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REVIEW

Groundnut (*Arachis hypogaea* L.) improvement in sub-Saharan Africa: a review

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ABSTRACT

Groundnut (*Arachis hypogaea* L.) is a multi-purpose legume crop widely cultivated in sub-Saharan Africa (SSA). However, yield levels of the crop has remained relatively low in SSA owing to a range of biotic, abiotic and socio-economic constraints. A dedicated groundnut improvement programme integrating new tools and methodologies to breed varieties suitable for current and emerging agro-ecologies and market needs is essential for enhanced and sustainable groundnut production in SSA. The objective of this review is to highlight breeding progress, opportunities and challenges on groundnut improvement with regard to cultivar development and deployment in SSA in order to guide future improvement of the crop. The review analysed the role of new tools in breeding such as, high-throughput and automated phenotyping techniques, rapid generation advancement, single seed descent approach, marker-assisted selection, genomic selection, next-generation sequencing, genetic engineering and genome editing for accelerated breeding and cultivar development of groundnut.

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Abiotic production constraints; aflatoxin content; groundnut breeding; genotyping; phenotyping

Introduction

Groundnut (Arachis hypogaea L., 2n = 4x = 40, AABB) is self-pollinating allotetraploid legume crop belonging to the *Fabaceae* family (Janila et al. 2013). Groundnut seeds are a rich source of oil (35–56%), protein (25–30%), carbohydrates (9.5–19.0%), minerals (P, Ca, Mg and K) and vitamins (E, K and B) (Gulluoglu et al. 2016). The crop has various industrial uses including products such as food, feed, paints, lubricants and insecticides (Variath and Janila 2017). Further, groundnut is an ideal crop in rotational systems to improve soil fertility due to its natural ability to fix atmospheric nitrogen (Jaiswal et al. 2017).

Groundnut yields in sub-Saharan Africa (SSA) are generally low (964 kg/ha) which is far less than potential yields of up to 3500 kg/ha reported elsewhere (African Institute of Corporate Citizenship 2016). The low yield levels of groundnut in SSA is attributed to various stresses such as abiotic (drought and low soil fertility) and biotic [pests such as aphids (*Aphis craccivora* Koch), leafminer (*Aproarema modicella* Deventer), thrips (*Thrips palmi* Karny, *Frankiniella schultzie* Trybom, *Scirtothrips dorsalis* Hood and *Caliothrips indicus) and* termites (Isoptera)], and diseases (i.e. groundnut rosette disease, leaf spot, rust). Further, farmers in the region are cultivating unimproved varieties using poor agronomic practices and with limited access to extension and advisory services (Alemayehu et al. 2014; Debele and Amare 2015; Coulibaly et al. 2017; Desmae and Sones 2017; Mastewal et al. 2017). For example, in Senegal, water stress occurring during flowering and seed filling period reduced groundnut shelled yield by 33 and 50%, respectively (Faye et al. 2016). Groundnut rosette disease causes more severe yield losses than any of the groundnut viral diseases in the region (Okello et al. 2010). Early and late leaf spots caused 100% yield loss in Ghana (Gaikpa et al. 2015).

In SSA, efforts are being made to improve groundnut yield levels which aided in the release of few genetically superior and improved groundnut varieties (Desmae et al. 2017). Reports showed that introduced groundnut varieties had considerable resistance to both biotic and abiotic stresses (Monyo and Varshney 2016; Coulibaly et al. 2017). In addition, groundnut varieties with some desirable quality attributes such as high oil content and larger seed size for confectionery purposes have also been recently popularised (Okello et al. 2016, 2018; Amare et al. 2017). Despite past successful efforts, there has been limited breeding progress in developing groundnut varieties combining desirable agronomic and quality attributes such as high fatty acid content in combination with high yield, short maturity, drought

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tolerance or resistance to foliar diseases which are the needs and preferences of farmers and groundnut value chains (Okello et al. 2010, 2018; Desmae et al. 2017). Therefore, it is an overriding consideration to develop varieties with various quality attributes to boost productivity and quality of the crop in order to satisfy farmer's demands and value chains for food security and regional and local markets. An integrated groundnut improvement incorporating conventional and molecular breeding tools may aid in accelerated groundnut cultivars development and deployment in SSA. Therefore, the objective of this review is to highlight breeding progress, opportunities and challenges on groundnut improvement with regards to cultivar development and deployment in SSA in order to guide future improvement of the crop.

Status of groundnut production

Area under groundnut cultivation and total production have shown marked increases during the period 1997–2016 in SSA (FAOSTAT 2016). For instance, Angola and Cameroon recorded rapid increase in both cultivated area and production between 1997 and 2016. Conversely, in Botswana and South Africa both cultivated area and production level declined between 1997 and 2016. Variable yield levels have also been observed for most SSA countries during the period 1997–2016. Angola recorded groundnut yield levels varying from 500 (during 1997) to 712 kg/ha (2016) which was a yield improvement of 30%. Cameroon recorded the lowest groundnut yield of 281 kg/ha in 1997 to the highest yield level of 1648 kg/ha in 2016, which was an increase of 83%. Contrastingly, South Africa and Mozambique showed a decline in groundnut yields between 1997 and 2016. Mozambique, Angola and Botswana recorded the lowest mean groundnut yields of 349, 442 and 491 kg/ha averaged across period 1997–2016, respectively. Ghana, Cameroon, Nigeria and South Africa have recorded the top yield levels > 1000 kg/ha across the same years. In general, increased groundnut production in SSA emanated from the expansion of agricultural lands. Some reports (Monyo and Varshney 2016; Kebede et al. 2017) indicated that groundnut yields of 1,700–2,500 kg per/ha can be realised using elite/improved varieties in SSA despite that farmers yet continue cultivating unimproved local varieties. Famer participatory variety selection is considered to be a useful tool to enhance access to improved seed and increased adoption rate of improved varieties in SSA (Ndjeunga 2010; Okello et al. 2010; Monyo and Varshney 2016; Motagi et al. 2016; Desmae et al. 2017).

Progress on groundnut variety development in SSA

In the last two decades, more than 100 improved and high yielding groundnut genotypes have been introduced, developed and released for cultivation in SSA (Desmae et al. 2017). Some of the released varieties are cultivated in several SSA countries (Table 1). For example, cultivar JL 24 is widely grown in Malawi, Mozambique and South Africa due to its considerable level of drought tolerance and early maturity (Desmae et al. 2017). The reported yield levels of this variety in Malawi, Mali and Niger is 1500, 2000 and 2000 kg/ha, in that order (Minde et al. 2008; Ndjeunga 2010). Variety ICIAR 19 BT is cultivated in Nigeria and Niger due to its early maturity, high yield levels, high oil content and resistance to groundnut rosette disease.

Table 1. Some of the major groundnut varieties cultivated in sub-Saharan Africa.

Name or code	Local names in different countries	Attributes	References
ICG 12991	Baka (Malawi) Serenut 4 T (Uganda), Nametil (Mozambique) and Zambia	Early maturity, drought tolerance	Deom et al. (2006), Muitia (2011), Kanyika et al. (2015)
JL 24	Sameké (Mali), Kakoma (Malawi), ICG 7827 (Mozambique), Luena (Zambia), JL24 (Congo), JL 24 (Sierra Leone), JL24 (South Africa)	Early maturity, drought tolerance, high oil content, high yield	Desmae et al. (2015)
ICIAR 19 BT	Samnut24 (Nigeria), ICIAR19BT (Niger)	Early maturity, high yield, high oil content, rosette disease resistance	Desmae et al. (2017)
ICGV-98412	Oboshie (Ghana), Babile-1 (Ethiopia)	High yield, large seeded for confectionery	Amare et al. (2016)
Mwenje and Nyanda	-	Resistant to aphids, Hilda and grain moth	www.seedcogroup.com
ICGV-SM 90704	Serenut 2 (Uganda), Mamane (Mozambique)	High yield, medium maturity, rosette disease resistance	Kanyika et al. (2015)
Harts	-	Tolerant to early and late leaf spot, high yielding	www.opot.co.za
ARC-Oleic2	-	High oleic acid content	www.opot.co.za
ARC-Opal1	-	Resistant to Botrytis stemrot	www.opot.co.za
ARC Sellie Plus	-	Low-oleic acid content, resistance to podworm	www.opot.co.za
Tufa	-	Drought tolerant, intermediate oleic-acid content	www.opot.co.za

Aflatoxin contamination caused by the fungus *Aspergillus flavus and* A. parasiticus is an important biotic factor affecting groundnut product quality and sustainable groundnut production in SSA (Waliyar et al. 1994; Monyo et al. 2012; Guchi 2015; Njoroge et al. 2017). It is also a potential threat to human and animal health globally (Waliyar et al. 2017). Further, aflatoxin contamination affects groundnut trade resulting in financial losses estimated at about US$750 million per annum in SSA (Kamika and Takoy, 2011). Breeding for aflatoxin resistant groundnut genotypes is vital for human health and to enhance world trade (Waliyar et al. 2017). Some genetic resources developed by the International Crops Research Institute for Semi-Arid Tropics (ICRISAT) such as ICGV 87084, ICGV 87094, and ICGV 87110 are reportedly resistant to *A. flavus*. Furthermore, 12 groundnut accessions with resistance to aflatoxin are developed by the Agricultural Research Council in South Africa (Cilliers and Swanevelder 2003). Improved Spanish groundnut cultivars such as ICGV 91278, ICGV 91283, and ICGV 91284 were selected by ICRISAT showing considerable resistance for aflatoxin-producing fungus (Upadhyaya et al., 2001b). Groundnut accessions ICGs 13,603, 1415, 14,630, 3584, 5195, 6703 and 6888 were recommended for production for their low levels of aflatoxin content (<4 µg kg^{-1}) which is far below the regulatory limits for EU (4 µg/kg), most developing countries (10 µg/kg), and the U.S.A. (20 µg/kg) (Magamba et al. 2017). Despite breeding progress, aflatoxin levels remain high in commercial groundnut products due to poor regulatory systems and other resource constraints. Effective post- and pre-harvest groundnut handling and processing are imperative to minimise aflatoxin contamination along the value chains of the crop (Magamba et al. 2017).

Genetic resources for groundnut breeding

Gene banks

Groundnut genetic resources are currently maintained at various gene banks and research institutions and programmes globally (Pandey et al. 2012; Desmae et al. 2017). The largest collection of groundnut accessions (~15,445) is held at ICRISAT gene bank in India (Pandey et al. 2012). Approximately 43% of groundnut collections at ICRISAT consists of landrace varieties, cultivars (7%), breeding lines (31%), and other genetic stocks (19%) (e.g. mutants and experimental germplasm) (Upadhyaya et al. 2002).

In SSA, most of the groundnut germplasm have been obtained from ICRISAT's regional gene banks such as Niamey located in Niger and from the U.S.A. (Okello et al. 2010; Monyo and Varshney 2016). Further, some SSA countries such as Malawi, Mali, Zimbabwe, Uganda and South Africa maintain groundnut genetic resources (Upadhyaya et al. 2001a; Okello et al. 2010) sourced from ICRISAT and U.S.A. In most cases, groundnut genetic resource held in various genebanks are available for research and breeding purposes subject to the signing of material transfer agreement. For example, in South Africa, almost all groundnut genetic resource held by the Agricultural Research Council are available on request (Cilliers and Swanevelder 2003). Groundnut genetic resource held by ICRISAT are also available by interested scientists for scientific studies or breeding purposes (Upadhyaya et al. 2001b). However, it is worth noting that material transfer can sometimes become more stringent especially if the germplasm has patent rights (Okello et al. 2010). Groundnut genetic resources currently held at various gene banks are sources of useful genes for the development of improved varieties with improved quality attributes and resistance to biotic and abiotic stress factors (Upadhyaya et al. 2005, 2014; Sharma et al. 2017a, 2017b).

Synthetics and wild species to tap new alleles for groundnut breeding

The primary gene pool of the cultivated groundnut is very narrow for some important characteristics such as resistance to foliar diseases (e.g. late leaf spot and rust) and insect pests (e.g. thrips) (Kumari et al. 2014; Favero et al. 2015; Michelotto 2017b). Wild species may offer wide variability, particularly for biotic and abiotic stress breeding (Sharma et al. 2017b). Utilisation of wild groundnut germplasm in breeding programmes has been restricted by reproductive barriers between wild and cultivated species. This presented technical difficulties in making large numbers of crosses due to ploidy differences between the two species (Kumari et al. 2014). Successful crosses between wild and cultivated species can be achieved through the development of synthetic groundnut (i.e. doubling of chromosome number of the hybrid which is developed from two diploid wild species) (Sharma et al. 2017b). Several amphidiploid and autotetraploid groundnuts have been developed using A- and B-genome accessions with high levels of resistance to multiple stresses (e.g. late leaf spot, stem rot and collar rot diseases) (Sharma et al. 2017b). Wild species such as *A. batizocoi*, *A. gregoryi*, and *A. magna* can be used as female parents and many A-genome species can be used as male parents to introgress desirable genes into the cultivated groundnut (Favero et al. 2015). Amphidiploid and autotetraploid groundnut have been developed by ICRISAT (Table 2) which serve as useful genetic resource

Table 2. List of synthetic tetraploid groundnuts developed at ICRISAT.

Sr. No.	Code	Origin	Species	Genome	References
1	ISATGR 1212	Synthetic amphidiploid	*A. duranenesis x A. ipaensis*	*AB*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
2	ISATGR 11A	Synthetic autotetraploid	*A. magna x A. valida*	*BB*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
3	ISATGR 5B	Synthetic autotetraploid	*A. magna x A. batizocoi*	*BB*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
4	ISATGR 9A	Synthetic amphidiploid	*A. batizocoi x A. cardenasii*	BA	Shilpa et al. (2013), Mallikarjuna et al. (2011)
5	ISATGR 11A	Synthetic autotetraploid	*A. magna x A. valida*	BB	Shilpa et al. (2013), Mallikarjuna et al. (2011)
6	ISATGR 40A	Synthetic amphidiploid	*A. ipaensis x A. duranensis*	BA	Shilpa et al. (2013), Mallikarjuna et al. (2011)
7	ISATGR 90B	Synthetic autotetraploid	*A. kempff-mercadoi x A. stenosperma*	AA	Shilpa et al. (2013), Mallikarjuna et al. (2011)
8	ISATGR 155	Autotetraploid	*A. diogoi x A. cardenasii*	*AA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
9	ISATGR 168B	Synthetic amphidiploid	*A. valida x A. duranensis*	*BA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
10	ISATGR 278-18	Synthetic amphidiploid	*A. duranensis x A. batizocoi*	*AB*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
11	ISATGR 265-5	Synthetic amphidiploid	*A. kempff-mercadoi x A. hoehnei*	*BA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
12	ISATGR 268-5	Synthetic amphidiploid	*A. batizocoi x A. cardenasii*	*BA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
13	ISATGR 10B	Synthetic autotetraploid	*A. magna x A. valida*	*BB*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
14	ISATGR 35A	Synthetic amphidiploid	*A. batizocoi x A. duranensis*	*BA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
15	ISATGR 206B	Synthetic amphidiploid	*A. duranensis x A. valida*	*AB*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
16	ISATGR 91A	Synthetic autotetraploid	*A. duranensis* × *A. cardenasii*	*AA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
17	ISATGR 154	Synthetic amphidiploid	*A. valida* × *A. duranensis*	*BA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)
18	ISATGR 48B	Synthetic amphidiploid	*A. valida* × *A. duranensis*	*BA*	Shilpa et al. (2013), Mallikarjuna et al. (2011)

to transfer useful genes into the cultivated groundnut (Mallikarjuna et al. 2011; Michelotto et al. 2016). Leaf rust and late leaf spot resistance were successfully introgressed into the cultivated groundnut varieties (e.g. ICGV 91114, ICGS 76, ICGV 91278, JL 24, and DH 86) using two synthetic resistance sources namely: ISATGR 278-18 and ISATGR 5B (Kumari et al. 2014). Resistance to thrips was introgressed into cultivated groundnut cultivars using amphidiploid species such as *A. batizocoi x A. kempff-mercadoi, A. gregoryi x A. stenosperma*, and *A. magna x A. cardenasii* (Michelotto et al. 2017). Introgression of root-rot nematode resistance gene (Rma) into tetraploid groundnut from synthetic allotetraploid donor (TxAG6) has been widely practiced in modern cultivars (Nagy et al. 2010). Chromosome pairing, pollen and pod fertility analysis in hybrids between *A. hypogaea* and *A. amphidiploids* revealed that amphidiploids can be used as a genetic bridge for the transfer of genes from wild species to the cultivated groundnut (Singh 1986). Tetraploid (2n = 4x = 40) peanut (*Arachis hypogaea* L. subsp. *hypogaea* var. *hypogaea*) lines GP-NC WS 16 and GP-NC WS 17 (SPT 06-07) with resistance to multiple diseases including early leaf spot (ELS), *Cylindrocladium* black rot, *Sclerotinia* blight, and tomato spotted wilt were derived from interspecific hybridisation from the diploid (2n = 2x = 20) wild species, *A. cardenasii* (Tallury et al. 2014). In general, the limited level of resistance for economically important traits such as resistance to leaf spot and rust in cultivated groundnut cultivars can be enhanced through the development of synthetic groundnuts. Recombination of cultivated and wild groundnut germplasm will likely improve agronomic, physiological and quality attributes resulting in the development of superior genotypes with resistance to biotic and abiotic stress factors to boost production in SSA.

Landraces and modern groundnut varieties

Landraces are a valuable source of genetic diversity and possess useful traits for breeding (Lopes et al. 2015; Corrado and Rao 2017). Landraces can be introduced in groundnut breeding programmes to incorporate unique genes such as resistance to biotic and abiotic stresses; and quality attributes. Significant genetic variation for quality attributes such as oil, zinc and iron contents exist among groundnut landrace varieties (Asibuo et al. 2008). Bolivian landraces of groundnut revealed larger diversity with respect to seed colour, seed size, seed weight, oleic and linoleic acid contents; and showing moderate to high level of resistance to late leaf spot (Husain and Mallikarjuna 2012). Mexican hirsuta groundnut landraces such as PI576633, PI576634, PI576635, PI576636, PI576637 and PI576638 were also identified to be superior in flavour and quality (Sanchez-Dominguez and Williams 1993). Many other sources of resistance to foliar diseases such as rust and late leaf spot were identified from South American landrace varieties (Singh and Nigam 2016). Several pure lines such as 48-7, 48-14, 48-15A, 48-21, 48-34, 48-35, 48-36, 48-37, 48-44, 48-45 and 48-70A with resistance to groundnut rosette disease were selections from landraces (Singh and Nigam 2016). In pigeon pea and chickpea, landraces or their selections were released directly as cultivated varieties (Asthana et al. 1996; Remanadan 1996). Some cowpea landrace varieties were released for commercial production in India (Sharma 1996). Landrace varieties are rarely used in breeding programmes despite possessing useful attributes. Collection and strategic conservation of groundnut landrace varieties and their exploitation in breeding programmes will aid identification of useful genes/traits for breeding for improved grain yield, quality attributes, biotic and

abiotic stress tolerance. Groundnut landrace varieties may also be useful for genetic mapping studies to unravel genetic control underlying of important traits (Varshney et al. 2013).

Breeding methods of groundnut

Groundnut improvement and cultivar development in SSA mainly depended on conventional breeding including pure line selection, mass selection, pedigree breeding and backcross breeding methods (Okello et al. 2010; Janila et al. 2013). For example, Serenut 5R a high yielding, early maturing, resistant to groundnut rosette disease and late leaf spot was released in Uganda using bulk selection (Table 3). Babile-1 with the accession number ICGV-98412, released in Ghana and Ethiopia, is high yielding, medium maturing and moderately resistant to late leaf spot. It was bred at the International Crop Research Institute for Semi-Arid Tropics, Patancheru, India (Table 3).

Genetic variability available in cultivated and wild *Arachis* have been extensively exploited through conventional breeding to develop improved varieties (Singh and Nigam 2016; Sharma et al. 2017b). Genetic variation for important traits such as plant height, number of primary branches per plant, number of mature and immature pods per plant, kernel yield per plant, hundred seed weight, haulm yield per plant and dry pod yield per plant have been reported in groundnut. This is useful for phenotypic analysis and breeding in this crop (Kushwah et al. 2017; Hampannavar et al. 2018). Further, traits like plant height, pods per plant, 100-pods weight, shelling percentage, harvest index and pod yield per plant have high heritability and considerably higher genetic advance (Nath and Alam 2002; HajHussein et al. 2018). High heritability estimate and genetic advance is an indication that variation is attributable to a high degree of genetic effect and selection can be effective (Johnson et al. 1955).

Knowledge on the degree of association between yield contributing characters and yield is very essential for the development of high yielding genotypes in groundnut. Correlation studies provide an opportunity to study the magnitude and direction of association of yield with its components traits and also among various yield-related components (Faye et al. 2015; Mhlaba et al. 2018). Groundnut pod yield per plant exhibited significant positive correlation with grain yield per plant, number of kernel per plant, hundred kernel weight, number of pods per plant, harvest index and shelling percentage (Kushwah et al. 2017; Zongo et al. 2017a; Hampannavar et al. 2018). This information could help in formulating effective selection criteria in groundnut improvement programme for genetic improvement for grain yield.

In general, groundnut breeding in SSA is mostly dependent on limited selection in segregating generations resulting in low selection efficiencies. Consequently, a limited number of improved groundnut genotypes were developed and deployed. In addition, the conventional breeding requires extended time to develop varieties. It also depends on the screening of a large number of breeding populations under multi-location trials due to the high genotype and environment interaction effect (Ngirazi et al. 2015; Kebede and Getahun 2017). Therefore, the integration of new breeding tools such as molecular markers and marker-assisted selection in groundnut breeding programmes could enhance the precision and speedy development of improved groundnut cultivars.

New and emerging tools for groundnut breeding

High-throughput automated phenotyping techniques

Plant phenotypic data collection with sufficient resolution and accuracy remains a major limiting factor for the effective use of genomic data for crop improvement (Bai et al. 2016). In developing countries where groundnut yield is low, the breeding focus is to improve yield and tolerance to biotic and abiotic stress factors. Selection of groundnut genotypes using pod yield has been slow and yielded highly variable results as yield is affected by genotype by environment interactions (Luis et al. 2016), which causes difficulties in selecting genotypes with wide adaptation resulting in delayed cultivar release.

Crop breeding strategies for higher yield and disease tolerance can be accelerated through the use of high-throughput phenotyping (Shakoor et al. 2017). Instead of using high-throughput phenotyping tools directly in breeding programmes, they may be more useful to enhance the efficiency of genomic tools during the establishment of marker-trait associations, genome-wide associations and training genomic selection models (Janila et al. 2016). Patrick et al. (2017) reported a rapid screening of tomato spot wilt disease resistance among twenty genotypes of groundnuts through the application of high-throughput phenotyping tool. High throughput phenotyping for total oil content in groundnut kernel through the application of near infrared spectrometry (NIRS) system was determined as reproducible, robust, rapid, cost-effective, and non-destructive, and can be used in conjunction with high oleic fatty acid

Table 3. List of improved groundnut varieties with resistance to biotic and abiotic stress tolerance and desirable agronomic attributes reported globally.

Name	Pedigree	Traits	Country	Organisation	Year of release	References
NuMex 01	NM Valencia A x Brantley	High oleic content	U.S.A.	New Mexico Agricultural State University	2013	Puppala and Tallury (2014)
NemaTAM	A.cardenasii Krapov. and W.C. Gregory x A. diogoi Hoehne	Resistant to root-knot nematode	U.S.A.	Texas Agricultural Experiment Station	2002	Simpson et al. (2003)
C724-19-15	C-99R X COAN	Resistant to root-knot nematode and tomato spotted wilt tospovirus	U.S.A.	USDA-ARS and Georgia Agricultural Experiment Station	2008	Holbrook et al. (2008)
Tifguard	C-99R X COAN	Resistant to root-knot nematode and tomato spotted wilt tospovirus	U.S.A.	University of Georgia Coastal Plain Experiment Station	2007	Holbrook et al. (2008)
TifGP-2		Resistant to root-knot nematode and tomato spotted wilt tospovirus	U.S.A.	USDA-ARS and Georgia Agricultural Experiment Station	2010	Holbrook et al. (2012)
ICGV-91114	ICGV 86055 x ICGV 86533	Tolerant to rust and drought	India	ICRISAT	2006	ICRSAT (2012)
"Webb" peanut	PI 667551	High-yielding, high-oleic fatty acid, nematode resistant	U.S.A.	Texas AgriLife Research	2001	Simpson et al. (2013)
TG-37A	TG-25 X variety TG-26	Mutant with semi-dwarfness, compact pod setting, high yield and smooth pod surface	India	Central Sub-Committee on Crop Standards, Release and Notification of Varieties, Ministry of Agriculture	2004	Kale et al. (2004)
Golden	Mutant	Mutant with high yielding and *Cercospora* leaf spot resistant	India	Barani Agricultural Research Institute (BARI)	2002	Naeem-UD-Din et al. (2009)
Binachinabadam-5	M6/250/54-20	Mutant with salinity tolerance		Bangladesh Institute of Nuclear Agriculture	2011	Azad et al. (2014)
Huayu 22		Mutant with high yield, good quality, several diseases resistance, drought tolerant and wide adaptable	China	Shandong Peanut Research Institute	2003	Wu et al. (2006)
Serenut 5R	ICGM 522 X RG 1	High yielding, early maturing, resistant to groundnut rosette disease resistant to late leaf spot	Uganda	National Semi-Arid Resources Research Institute	2010	Okello et al. (2016)
CG-8	ICGV-SM 08501,	–	Malawi	ICRISAT	2014	Setimela et al. (2017)
CG-9	ICGV-SM 08503	–	Malawi	ICRISAT	2014	Setimela et al. (2017)
CG-10	ICGV-SM 01724	–	Malawi	ICRISAT	2014	Setimela et al. (2017)
CG-11	ICGV-SM 01731	–	Malawi	ICRISAT	2014	Setimela et al. (2017)
CG-13	ICGV-SM 99551	Short duration	Malawi	ICRISAT	2014	Setimela et al. (2017)
CG-14	ICGV-SM 99556	–	Malawi	ICRISAT	2014	Setimela et al. (2017)
CG-12	ICGV-SM 01514	–	Malawi	ICRISAT	2014	Setimela et al. (2017)
NARINUT 2015	ICGV-SM 01731	Rosette disease tolerant	Tanzania	ICRISAT	2015	Setimela et al. (2017)
KUCHELE 2015	ICG 8326		Tanzania	ICRISAT	2015	Setimela et al. (2017)
NACHI 2015	ICGV-SM 90704	–	Tanzania	ICRISAT	2015	Setimela et al. (2017)
Serenut 6T	ICGV 93437 × ICGV-SM 93561	High-yielding, early maturing and resistant to groundnut rosette disease	Uganda	National Semi-Arid Resources Research Institute	2010	Okello et al. (2018)
ICGV 91278	JL 24'/UF 71513-1	Aflatoxin resistant	India	ICRISAT	1999	Upadhyaya et al. (2001b)
ICGV 9128	U 4-7-5/JL 24	Aflatoxin resistant	India	ICRISAT	1999	Upadhyaya et al. (2001b)
ICGV 91284	J 11'/ICGV 86184	Aflatoxin resistant	India	ICRISAT	1999	Upadhyaya et al. (2001b)

screening to provide for simultaneous phenotyping of total oil and high oleic acid contents (Sundaram et al. 2010; Awada et al. 2018). Adoption of high-throughput automated technologies is hypothesised to result in faster development of well-adapted and high-performing cultivars (Awada et al. 2018). However, the

application of high-throughput phenotyping techniques in genetic improvement of groundnut and other crops are still very limited. This is probably because automated phenotyping is an emerging breeding approach and has not yet been adopted by plant breeders and crop improvement programmes (Awada et al. 2018).

Genomic tools

Marker-assisted selection

Molecular breeding refers to the technique of using DNA markers that are tightly linked to phenotypic traits to assist in a selection scheme for a particular breeding objective (Jaradat 2016). Molecular markers and genetic linkage maps are pre-requisites for molecular breeding (Varshney et al. 2009). Marker-assisted selection (MAS) refers to the selection of superior genotypes using molecular markers (Kumpatla 2012). Compared with conventional phenotypic selection, MAS is not influenced by environmental conditions because it detects the structural polymorphisms at the molecular level. Further MAS is cheaper and less labour intensive, allows selection in off-season nurseries and has a potential to accelerate the breeding process (Kumpatla 2012).

Due to low levels of molecular polymorphism among cultivated groundnut varieties, MAS in groundnut has not been used extensively compared with other major crops (Burow et al. 2013). Similarly, a low level of variability in cultivated groundnut have been reported using molecular markers (Bhagwat et al. 1997). The cultivated groundnut has been analysed by several marker systems such as Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNA (RAPD), Amplified Fragment Length Polymorphism (AFLP), Single Nucleotide Polymorphism (SNPs) and Simple Sequence Repeat markers (SSR) (Stalker and Mozingo 2001; Zhao et al. 2016). Currently, SSR markers are commonly used in groundnut genetic analysis and breeding due to their co-dominance, simplicity, high polymorphism, repeatability, multi-allelic nature and transferability within the genus *Arachis* (He et al. 2003; Pandey et al. 2012; Wang et al. 2018). Mondal et al. (2012) identified three and four SSR alleles which were found associated with rust and late leaf spot resistance in groundnut, respectively. About 376 highly informative SSR markers linked to resistance to early leaf spot, groundnut rosette disease, and rust and aflatoxin contamination across African cultivated groundnut varieties were identified useful to identify suitable parents for mapping populations or breeding (Kanyika et al. 2015). There is approximately 14 392 publicly available SSR markers in the *A. hypogeae* database (Wang et al. 2018). Recently, about 210 new SSRs were developed for *A. hypogaea* useful for genetic diversity analysis and cultivar development (Wang et al. 2018). In addition, SSR markers have been developed specifically for different *Arachis* species such as *A. duranensis* *A. paensis* and *A. stenosperma* (Zhao et al. 2012).

Table 4 lists some molecular markers developed for groundnut breeding. Four SSR markers (e.g. IPAHM103, GM2079, GM1536 and GM2301) associated with groundnut leaf rust resistance were identified by Varshney et al. (2014). SSR markers pPGPseq-17F6, pPGPseq-2F05, pPGPseq-8E12, pPGPseq-13A10 and pPGPseq-16C6 are reportedly well-associated with rust resistance (Shoba et al. 2012). Zongo et al. (2017b) identified marker GM1911 associated to early leaf spot resistance in groundnut. Further, SSR markers such as pPGPseq-2B10, pPGPseq-2F05, Ppgp13A7, PM 3751_{62}, pPGPseq5D5$_{220}$ and PM384_{100} are also linked to late leaf resistance (Mace et al. 2006; Shoba et al. 2012). SSR markers such as SSR_F149451, Cer14, pPGP-seq2H08, SSR_DX508223 and SSR_FI500754 linked to plant growth habit and SSR markers PM50, SSR GW391728, SSR G0340377 and pPGP_seq2H08 linked seed size have been identified in groundnut. Two transposable element markers namely: TE 360 and TE 498, were found to be linked to rust resistance gene (Mondal et al. 2014). SSR marker GM 1991 is reportedly linked to a drought tolerant QTL in groundnut (Guo et al. 2012). Chu et al. (2007) identified marker S197 as a reliable predictor for nematode resistance.

Other molecular tools such as diversity arrays technology (DArT) are useful in groundnut improvement programmes. Shasidhar et al. (2017) developed two genetic maps based on the DArT and diversity arrays technology sequencing (DArTseq) markers and identified genomic regions linked to groundnut oil content and fatty acids. However, genetic studies revealed low polymorphism and the moderate level of genetic diversity among diploid and tetraploid groundnut genetic pool (Varshney et al. 2010) indicating utilisation of DArT marker system may limit efficient genetic analysis of groundnut genetic resources for cultivar development (Pandey et al. 2012). Development of highly discriminative and informative DArT markers is useful for genetic analysis and breeding in groundnut.

MAS helps to develop ideal groundnut cultivar with inbuilt resistance and improved pod and kernel features (Mothilal 2012). Introgression of nematode resistance through an amphidiploid pathway into cultivated groundnut was successfully implemented using MAS and subsequently nematode resistant groundnut cultivar, NemaTAM was developed (Holbrook et al. 2011).

Table 4. Some molecular marker systems developed for genetic analysis and breeding in groundnut.

		Marker sequence		
Marker name	Marker type	Forward primer	Reverse primer	References
IPAHM103	SSR	GCATTCACCACCATAGTCCA	TCCTCTGACTTTCCTCCATCA	Varshney et al. (2014)
GM1536	SSR	AAAGCCCTGAAAAGAAAGCAG	ATGCATTTGCAGGTTCTGGT	Varshney et al. (2014)
GM2301	SSR	GTAACCACAGCTGGCATGAAC	CTTCAAGAACCCACCAACAC	Varshney et al. (2014)
GM2079	SSR	GGCCAAGGAGAAGAAGAAAGA	GAAGGAGTAGTGGTGCTGCTG	Varshney et al. (2014)
GM1991	SSR	GAAAATGATGCCGAGAAATGT	GGGGAGAGATGCAGAAAGAGA	Guo et al. (2012)
GM 1911	SSR	CAGCTTTCTTTCAATTCATCCA	CACTTCGTGTTCTTCCTGCTC	Guo et al. (2012)
TE 360	TEM	GGATATGATGCCCATAGCTGA	TGCTGACTACTTGCAATGCC	Mondal et al. (2014)
TE 498	TEM	ATGACTTACATGTAGCAATTG	TGAAAGGAGTCAAAGGTCATG	Mondal et al. (2014)
S197	RAPD	CTGTCGAACCATGGAAGAAGATCC	CCAACTTGATGGTAGAAGTATGCTT	Chu et al. (2007)
AHCW0061	SSR	TCATGTGAATTTGTGGACGGT	CCAGGTTTTTGAGGTCCCTGA	Wang et al. (2018)
AHCW0310	SSR	GTTCAAGGGCTGTGCATTGG	GGGTTCGACTCCCGTCTTAT	Wang et al. (2018)
AHCW0545	SSR	ACAGAAGAAGAAACAGCGCG	TTCCGTCATGTGCTTCGGAA	Wang et al. (2018)
AHCW0618	SSR	AAATTTGAGCACGCATCCCC	TGTCTTTTTCCTCGCCTTTGT	Wang et al. (2018)
AHCW0700	SSR	TGGAAGTTTCACGGGACAGG	GTAGCAAGCTTCCCCACCAT	Wang et al. (2018)
AHCW0768	SSR	GGACCCATTTTTGCAAGAGAGA	CGGATTGCAACATTGGCGAA	Wang et al. (2018)
AHCW1250	SSR	ACAGCTGCCTCTTCTCTGTG	CCCACTCAAAATCGGATTTGGA	Wang et al. (2018)
AHCW1510	SSR	TCCTGCACCATGACCATGAA	TGTTCGGCACCAATCTGTCA	Wang et al. (2018)
AHCW1765	SSR	CGCTGGTCTGGCATTTAACG	AAGGGAGGAGGAGTTGGGTT	Wang et al. (2018)
AHCW1862	SSR	TGTTCAGGGATGTGTTTGGACT	GGGCAAGCTCTTTAAACTGCA	Wang et al. (2018)
Cer14	SSR	AGCTGCTTTGACCAGCCGGG	CGCAAGCTTCCTTGTAGATGGTGGT	Mondal et al. (2012)
SSR_DX508223	SSR	GGATTAGGGTTATGAGTTAGGAAACAC	GCTGATGATTGGTTCGGGTAT	Bhad et al. (2016)
SSR_FI500754	SSR	AAGTGGCAGAATCACAGATGG	AGGGTAGAGGTTGGAGAGAAGG	Bhad et al. (2016)
SSR_FI499451	SSR	GTAAGCCACTCTATCACCCCAG	ACAGCCTCACAAATCCAAGAAT	Bhad et al. (2016)
pPGPseq_2H08	SSR	TAAGTGGGGTGGGAGTGGAC	AGCAGTTTGCGTAAGCATTTG	Ferguson et al. (2004)
RGC 24	SSR	TTTGACGGTATGTGCTTTCTTG	TGCCACGACCAAACCAATC	Bhad et al. (2016)
PM 50	SSR	CAATTCATGATAGTATTTTATTGGACA	CTTTCTCCTCCCCAATTTGA	Bhad et al. (2016)
SSR_GW391728	SSR	TCATCATCTGCTAGGGTTATGG	GGTTCCACCTCTTGTCCAGTAT	Mondal et al. (2012)

SSR, simple sequence repeat markers, *TEM*, Transposable element markers, *RAPD*, Random Amplified Polymorphic DNA

Marker-assisted backcrossing (MABC) has been commonly used in groundnut improvement, for instance, high oleic acid content and nematode resistant variety, 'Tifguard' was developed through the application of this technique (Tiwari et al. 2017). Introgression of rust resistance from 'GPBD 4' groundnut cultivar into susceptible varieties ICGV 91114, JL 24 and TAG 24 were employed through MABC which resulted in the development of improved rust resistance groundnut lines (Varshney et al. 2014).

In developing countries including SSA, application of MAS in groundnut improvement is very limited. This is mainly due to the lack of human capital and infrastructure (Janila et al. 2016). However, some successes have been reported. For example, high oleic acid content governing genes, *ahFAD2A* and *ahFAD2B,* were transferred from high-oleic parents (UF-85, Guat and Atete) to low-oleic commercially produced South African cultivars (e.g. Akwa, Kwarts and Harts) through the application of MAS (Mienie and Pretorius 2013). AFPL markers linked to resistance to groundnut rosette disease were successfully identified and mapped in South Africa (Herselman et al. 2004). In Malawi, two groundnut genotypes, RG1 and ICG 1291, were identified as resistant to groundnut rosette disease using SSR markers (Chintu 2013). Selected advanced groundnut lines with different phenotypic attributes were characterised at the molecular level using SSR markers in Ghana (Oteng-Frimpong et al. 2015). Integration of MAS into groundnut breeding programmes in SSA will have greater implication on groundnut improvement in the future.

Marker-assisted backcrossing is routinely applied in breeding programmes for gene introgression (Frisch and Melchinger 2005). MABC aims to transfer one or a few genes/QTLs of interest from agronomically inferior (donor parent) into a superior cultivar or elite breeding line (serving as the recurrent parent) to improve the targeted trait (Jiang, 2013). MABC was used to develop foliar fungal disease resistant lines (Varsheney et al. 2014; Janila et al. 2016) and high oleic lines in Spanish and Virginia bunch types (Janila et al. 2016). However, MABC is not the best approach to develop commercial varieties as compared to MAS which allows improvement of other desirable traits in addition to the target trait selects using markers.

MAS and MABC are not well-suited for analysis of quantitative traits (Sorrells 2015). In such cases, genomic selection is a promising breeding strategy for rapid improvement of quantitative traits. Genomic selection (GS) relies on the development of selection models based on dense genetic markers distributed across the whole genome and phenotyping of a training population for selection of individuals with high genome-estimated breeding values in the breeding population (Resende et al. 2012). GS can therefore provide effective selection using polygenic traits with low heritability (Sun 2014).

In general, MAS has been useful in groundnut breeding. However, in order to develop sufficient genomic

resources for groundnut, MAS has to be widely applied to identify markers linked to other important traits such as drought tolerance and aphid (*Aphis craccivora*) resistance which are becoming a major bottleneck for groundnut production in SSA. Thus, integration of MAS into groundnut breeding programmes in the region will have greater implication on groundnut improvement in the future. In general, molecular markers developed specifically for groundnut provide opportunities to characterise groundnut genetic resources for biotic stress and abiotic stress constraints, agronomic attributes and grain quality traits. This will result in identification and selection of genetically unrelated genotypes possessing key attributes for strategic crossing to develop high-yielding genotypes with key farmer preferred traits and also for industrial purposes (Pandey et al. 2012). Further, to accelerate cultivar development in SSA, access to research funding and technology especially genomic tools will aid mapping of the groundnut genetic pool for accelerated selection and breeding.

Next generation sequencing (NGS)

NGS technologies are highly dependent on massive parallel sequencing, high resolution imaging, and complex algorithms to deconvolute signal data to generate sequence data. NGS technologies offer a wide variety of applications such as whole genome *de novo* and re-sequencing, transcriptome sequencing (RNA-seq), micro-RNA sequencing, amplicon sequencing, targeted sequencing, chromatin immuno precipitated DNA sequencing (ChIP-seq), and methylome sequencing (Kumpatla et al. 2012). Genotyping- by-sequencing and whole-genome resequencing, can lead to the development of molecular markers suited to studies of genetic relationships among breeding materials, genetic mapping of target genes and genome-wide association studies. This can facilitate the selection of individuals with resistant to climatic stress and to pathogens causing substantial losses in agriculture (David and Repkova 2017). NGS technology has been applied for the identification of genes related to resistance to biotic stress in wild groundnut relatives (Brasileiro et al. 2014). For example, quantitative trait loci (QTLs) linked to leaf spot resistance were identified in groundnut through SNP-based next generation sequencing (Liang et al. 2017). Three different viruses from three families of forage groundnut (*A. pintoi*) were identified through the application of NGS (Sanchez et al. 2016). Complete chloroplast genome sequences of seven *Arachis* species were generated using NGS sequencing (Yin et al. 2017). The genetic relationship among groundnut genotypes can also be studied using NGS. In general, inclusion of NGS in groundnut breeding programmes in SSA which currently relies mostly on conventional breeding methods will assist in rapid development of genomic tools for groundnut improvement and cultivar development.

Mutation breeding in groundnut

Groundnut has narrow genetic base because of its monophyletic origin, limited gene flow due to ploidy barrier and self-pollination (Yusuf et al. 2017). Mutation breeding serves as an alternative approach to conventional plant breeding to increase genetic variability and could confer specific improvement without significantly altering phenotype expression (Kulthe and Kothekar 2011). Physical mutagens such as X-ray, gamma rays, β-rays, fast neutrons and chemical mutagens like, ethyl methane sulphonate, ethidium bromide, acryflavine, diethyl methane sulphonate (DES), N- nitroso-N- methyl – urea, Nethyl–N-nitroso-urea, ethylene imine and sodium azide have been successfully used to create genetic variability in groundnut (Kumari 2008; Bhagwan and Akkiraju 2015; Gunasekaran and Pavadai 2015; Habtamu 2016).

About 72 groundnut varieties have been developed through mutation breeding (Janila et al. 2013). Table 3 lists some improved groundnut varieties with resistance to biotic (e.g. leaf spot and aflatoxin) and abiotic stress (e.g. drought and salinity) tolerance and improved quality attributes (e.g. increased seed size, high oleic to linoleic ratio). Several of these varieties were developed using mutation breeding. For example, TG-37A and Golden groundnut mutants were developed and released in India. TG-37A is a semi-dwarf, compact pod setting, high yielding and with smooth pod surface, while variety Golden is high yielding and *Cercospora* leaf spot resistant. Mutants such as Huayu 22 and Fu 22, were released in China. Huayu 22 is high yielding, high quality and resistant to several diseases and with wide adaptation. Mutant variety Fu 22 is known for its tolerance against *A. flavus* (Maluszynski 2001).

Groundnut varieties with high oleic to linoleic acid ratio have become preferred by the groundnut industry due to their increased shelf life and improved health benefits (Chamberlin et al. 2011). Mondal and Badigannavar (2013) reported a groundnut mutant variety with 78% improvement in oleic acid content compared with its parental genotype. Similarly, Nadaf et al. (2009) reported high oleic to linoleic acid ratio in selected groundnut mutants. The first high oleic groundnut variety released in the world was SunOleic 95R, which was derived from a cross between a high oleic breeding line F435 and a component line 'Sunrunner' (Gorbet and Knauft 1997). Further, NuMex 01 is a high oleic acid Valencia groundnut variety developed by the New

Mexico Agricultural State University (Puppala and Tallury 2014).

Significant genetic variability was created for morpho-physiological traits such as pod yield and related traits, and oil content of groundnut through gamma irradiation (Rashid et al. 2012). Similarly, Ahmed and Mohamed (2009) reported a higher number of pods and seed yield per plant in groundnut mutants than their parents. Sui et al. (2015) reported that the use of Pingyangmycin-based *in vitro* mutagenesis in combination with directed screening with Hydroxyproline is effective for development of potential drought-tolerant mutants of groundnut. Induced mutagenesis particularly through combination of gamma rays and sodium azide was successful in developing mutants in groundnut with wide genetic variability (Mondal et al. 2007).

Increased pod yield, a greater number of pods per plant, higher pod filling ability, increased pod size, resistance to foliar diseases and drought tolerance are important farmers' preferred traits of groundnut in SSA (Ntare et al. 2007; Ndjeunga et al. 2010). But due to the narrow genetic base of the crop, foliar diseases (e.g. rust and late leaf spot) cause significant yield losses (Kumari et al. 2014). In SSA, mutation breeding technology has been adopted in groundnut improvement programmes. For instance, groundnut yield has been improved with the aid of mutation breeding in Uganda (Busolo-Bulafu 1991). In Egypt, groundnut mutants achieved higher pod yield, a larger number of pods, higher seed set per plant and improved shelling percentage than their parents (Ahmed and Mohamed 2009). Genetic variations induced by mutation represent a more efficient source of genetic variability than gene pools conserved by nature (Brock 1977). Thus, mutation breeding can be used as an alternative technique to induce genetic variation for desired characters. Further, mutation breeding offers an alternative and novel approach for creating unique phenotypes which can be exploited for breeding. However, some challenges including access to mutation induction facilities limits the use of this technology for groundnut improvement in SSA. The low cost of other mutation breeding technologies such ethyl methane sulphonate mutagenesis (EMS) offers opportunities for groundnut improvement in the region. Approximately 3400 groundnut mutants have been developed using EMS delivering useful genetic variation in groundnut breeding (Knoll et al. 2011).

Rapid generation advancement

Rapid generation advancement (RGA) approach uses single seed descent as the breeding method in a small screen house or glass house space (Collard et al. 2017). Using RGA, many breeding programmes in chickpea successfully take two generations per year i.e. one in the field during the crop season and the other in off-season either in the greenhouse or in an off-season nursery (Gaur et al. 2007). In tomato, it was reported that RGA can produce a maximum of five generations per year compared to a maximum of three generations using conventional breeding methods (Bhattarai et al. 2009). In groundnut, RGA was used in breeding high oleic groundnut varieties in Spanish and Virginia Bunch varieties using controlled environment facilities that facilitated three cycles per year instead of two (ICRISAT 2017). The aim of RGA is to accelerate breeding cycles and breeding progress in many crops (Tanaka et al. 2016). Therefore, the method offers opportunities for rapid generation advancement to develop breeding populations for accelerated cultivar development (Bhattarai et al. 2009). The urgent need to develop superior and improved groundnut varieties for SSA requires accelerated methods such as RGA in cultivar development and release to boost production. The breeding procedure is reportedly cost effective and time saving (Collard et al. 2017) and should provide opportunities to accelerate groundnut breeding in the region.

Shuttle breeding uses diverse ecological environments to develop improved varieties with higher adaptability (Ortiz et al. 2007). Promising genotypes are grown simultaneously across different sites to select high-yielding genotypes (Ortiz et al. 2007). As a result, shuttle breeding can be used to develop drought tolerant, early-maturing groundnut varieties with high-yield, good seed quality, diseases and insect pest resistance and wide adaptability. In wheat (*Triticum aestivum* L.) shuttle breeding has been employed by the International Maize and Wheat Improvement Centre (CIMMYT) to develop wheat genotypes possessing biotic and abiotic stress tolerance, high-yield potential and good end-user quality attributes for cultivation across diverse environments (Crespo-Herrera et al. 2018; Hernández-Espinosa et al. 2018). This is achieved through the introduction of new and novel sources of genetic variation from wild species, landraces, and other sources of useful alleles (i.e. mutants) to develop well-adapted genotypes (Ortiz et al. 2007).

In SSA, groundnut breeding programmes can benefit from shuttle breeding for advancing the generations that can contribute to the enhanced rate of genetic gain especially for yield. Further, the development of efficient shuttle breeding method with RGA could help significantly to reduce groundnut breeding cycles in SSA. Despite these opportunities, limited collaborative research among groundnut breeders in SSA hinder accelerated cultivar development and release. There is a need

for financial support by key groundnut producing countries in SSA for collaborative groundnut improvement that may accelerate breeding of highly-adapted and high-yielding genotypes in the region.

Single seed descent method in groundnut breeding

Genetic gains for key traits can be delayed due to the long breeding generation required in the traditional breeding methods. Some 10–16 breeding generations are required for genetic advancement and to select desirable recombinants resulting from crosses (Saxena et al. 2017). Single Seed Descent (SSD) is most suitable for handling large segregating populations (Wells and Weiser 1989) and for accelerated cultivar development. SSD optimises resources allocation without compromising on genetic variability and genetic advancement. It reduces time for cultivar development and saves cost associated with the advancement of early generations (Teerawat and Charassri 2010). SSD has been successfully used in groundnut breeding programmes, where multiple generations per year have accelerated using the inbreeding process to progress fixed lines to multi-site evaluation trials (Holbrook and Culbreath 2008). In safflower (*Carthamus tinctorius* L.), SSD resulted in development of lines with higher yield and oil content producing compared with parental genotypes (Martinez et al. 1986). In pigeon pea [*Cajanus cajan* (L.) Millsp] development of RGA technology that integrates germination of immature seeds with single seed descent method resulted in about 3–4 generations advanced in 1 year (Saxena et al. 2017). In cowpea (*Vigna unguiculata* L. Walp) SSD allowed a more rapid generation than pedigree selection resulting in the development of superior genotypes (Obisesan 1992). This method could be appropriate for groundnut breeding. There is a need for a standardised and efficient SSD protocol to accelerate cultivar development in SSA.

Genetic engineering and genome editing

Genetic engineering (i.e. recombinant DNA technology, gene modification, and gene therapy) refers to the process of inserting new genetic information into existing cells in order to modify a specific organism for the purpose of changing its characteristics (Nakashima 2018). Genetic engineering techniques such as the use of *Agrobacterium tumefaciens* mediated transformation and DNA-bombardment-mediated transformation are used as powerful tools to accelerate groundnut improvement (Shilpa et al. 2013). The success of genetic transformation depends on a reliable tissue culture regeneration system, gene construct(s), suitable vector (s) for transformation and efficient procedures to introduce desired genes into target plants (Banavath et al. 2018). Groundnut tissues such as leaf sections, cotyledonary nodes, longitudinal cotyledon halves, embryo axes, embryo leaflets, and hypocotyls have been used for genetic transformation (Holbrook et al. 2011).

Genetic engineering of groundnut is one of the potential option for improving abiotic stress tolerance and food safety (i.e. aflatoxin contamination) (Banavath et al. 2018). Resistance to several fungal diseases (late leaf spot and rust), virus diseases (bud necrosis and tomato spotted wilt virus) and insect pests (white grub, gram pod borer) have been achieved through the application of genetic engineering in groundnut (Shilpa et al. 2013). Table 5 summarises some successful groundnut genetic transformation studies.

Genome editing is used to obtain new allelic forms which is targeted gene modification to obtain a generation of new allelic variants in the genomes of cultivated individuals (David and Repkova 2017). Various novel genome editing tools have been developed including zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and clustered regularly interspaced short palindromic repeats/Cas9 (CRISPR/Cas9) (Kamburova et al. 2017). These tools make double-strand breaks (DSB) in DNA followed by repairing employing error-prone non-homologous end joining (NHEJ) or homology directed repair (HDR) mechanism which leads to mutation in specific location in the genome (Mishra and Zhao 2018). In groundnut, a TIR-NBS-LRR candidate gene for nematode resistance was transferred using CRISPR/Cas9 vector (Guimaraes et al. 2015). Groundnut allergy is a life-threatening food allergy. QTLs associated with aflatoxin resistance have been identified in groundnut (Guo et al. 2008). For hypoallergenic groundnuts to be safe for consumption, all genes coding for allergens can be silenced or removed resulting in aflatoxin free groundnuts, and genome editing offers an effective tool (Van de Wiel et al. 2017). Groundnut breeding programmes in SSA could hugely benefit from genetic engineering and genome editing technology to produce non-toxic groundnuts for consumption and increased trade.

In conclusion, groundnut breeding in SSA is mainly dependent on limited phenotypic selection in segregating generations resulting in low selection efficiencies. Consequently, a limited number of improved groundnut genotypes were developed and deployed. To develop climate resilient, improved varieties with resistance to biotic and abiotic stress tolerance and quality attributes there is need to employ advanced techniques in the breeding processes. These include high-throughput

Table 5. Summary of some successful groundnut genetic transformation studies.

Genotype	Explant	Transformation method	Promoter	Transgene	Selectable Marker	References
TMV-2	Embryo part	*Agrobacterium* mediated	*CaMV 35S*	Tobacco Chitinase	*npt-II*	Rohini et al. (2001)
JL-24	Cotyledon	PROK II binary vector	*CaMV 35S*	*IPCVcp*	*npt-II*	Sharma et al. (2000)
K6	IL	*Agrobacterium* mediated	*CaMV 35S*	*TSV-CP*		Mehta et al. (2013)
k-134	DEC	*Agrobacterium* mediated	*CaMV 35S*	*TSV-CP*	*npt-II*	Mehta et al. (2013)
New Mexico Valencia A	Cotyledon	*Agrobacterium* mediated	*CaMV 35S*	*vp1*	*Npt-II*	Qin et al. (2013)
Georgia runner	E AX	Microprojectile bombardment	*ACT-2*	*Mer A*	GUS	Yang et al. (2003)
BARI-2000	Cotyledon	*Agrobacterium* mediated	*CaMV 35S*	*AtNHX1 0029*	*npt-II*	Asif et al. (2011)
J-11	Cotyledon	*Agrobacterium* mediated	*CaMV 35S*	*IPCVcp*	*npt-II*	Sharma et al. (2000)
Florunner	E AX	*Agrobacterium* mediated	*CaMV 35S*	*tswv-np + gus + bar*		Brar et al. (1994)
NC-7	Somatic embryo	*Agrobacterium* mediated	*CaMV 35S*	PStV CP4	*hph*	Partridge-Telenko et al. (2011)

E AX, embryo axes, *DEC*, de-embryonated, *IL*, immature leaf, *CaMV*, Cauliflower Mosaic Virus, *ACT-2*, *Arabidopsis* thaliana.

and automated phenotyping techniques, rapid generation advancement, single seed descent approach, marker assisted selection, genomic selection, genetic engineering and genome editing. Integrating new breeding tools in the groundnut breeding programmes will assist in rapid identification and selection of promising groundnut genotypes possessing useful agronomic attributes to facilitate the development of genetically superior and improved cultivars to boost production in the region. Limited collaborative research and a lack of sustainable funding from groundnut producing countries hindered the progress of groundnut variety release in SSA. Moreover, breeding programmes in SSA need to be well-equipped with both human capital and infrastructure through research collaboration and partnerships with potential institutes working on groundnut improvement.

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