and Nigeria: ICRISAT.
- Nigam, S. N. (2014). *Groundnut at a glance*. 121 pp.
- Nigam, S. N., & Bock, K. R. (1990). Inheritance of resistance to groundnut rosette virus in groundnut (*Arachis hypogaea* L.). *Annals of Applied Biology*, *117*, 553–560. [https://doi.org/10.1111/j.1744-7348.1990.tb](https://doi.org/10.1111/j.1744-7348.1990.tb04821.x) [04821.x](https://doi.org/10.1111/j.1744-7348.1990.tb04821.x)
- Nigam, S. N., Chandra, S., Sridevi, K. R., Bhukta, M. R., Reddy, A. G. S., Rachaputi, N. R., … Nagda, A. K. (2005). Efficiency of physiological trait‐based and empirical selection approaches for drought tolerance in groundnut. *Annals of Applied Biology*, *146*, 433–439. [https://doi.](https://doi.org/10.1111/j.1744-7348.2005.040076.x) [org/10.1111/j.1744-7348.2005.040076.x](https://doi.org/10.1111/j.1744-7348.2005.040076.x)
- Nigam, S. N., Nageswara Rao, R. C., & Wright, G. C. (2002). *Field Screening for drought tolerance in groundnut*. In: Field Screening for Drought Tolerance Proceedings of an International Workshop on International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India, pp. 147-151. ISBN 92-9066- 448-7.
- Nigam, S. N., Upadhyaya, H. D., Chandra, S., Rao, R. C. N., Wright, G. C., & Reddy, A. G. S. (2001). Gene effects for specific leaf area and harvest index in three crosses of groundnut (*Arachis hypogaea*). *Annals of Applied Biology*, *139*, 301–306. [https://doi.org/10.1111/j.1744-7348.](https://doi.org/10.1111/j.1744-7348.2001.tb00143.x) [2001.tb00143.x](https://doi.org/10.1111/j.1744-7348.2001.tb00143.x)
- Nigam, S. N., Waliyar, F., Aruna, F. R., Reddy, S. V., Lava Kumar, P., Craufurd, P. Q., … Upadhyaya, H. D. (2009). Breeding peanut for resistance to aflatoxin contamination at ICRISAT. *Peanut Science*, *36*, 42– 49.<https://doi.org/10.3146/AT07-008.1>
- Ntare, B. R., Ndjeunga, J., Waliyar, F., Kodio, O., Echekwu, C. A., Kapran, I., … Sako, K. (2007). *Farmer participatory evaluation and dissemination of improved groundnut varieties in West Africa*. ICRISAT, 36 pp.
- Ntare, B. R., Olorunju, P. E., & Hildebrand, G. L. (2002). Progress in breeding early maturing peanut cultivars with resistance to groundnut rosette disease in West Africa. *Peanut Science*, *29*, 17–23. [https://doi.](https://doi.org/10.3146/pnut.29.1.0004) [org/10.3146/pnut.29.1.0004](https://doi.org/10.3146/pnut.29.1.0004)
- Ntare, B. R., Waliyar, F., Mayeux, A. H., & Bissala, H. Y. (2006). Strengthening conservation and utilization of groundnut (*Arachis hypogaea* L.) genetic resources in West Africa. *Plant Genetic Resources Newsletter*, *147*, 18–24.
- Olorunju, P. E., Kuhn, C. W., Demski, J. W., Misari, S. M., & Ansa, O. A. (1992). Inheritance of resistance in peanut to mixed infection of groundnut rosette virus (GRV) and groundnut rosette assistor virus and single infection of GRV. *Plant Disease*, *76*, 95–100. [https://doi.](https://doi.org/10.1094/PD-76-0095) [org/10.1094/PD-76-0095](https://doi.org/10.1094/PD-76-0095)
- Oteng-Frimpong, R., Sriswathi, M., Ntare, B. R., & Dakora, F. D. (2015). Assessing the genetic diversity of 48 groundnut (*Arachis hypogaea* L.) genotypes in the Guinea savanna agro‐ecology of Ghana, using microsatellite‐based markers. *African Journal of Biotechnology*, *14*, 2484–2493.
- Padmaja, D., Eswari, K. B., BrahmeswaraRao, M. V., & Madhusudhan Reddy, S. (2013). Genetic relationship of yield attributing traits and late leaf spot tolerance with pod yield in BC1F2 population of (JL 24 x ICG 11337) x JL 24 of groundnut. *International Journal of Innovative Research and Development*, *2*, 191–196.
- Padmaja, D., Eswari, K. B., BrahmeswaraRao, M. V., & Prasad, G. (2015). Genetic variability studies in F2 population of Groundnut *(Arachis hypogeaea L.)*. *Helix*, *2*, 668–672.
- Pandey, M. K., Agarwal, G., Kale, S. M., Clevenger, J., Nayak, S. N., Sriswathi, M., … Varshney, R. K. (2017). Development and evaluation of a high density genotyping 'Axiom_Arachis SNPs for accelerating genetics and breeding in groundnut. *Scientific Reports*, *7*, 40577. <https://doi.org/10.1038/srep40577>
- Pandey, M. K., Guo, B., Holbrook, C. C., Janila, P., Zhang, X., Bertioli, D. J., … Varshney, R. K. (2014). Molecular markers, genetic maps and

QTLs for molecular breeding in peanut. In N. Mallikarjuna, & R. K. Varshney (Eds.), *Genetics, genomics and breeding of peanuts* (pp. 79– 113). Boca Raton, FL: CRC Press.

- Pandey, M. K., Khan, A. W., Singh, V. K., Vishwakarma, M. K., Shasidhar, Y., Kumar, V., … Varshney, R. K. (2017). QTL‐seq approach identified genomic regions and diagnostic markers for rust and late leaf spot resistance in groundnut *(Arachis hypogaea* L.). *Plant Biotechnology Journal*, *15*, 927–941.<https://doi.org/10.1111/pbi.12686>
- Pandey, M. K., Monyo, E., Ozias-Akins, P., Liang, X., Guimarães, P., Nigam, S. N., … Varshney, R. K. (2012). Advances in *Arachis* genomics for peanut improvement. *Biotechnology Advances*, *30*, 639–651. <https://doi.org/10.1016/j.biotechadv.2011.11.001>
- Pandey, M. K., Upadhyaya, H. D., Rathore, A., Vadez, V., Sheshshayee, M. S., Sriswathi, M., … Varshney, R. K. (2014). Genome wide association studies for 50 agronomic traits in peanut using the 'reference set' comprising 300 genotypes from 48 countries of the semi‐arid tropics of the world. *PLoS One*, *9*(8), e105228. [https://doi.org/10.1371/jour](https://doi.org/10.1371/journal.pone. 0105228) [nal.pone. 0105228](https://doi.org/10.1371/journal.pone. 0105228)
- Pandey, M. K., Wang, H., Khera, P., Vishwakarma, M. K., Kale, S. M., Culbreath, A. K., … Guo, B. (2017). Genetic dissection of novel QTLs for resistance to leaf spots and tomato spotted wilt virus in peanut (*Arachis hypogaea* L.). *Frontiers in Plant Science*, *8*, 25. [https://doi.org/10.](https://doi.org/10.3389/fpls.2017.00025) [3389/fpls.2017.00025](https://doi.org/10.3389/fpls.2017.00025)
- Pandey, M. K., Wang, M. L., Qiao, L., Feng, S., Khera, P., Wang, H., … Guo, B. (2014). Identification of QTLs associated with oil content in RIL populations and mapping FAD2 genes and their relative contribution towards oil quality. *BMC Genetics*, *15*, 133. [https://doi.org/10.](https://doi.org/10.1186/s12863-014-0133-4) [1186/s12863-014-0133-4](https://doi.org/10.1186/s12863-014-0133-4)
- Patil, A. S., Punewar, A. A., Nandanwar, H. R., & Shah, K. P. (2014). Estimation of Variability parameters for yield and its component traits in groundnut (*Arachis hypogaea* L.). *Bioscan*, *9*, 749–754.
- Pattanashetti, S. K., Gowda, M. V. C., & Girija, Pattanashetti (2008). Inheritance of morphological traits and pod features in groundnut (*Arachis hypogaea* L.). *Indian Journal of Genetics and Plant Breeding*, *68*, 157–162.
- Peng, Z., Fan, W., Wang, L., Paudel, D., Leventini, D., Tillman, B. L., & Wang, J. (2017). Target enrichment sequencing in cultivated peanut (*Arachis hypogaea* L.) using probes designed from transcript sequences. *Molecular Genetics and Genomics*, *5*, 1–11. [https://doi.org/](https://doi.org/10.1007/s00438-017-1327-z) [10.1007/s00438-017-1327-z](https://doi.org/10.1007/s00438-017-1327-z)
- Peng, Z., Gallo, M., Tillman, B. L., Rowland, D., & Wang, J. (2016). Molecular marker development from transcript sequences and germplasm evaluation for cultivated peanut (*Arachis hypogaea* L.). *Molecular Genetics and Genomics*, *291*, 363–381. [https://doi.org/10.1007/](https://doi.org/10.1007/s00438-015-1115-6) [s00438-015-1115-6](https://doi.org/10.1007/s00438-015-1115-6)
- Pittman, R. N. (1995). *United States peanut descriptors*. USDA-ARS-132. Washington, DC.: U.S. Government Printing Office.
- Qin, H., Feng, S., Chen, C., Guo, Y., Knapp, S., Culbreath, A., … Guo, B. (2012). An integrated genetic linkage map of cultivated peanut (*Arachis hypogaea* L.) constructed from two RIL populations. *TAG. Theoretical and Applied Genetics.*, *124*, 653–664. [https://doi.org/10.1007/](https://doi.org/10.1007/s00122-011-1737-y) [s00122-011-1737-y](https://doi.org/10.1007/s00122-011-1737-y)
- Ravi, K., Vadez, V., Isobe, S., Mir, R. R., Guo, Y., Nigam, S. N., … Varshney, R. K. (2011). Identification of several small main‐effect QTLs and a large number of epistatic QTLs for drought tolerance related traits in groundnut (*Arachis hypogaea* L.). *TAG. Theoretical and Applied Genetics.*, *122*, 1119–1132. [https://doi.org/10.1007/s00122-010-](https://doi.org/10.1007/s00122-010-1517-0) [1517-0](https://doi.org/10.1007/s00122-010-1517-0)
- Reddy, P. S. (1988). Genetics, breeding and varieties. In P. S. Reddy (Ed.), *Groundnut* (pp. 200–317). Indian Council of Agricultural Research: New Delhi.
- Reddy, L. J., Nigam, S. N., Dwivedi, S. L., & Gibbons, R. W. (1987). *Breeding groundnut cultivars resistant to rust (Puccinia arachidis Speg.)*. In: Groundnut Rust Disease: Proc Discuss Group Meet. 24-28 September, 1984, ICRISAT, Patancheru, AP 502324, India. Pp 17-25.
- Reddy, L. J., Nigam, S. N., Rao, R. C. N., & Reddy, N. S. (2001). Registration of ICGV 87354 peanut germplasm with drought tolerance and rust resistance. *Crop Science*, *41*, 274–275.
- Reddy, L. J., Nigam, S. N., & Reddy, A. G. S. (1995). Stability of, pod yield for foliar disease resistant groundnut varieties. *International Arachis Newsletter*, *17*, 13–15.
- Roomi, S., Sabiha, B., Iqbal, A., Suleman, M., Muhammad, I., Zia, M. A., … Tabbasam, N. (2014). SSR based genetic diversity analysis in a diverse germplasm of groundnut (*Arachis hypogaea* L.) from Pakistan. *Australian Journal of Crop Science*, *8*, 55–61.
- Sanogo, O. (2016). *Early generation selection for drought related traits in groundnut (Arachis hypogaea L.) in Mali*. PhD Thesis, University of Ghana. Pp 247.
- Sarvamangala, C., Gowda, M. V. C., & Varshney, R. K. (2011). Identification of quantitative trait loci for protein content, oil content and oil quality for groundnut (*Arachis hypogaea* L.). *Field Crops Research*, *122*, 49–59.<https://doi.org/10.1016/j.fcr.2011.02.010>
- Selvaraj, M. G., Narayana, M., Schubert, A. M., Ayers, J. L., Baring, M. R., & Burow, M. D. (2009). Identification of QTLs for pod and kernel traits in cultivated peanut by bulked segregant analysis. *Electronic Journal of Biotechnology*, *12*,<https://doi.org/10.2225/vol12>
- Sharma, K. K., Pothana, A., Prasad, K., Shah, D., Kaur, J., Bhatnagar, D., … Bhatnagar-Mathur, P. (2018). Peanuts that keep aflatoxin at bay: A threshold that matters. *Plant Biotechnology Journal*, *16*, 1024–1033. <https://doi.org/10.1111/pbi.12846>
- Shasidhar, Y., Vishwakarma, M. K., Pandey, M. K., Janila, P., Variath, M. T., Manohar, S. S., … Varshney, R. K. (2017). Molecular mapping of oil content and fatty acids using dense genetic maps in groundnut (Arachis hypogaea L.). *Frontiers in Plant Science*, *8*, 794. [https://doi.](https://doi.org/10.3389/fpls.2017.00794) [org/10.3389/fpls.2017.00794](https://doi.org/10.3389/fpls.2017.00794)
- Shirasawa, K., Bertioli, D. J., Varshney, R. K., Moretzsohn, M. C., Leal-Bertioli, S. C., Thudi, M., … Isobe, S. (2013). Integrated consensus map of cultivated peanut and wild relatives reveals structures of the A and B genomes of *Arachis* and divergence of the legume genomes. *DNA Research*, *20*, 173–184. [https://doi.org/10.1093/dnares/](https://doi.org/10.1093/dnares/dss042) [dss042](https://doi.org/10.1093/dnares/dss042)
- Shirasawa, K., Koilkonda, P., Aoki, K., Hirakawa, H., Tabata, S., Watanabe, M., … Isobe, S. (2012). In silico polymorphism analysis for the development of simple sequence repeat and transposon markers and construction of linkage map in cultivated peanut. *BMC Plant Biology*, *12*, 80.<https://doi.org/10.1186/1471-2229-12-80>
- Simpson, C. E. (2001). Use of wild Arachis species/introgression of genes into *A. hypogaea* L. *Peanut Science*, *28*, 114–116. [https://doi.org/10.](https://doi.org/10.3146/i0095-3679-28-2-12) [3146/i0095-3679-28-2-12](https://doi.org/10.3146/i0095-3679-28-2-12)
- Simpson, C. E., Burow, M. D., Paterson, A. H., Starr, J. L., & Church, G. T. (2003). Registration of NemaTAM peanut. *Crop Science*, *43*, 1561. <https://doi.org/10.2135/cropsci2003.1561>
- Simpson, C. E., & Starr, J. L. (2001). Registration of `COAN' Peanut. *Crop Science*, *41*, 918.<https://doi.org/10.2135/cropsci2001.413918x>
- Songsri, P., Jogloy, S., Kesmala, T., Vorasoot, N., Akkasaeng, C., Patanothai, A., & Holbrook, C. C. (2009). Heritability of drought resistance traits and correlation of drought resistance and agronomic traits in peanut. *Crop Science*, *48*, 2245–2253.
- Stalker, H. T., Tallury, S. P., Ozias-Akins, P., Bertioli, D., & Leal‐Bertioli, S. C. (2013). The value of diploid peanut relatives for breeding and genomics. *Peanut Science*, *40*, 70–88. [https://doi.org/10.3146/PS13-](https://doi.org/10.3146/PS13-6.1) [6.1](https://doi.org/10.3146/PS13-6.1)
- Subrahmanyam, P., Hildebrand, G. L., Naidu, R., Reddy, L. J., & Singh, A. K. (1998). Sources of resistance to groundnut rosette disease in global groundnut germplasm. *Annals of Applied Biology*, *132*, 473–485. <https://doi.org/10.1111/j.1744-7348.1998.tb05223.x>
- Subrahmanyam, P., McDonald, D., Waliyar, F., Reddy, L. J., Nigam, S. N., Gibbons, R. W., … Subba Rao, P. V. (1995). *Screening methods and sources of resistance to rust and late leaf spot of groundnut*. In: Information bulletin, No 47, ICRISAT, Patancheru, India.
- Subrahmanyam, P., Moss, J. P., McDonald, D., Subba Rao, P. V., & Rao, V. R. (1985). Resistance to Cercosporidium personatum leafspot in wild *Arachis* species. *Plant Disease*, *69*, 951–954.
- Subrahmanyam, P., van Wyk, P. S., Kisyombe, C. T., Cole, D. L., Hildebrand, G. L., Chiyembekeza, A. J., & Van der Merwe, P. J. A. (1997). Diseases of groundnut in the Southern African Development Community (SADC) region and their management. *International Journal of Pest Management*, *43*, 261–273. [https://doi.org/10.1080/](https://doi.org/10.1080/096708797228555) [096708797228555](https://doi.org/10.1080/096708797228555)
- Sujay, V., Gowda, M. V. C., Pandey, M. K., Bhat, R. S., Khedikar, Y. P., Nadaf, H. L., ... Varshney, R. K. (2012). Quantitative trait locus analysis and construction of consensus genetic map for foliar disease resistance based on two recombinant inbred line populations in cultivated groundnut (*Arachis hypogaea* L.). *Molecular Breeding*, *30*, 773–788. <https://doi.org/10.1007/s11032-011-9661-z>
- Thirumala Rao, V., Venkanna, V., Bhadru, D., & Bharathi, D. (2014). Studies on variability, character association and path analysis on Groundnut (*Arachis hypogaea* L.). *International Journal of Pure & Applied Bioscience*, *2*, 194–197.
- Tseng, Y.-C., Tillman, B. L., Peng, Z., & Wang, J. (2016). Identification of major QTLs underlying tomato spotted wilt virus resistance in peanut cultivar Florida‐EPTM '113'. *BMC Genetics*, *17*, 128. [https://doi.org/](https://doi.org/10.1186/s12863-016-0435-9) [10.1186/s12863-016-0435-9](https://doi.org/10.1186/s12863-016-0435-9)
- Upadhyaya, H. D. (2005). Variability for drought resistance related traits in the mini core collection of peanut. *Crop Science*, *45*, 1432–1440. <https://doi.org/10.2135/cropsci2004.0389>
- Upadhyaya, H.D., Bhattacharjee, R., Hoisington, D. A., Chandra, S., Varshney, R. K., Singh, S., … Bertioli, D. (2006). *Molecular characterization of groundnut (Arachis hypogaea L.) composite collection*. Generation Challenge Program Annual Research Meeting, 12-16 September 2006, Sao Paulo, Brazil.
- Upadhyaya, H. D., Bramel, P. J., Ortiz, R., & Singh, S. (2002). Developing a mini core of peanut for utilization of genetic resources. *Crop Science*, *42*, 2150–2156.<https://doi.org/10.2135/cropsci2002.2150>
- Upadhyaya, H. D., Dronavalli, N., Singh, S., & Dwivedi, S. L. (2012). Variability and stability for kernel iron and zinc contents in the ICRISAT mini core collection of peanut. *Crop Science*, *52*, 2628–2637. <https://doi.org/10.2135/cropsci2012.05.0306>
- Upadhyaya, H. D., Dwivedi, S. L., Sharma, S., Lalitha, N., Singh, S., Varshney, R. K., & Gowda, C. L. L. (2014). Enhancement of the use and impact of germplasm in crop improvement. *Plant Genetic Resources*, *12*, 155–159.<https://doi.org/10.1017/S1479262114000458>
- Upadhyaya, H. D., Dwivedi, S. L., Vadez, V., Hamidou, F., Singh, S., Varshney, R. K., & Liao, B. (2014). Multiple resistant and nutritionally dense germplasm identified from mini core collection in peanut. *Crop Science*, *54*, 679–693. [https://doi.org/10.2135/cropsci2013.07.](https://doi.org/10.2135/cropsci2013.07.0493) [0493](https://doi.org/10.2135/cropsci2013.07.0493)
- Upadhyaya, H. D., Gopal, K., Nadaf, H. L., & Vijayakumar, S. (1992). Combining ability studies for yield and its components in groundnut. *Indian J. of Genet. Plant Breeding.*, *52*, 1–6.
- Upadhyaya, H. D., MallikarjunaSwamy, B. P., Goudar, P. V. K., Kullaiswamy, B. Y., & Singh, S. (2005). Identification of diverse groundnut germplasm through multienvironment evaluation of a core collection for Asia. *Field Crops Research*, *93*, 293–299. [https://doi.](https://doi.org/10.1016/j.fcr.2004.10.007) [org/10.1016/j.fcr.2004.10.007](https://doi.org/10.1016/j.fcr.2004.10.007)
- Upadhyaya, H. D., Mukri, G., Nadaf, H. L., & Singh, S. (2012). Variability and stability analysis for nutritional traits in the mini core collection of peanut. *Crop Science*, *52*, 168–178. [https://doi.org/10.2135/cropsc](https://doi.org/10.2135/cropsci2011.05.0248) [i2011.05.0248](https://doi.org/10.2135/cropsci2011.05.0248)
- Upadhyaya, H. D., & Nigam, S. N. (1994). Inheritance of two components of early maturity in groundnut (*Arachis hypogaea* L.). *Euphytica*, *78*, 59–67.
- Upadhyaya, H. D., & Nigam, S. N. (1998). Epistasis for vegetative and reproductive traits in peanut. *Crop Science*, *38*, 44–49. [https://doi.](https://doi.org/10.2135/cropsci1998.0011183X003800010008x) [org/10.2135/cropsci1998.0011183X003800010008x](https://doi.org/10.2135/cropsci1998.0011183X003800010008x)
- Upadhyaya, H. D., & Nigam, S. N. (1999). Inheritance of fresh seed dormancy in peanut. *Crop Science*, *39*, 98–101. [https://doi.org/10.2135/](https://doi.org/10.2135/cropsci1999.0011183X003900010015x) [cropsci1999.0011183X003900010015x](https://doi.org/10.2135/cropsci1999.0011183X003900010015x)
- Upadhyaya, H. D., Ortiz, R., Bramel, P. J., & Singh, S. (2003). Development of a groundnut core collection using taxonomical, geographical and morphological descriptors. *Genetic Resources and Crop Evolution*, *50*, 139–148.<https://doi.org/10.1023/A:1022945715628>
- Upadhyaya, H. D., Reddy, L. J., Gowda, C. L. L., & Singh, S. (2006). Identification of diverse groundnut germplasm: Sources of early‐maturity in a core collection. *Field Crops Research*, *97*, 261–267. [https://doi.org/](https://doi.org/10.1016/j.fcr.2005.10.010) [10.1016/j.fcr.2005.10.010](https://doi.org/10.1016/j.fcr.2005.10.010)
- Upadhyaya, H. D., Sharma, S., Singh, S., & Singh, M. (2011). Inheritance of drought resistance related traits in two crosses of groundnut (*Arachis hypogaea* L.). *Euphytica*, *177*, 55–66. [https://doi.org/10.1007/](https://doi.org/10.1007/s10681-010-0256-2) [s10681-010-0256-2](https://doi.org/10.1007/s10681-010-0256-2)
- Varshney, R. K. (2016). Exciting journey of 10 years from genomes to fields and markets: Some success stories of genomics‐assisted breeding in chickpea, pigeon pea and groundnut. *Plant Science*, *242*, 98– 107.<https://doi.org/10.1016/j.plantsci.2015.09.009>
- Varshney, R. K., Bertioli, D. J., Moretzsohn, M. C., Vadez, V., Krishnamurthy, L., Aruna, R., … Hoisington, D. A. (2009). The first SSR‐based genetic linkage map for cultivated groundnut (*Arachis hypogaea* L.). *TAG. Theoretical and Applied Genetics.*, *118*, 729–739. [https://doi.org/](https://doi.org/10.1007/s00122-008-0933-x) [10.1007/s00122-008-0933-x](https://doi.org/10.1007/s00122-008-0933-x)
- Varshney, R. K., Pandey, M. K., Janila, P., Nigam, S. N., Sudini, H., Gowda, M. V. C., … Nagesh, P. (2014). Marker‐assisted introgression of a QTL region to improve rust resistance in three elite and popular varieties of peanut (*Arachis hypogaea* L.). *TAG. Theoretical and Applied Genetics.*, *127*, 1771–1781. [https://doi.org/10.1007/s00122-014-](https://doi.org/10.1007/s00122-014-2338-3) [2338-3](https://doi.org/10.1007/s00122-014-2338-3)
- Vishwakarma, M. K., Kale, S. M., Sriswathi, M., Naresh, T., Shasidhar, Y., Garg, V., … Varshney, R. K. (2017). Genome‐wide discovery and deployment of insertions and deletions markers provided greater insights on species, genomes, and sections relationships in the genus *Arachis*. *Frontiers in Plant Science*, *8*, 2064. [https://doi.org/10.3389/](https://doi.org/10.3389/fpls.2017.02064) [fpls.2017.02064](https://doi.org/10.3389/fpls.2017.02064)
- Vishwakarma, M. K., Pandey, M. K., Shasidha, Y., Manohar, S. S., Nagesh, P., Janila, P., & Varshney, R. K. (2016). Identification of two major quantitative trait locus for fresh seed dormancy using the diversity arrays technology and diversity arrays technology‐seq based genetic map in Spanish‐type peanuts. *Plant Breeding*, *135*, 367–375. [https://d](https://doi.org/10.1111/pbr.12360) [oi.org/10.1111/pbr.12360](https://doi.org/10.1111/pbr.12360)
- Waliyar, F., Kumar, K. V. K., Diallo, M., Traore, A., Mangala, U. N., Upadhyaya, H. D., & Sudini, H. (2016). Resistance to pre‐harvest aflatoxin contamination in ICRISAT's groundnut mini core collection. *European Journal of Plant Pathology*, *145*, 901–913. [https://doi.org/10.1007/](https://doi.org/10.1007/s10658-016-0879-9) [s10658-016-0879-9](https://doi.org/10.1007/s10658-016-0879-9)
- Wang, M. L., Khera, P., Pandey, M. K., Wang, H., Qiao, L., Feng, S., … Guo, B. (2015). Genetic mapping of QTLs controlling fatty acids provided insights into the genetic control of fatty acid synthesis pathway in peanut (*Arachis hypogaea* L.). *PLoS One*, *10*(4), e0119454. [https://d](https://doi.org/10.1371/journal.pone.0119454) [oi.org/10.1371/journal.pone.0119454](https://doi.org/10.1371/journal.pone.0119454)
- Wang, H., Pandey, M. K., Qiao, L., Qin, H., Culbreath, A. K., He, G., … Guo, B. (2013). Genetic mapping and quantitative trait loci analysis for disease resistance using F2 and F5 generation‐based genetic maps derived from 'Tifrunner' × 'GT‐C20' in peanut. *The Plant Genome*, *6*, 1–10.
- Wang, H., Penmetsa, R. V., Yuan, M., Gong, L., Zhao, Y., Guo, B., … He, G. (2012). Development and characterization of BAC‐end sequence derived SSRs, and their incorporation into a new higher density genetic map for cultivated peanut (*Arachis hypogaea* L.). *BMC Plant Biology*, *12*, 10.<https://doi.org/10.1186/1471-2229-12-10>
- Wang, M. L., Sukumaran, S., Barkley, N. A., Chen, Z., Chen, C. Y., Guo, B., … Yu, J. (2011). Population structure and marker–trait association analysis of the US peanut (*Arachis hypogaea* L.) mini core collection. *TAG. Theoretical and Applied Genetics.*, *123*, 1307–1317. [https://doi.](https://doi.org/10.1007/s00122-011-1668-7) [org/10.1007/s00122-011-1668-7](https://doi.org/10.1007/s00122-011-1668-7)
- Williams, J. H., Rao, R. C. N., & Rao, M. H. V. (1985). Breeding for drought tolerance on groundnut (*Arachis Hypogaea* L.). In: Proceedings of the Workshop on Varietal Improvement for Rice-based Farming Systems, 11-15 Mar 1985, Phitsanulok, Thailand.
- Wilson, J. N., Chopra, R., Baring, M. R., Selvaraj, M. G., Simpson, C. E., Chagoya, J., & Burow, M. D. (2017). Advanced backcross quantitative trait loci (QTL) analysis of oil concentration and oil quality traits in peanut (*Arachis hypogaea* L.). *Tropical Plant Biology*, *10*, 1–17. <https://doi.org/10.1007/s12042-016-9180-5>
- Wynne, J. C., Beute, M. K., & Nigam, S. N. (1991). Breeding for disease resistance in peanut (*Arachis hypogaea* L.). *Annual Review of Phytopathology*, *29*, 279–303. [https://doi.org/10.1146/annurev.py.29.](https://doi.org/10.1146/annurev.py.29.090191.001431) [090191.001431](https://doi.org/10.1146/annurev.py.29.090191.001431)
- Yeri, S. B., & Bhat, R. S. (2016). Development of late leaf spot and rust resistant backcross lines in Jl 24 variety of groundnut (Arachis hypogaea L.). *Electronic Journal of Plant Breeding*, *7*, 37–41. [https://doi.](https://doi.org/10.5958/0975-928X.2016.00005.3) [org/10.5958/0975-928X.2016.00005.3](https://doi.org/10.5958/0975-928X.2016.00005.3)
- Zhang, X., Zhang, J., He, X., Wang, Y., Ma, X., & Yin, D. (2017). Genome‐ wide association study of major agronomic traits related to domestication in peanut. *Frontiers in Plant Science*, *8*, 1611. [https://doi.org/](https://doi.org/10.3389/fpls.2017.01611) [10.3389/fpls.2017.01611](https://doi.org/10.3389/fpls.2017.01611)
- Zhao, C., Qiu, J., Agarwal, G., Wang, J., Ren, X., Xia, H., … Wang, X. (2017). Genome‐wide discovery of microsatellite markers from diploid progenitor species, *Arachis duranensis* and *A. ipaensis*, and their application in cultivated peanut (*A. hypogaea*). *Frontiers in Plant Science*, *8*, 1209.<https://doi.org/10.3389/fpls.2017.01209>
- Zhou, X., Xia, Y., Liao, J., Liu, K., Li, Q., Dong, Y., … Jiang, H. (2016). Quantitative trait locus analysis of late leaf spot resistance and plant‐ type‐related traits in cultivated peanut (*Arachis hypogaea* L.) under multi‐environments. *PLoS One*, *11*(11), e0166873. [https://doi.org/10.](https://doi.org/10.1371/journal.pone.0166873) [1371/journal.pone.0166873](https://doi.org/10.1371/journal.pone.0166873)
- Zhou, X., Xia, Y., Ren, X., Chen, Y., Huang, L., Huang, S., … Jiang, H. (2014). Construction of a SNP‐based genetic linkage map in cultivated peanut based on large scale marker development using nextgeneration double‐digest restriction‐site‐associated DNA sequencing (ddRADseq). *BMC Genomics*, *15*, 351. [https://doi.org/10.1186/1471-](https://doi.org/10.1186/1471-2164-15-351) [2164-15-351](https://doi.org/10.1186/1471-2164-15-351)

How to cite this article: Desmae H, Janila P, Okori P, et al. Genetics, genomics and breeding of groundnut (*Arachis hypogaea* L.). *Plant Breed*. 2019;138:425–444. [https://doi.org/](https://doi.org/10.1111/pbr.12645) [10.1111/pbr.12645](https://doi.org/10.1111/pbr.12645)