

REVIEW

Potential of genomics for the improvement of underutilized legumes in sub-Saharan Africa

Rajneesh Paliwal  | Taofeek Tope Adegboyega | Michael Abberton |
Ben Faloye | Olaniyi Oyatomi

Genetic Resources Center, International Institute of Tropical Agriculture, Ibadan, Nigeria

Correspondence

Michael Abberton, Genetic Resources Center, International Institute of Tropical Agriculture, Ibadan, Nigeria.

Email: m.abberton@cgiar.org

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Abstract

Underutilized, or orphan legumes, are widely distributed across farming landscapes in sub-Saharan Africa (SSA) but often have low yields and do not fulfill their potential due to very limited research, breeding, development, marketing, and awareness of their benefits. These advantages include nutritional quality and climate resilience. In this review, we focus on Bambara groundnut, African yam bean, and Kersting's groundnut. Knowledge of the challenges and rewards of exploiting them will provide opportunities for concerted approaches to their revival and contribution to future global food systems, especially in the context of climate change. This review identifies the institutional and noninstitutional challenges, the constraints, the prospects, and the rewards that can be derived from exploiting orphan legumes in SSA. The genetic resources center (GRC) of the International Institute of Tropical Agriculture (IITA) conserves a diverse collection of about 2500 accessions of these crops with the majority from Africa. In this review, we focus on the ex situ conservation of the genetic resources of these indigenous African legume crops, their characterization and evaluation, prospects for the development of improved cultivars, and the role they could play, particularly with respect to nutrition and adaptation to climate change. We emphasize progress made in recent years concerning the assembly of information required for application of genomics tools to these crops and how this will underpin the development of improved varieties.

KEYWORDS

breeding, climate change, food and nutrition security, genetic resources

1 | INTRODUCTION

By 2050, Africa is projected to add about half of the world's increase in population (Frayne, Crush, & McLachlan, 2017). At the same time, the production of staple crops is expected to decline due to climate

change (Dinesh et al., 2015). Currently, the highest hidden hunger index (HHI, a combination of zinc, iron, and vitamin A deficiency) is reported in 31 of 36 countries of the SSA region, which contains 91% of the global HHI-affected preschool children (Muthayya et al., 2013). These factors are challenges to the achievement of sustainable development goals (SDGs) of zero hunger (SDG2) and good health and well-being (SDG3; Stuart, 2017). Orphan legumes have the potential

Rajneesh Paliwal and Taofeek Tope Adegboyega authors contributed equally to this work.

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to provide sustainability of the agri-food system in SSA because of their cultural linkage with regional food habits of the communities, nutrient density nature, diversity, and resilience to climate change. Foods of these indigenous legume crops are rich in proteins, minerals, vitamins, and antioxidants. In this review, we focus on the challenges and rewards from exploiting orphan legumes towards addressing malnutrition and hidden hunger through nutritious, economical, climate-resilient, and smart agriculture food systems in SSA. These African domesticated legumes have useful properties but do not have high demand compared to major staple crops of the world due in part to supply limits. However, these legumes have important roles in many developing countries for their nutrition, food security, and the income of smallholder farmers. Unfortunately, these legumes have been largely ignored by crop researchers, industry, and policymakers because of limited economic importance at the commodity level in the global market. These underutilized indigenous legumes are better adapted compared to other major legume crops in poor soils and are tolerant of abiotic stresses including drought. Table 1 describes the general/scientific names, global production area, major countries of cultivation, and important features of selected orphan legumes in SSA.

GRC presently maintains a collection of 6747 accessions of different underutilized legumes. The details of conserved accessions of African yam bean, Bambara groundnut, and Kersting's groundnut are given in Table S1. Substantial numbers of the collections of Bambara groundnut (19%), African yam bean (97.4%), and Kersting's groundnut (100%) were collected from Nigeria. GRC, with partners, is studying morphological and yield related traits and climate adaptive traits in Bambara groundnut and African yam bean. Molecular characterization is also in progress for genetic diversity studies and quantitative trait loci (QTL) discovery for drought and other useful traits including nutrition in these two crops.

2 | AFRICAN YAM BEAN

African yam bean (*Sphenostylis stenocarpa* Hochst Ex A. Rich Harms) is an underutilized indigenous legume of sub-Saharan Africa. It is an

annually prostrate or climbing vine that produces both nutritious seeds and tubers (Figure 1). Okigbo (1973) and Duke (1981) gave a detailed botanical characterization of this crop. It produces linear pods of about 20 to 30 cm length. The nutritional content of its seeds and tubers could help provide more nutritious diets under climate change to the food basket of the smallholder farmers of SSA. It is considered a neglected crop with very limited research attention and no breeding (Anonymous, 2012).

Its seed, tubers, and leaves are nutritionally rich. It is mainly grown West Africa but also in East and Central Africa for its tubers. The fully matured pod houses 20–30 seeds depending on genotype. Seeds of African yam bean are usually brown, cream, and orange brown or mottled and ovoid in shape. African yam bean is interplanted with yams (*Dioscorea spp.*) and some other vegetables in village settings (Ezueh, 1984). The number of days to flowering in African yam bean ranges between 80 and 130 days after planting whereas physiological seed maturity ranges between 150 and 300 days, depending on the genotype. Seed yield varies per location, as an example, from 63 lines evaluated at the International Institute of Tropical Agriculture (IITA), Ibadan, Western Nigeria, the best line yielded 1860 kg per ha whereas at Nsukka, Eastern Nigeria, a seed yield of about 2000 kg per ha has been recorded. The spindle shaped tubers usually occur in small quantities and range from 5 to 7.5 cm length, weighing between 50 and 300 g each (NAS, 1979).

A number of reports have confirmed that the tuberous roots of African yam bean are a good source of carbohydrates in West Africa (Ezueh, 1984; Okigbo, 1973; Potter & Doyle, 1992). The underutilization of African yam bean may be due in part to some production and utilization constraints, such as long duration of cooking, low yields, antinutritional factors, and long maturity period (Nnamani et al., 2017; Ojuederie, Balogun, & Abberton, 2016).

GRC conserved 456 accessions of African yam bean, of which 444 were collected from Nigeria. This collection needs to be expanded to become more comprehensive particularly to include accessions from other African countries, especially Ethiopia, which was the center of origin with broad genetic diversity. GRC has assessed the variation in 127 of 456 African yam bean accessions.

TABLE 1 Specific selected African orphan legumes common in sub-Saharan Africa and their location and important features

General name	Scientific name	Major cultivating countries in SSA	Important features	Reference
African yam bean	<i>Sphenostylis stenocarpa</i> (Hochst. Ex A. Rich Harms)	Origin in Ethiopia, but now widely cultivated in tropical Africa, especially West Africa (Cameroon, Ghana, and Nigeria)	Balanced nutrition, feed for animals, N fixation, and can grow in marginal soils.	(Potter & Doyle, 1992)
Bambara groundnut	<i>Vigna subterranea</i> (L.) Verdc.	Extensively grown in sub-Saharan Africa particularly Niger, Nigeria, Cameroon, Nigeria, Burkina Faso, Mali, Togo and DR Congo. In Southeast Asia (Thailand and Indonesia).	Drought tolerant, nutritious, Africa's estimated marginal yield of 0.3 million tonnes.	(Council, 2006; Faostat, 2017; Hillocks et al., 2012; Mayes et al., 2019)
Kersting's groundnut	<i>Macrotyloma geocarpum</i> (Harms)	Grown in arid and semi-arid regions of West Africa.	A source of high-quality protein for food and feed for the tropics.	(Aremu et al., 2006).



FIGURE 1 African yam bean (a) flowering stage, (b) pod formation stage, (c) pod maturation stage, (d) seed coat color, and (e) tuber. Image source: Genetic Resources Centre, International Institute of Tropical Agriculture, Ibadan, Nigeria

Passport data for these accessions is shown in Table S2. Initial characterization was carried out according to the established crop descriptors at GRC, IITA (Table 2).

3 | BAMBARA GROUNDNUT

The genus *Vigna* consist of 39 species, including important crops such as cowpea (*Vigna unguiculata* L. Walp), Mungbean (*Vigna radiata*), and Bambara groundnut (*Vigna subterranea* L. Verdc; Goel, Riana, & Ogihara, 2002; Vijaykumar, Saini, & Jawali, 2009). Bambara groundnut and cowpea were originated in Africa, whereas mung bean is from Asia (Doi, Kaga, Tomooka, & Vaughan, 2002; Smartt, 1985). These are valuable species, in many developing countries, especially in Africa and Asia, because of their high nutritional value and, of course, nitrogen fixation.

Bambara groundnut is a crop that survives harsh weather. It originated in West Africa and has a growing cycle and harvest time ranging from 4 to 6 months depending on genotype and end use (Figure 2). It is considered to be the third most important legume in sub-Saharan Africa after cowpea and groundnut (Linnemann & Azam-Ali, 1993). Bambara groundnut has low commercial value, but its nutritious green and matured pods are sought after by farmers for household consumption. There is variation between landraces in the growing degree days to maturity and many other physiological traits.

Bambara groundnut seed is regarded as a very well balanced food because of its nutrient composition. Its protein content ranges between 18% to 24% (Mayes et al., 2019), and it is rich in eight of the

nine essential amino acids, including lysine, methionine, isoleucine, leucine, threonine, phenylalanine, and valine, whereas tryptophan is the limiting amino acid (Yao et al., 2015). Carbohydrate content ranges between 51% and 70% (Halimi, Barkla, Mayes, & King, 2019). Moreover, the iron content, potassium, sodium, and calcium content ranged from 4.9 to 48 mg/100 g, 11.44 to 19.35 mg/100 g, 2.9 to 12.0 mg/100 g, and 95.8 to 99 mg/100 g, respectively. All of these values compare favorably to the major food legumes (Amarteifio, Tibe, & Njogu, 2006; Fasoyiro, Ajibade, Omole, Adeniyani, & Farinde, 2006). The crop provides energy ranging from 367 to 414 kcal/100 mg (Boateng, Addo, Okyere, Berchie, and Tetteh (2013). The gross energy value of its seed is higher than any other legume crop (Anchirinah, Bennet-Lartey, & Yiridoe, 2001; Feldman, Ho, Massawe, & Mayes, 2019; Rowland, 1993).

Bambara groundnut has diverse uses in Nigeria. In the eastern part of the country, it is traditionally used in the preparation of various recipes to add relish, roasted and consumed with palm kernel (Adu-Dapaah & Sangwan, 2004) or roasted and chewed with palm kernel. Its young green pods are boiled with salt and pepper and eaten as a snack, whereas dry seeds can be processed to flour and used for the preparation of different forms of food including Okpa and cake (bean porridge; Kaptso, Njintang, Hounhouigan, Scher, & Mbofung, 2007) in the middle belt and eastern part of Nigeria (Okpuzor, Ogbunugafor, Okafor, & Sofidiya, 2010). It is also reported that a blend of Bambara groundnut flour with Ojojo made from water yam (*Dioscorea alata*) increases the food protein content (Alakali, Okache, & Agomuo, 2016).

Bambara groundnut is widely produced in Africa, up to about 0.3 million tonnes annually (Hillocks, Bennett, & Mponda, 2012; Mubaiwa,

S. No	AYB descriptors	S. No	AYB descriptors
1	Days to physiological maturity	31	Seed length/width ratio
2	Internode length	32	Seed length/thickness ratio
3	Leaf number per meter length	33	Seed width/thickness ratio
4	Number of seeds per plant	34	Shelling percentage
5	Seed weigh per plant	35	Seed set percentage
6	Pod dehiscence	36	Leave color
7	Seed cavity ridges on pods	37	Hypocotyl pigmentation
8	Pod length	38	Pigmentation of the stem
9	Pod beak length	39	Pigmentation of the branches
10	Pod weight	40	Pigmentation of the petiole
11	Locules per pod	41	Pigmentation of the peduncle
12	Pods per peduncle	42	Pigmentation intensity of the stem
13	Pods per plant	43	Pigmentation intensity of the branches
14	Splitting of testa	44	Pigmentation intensity of the petiole
15	Seed shapes	45	Pigmentation intensity of the peduncle
16	Testa basal color	46	Days to peduncle initiation
17	Testa color variegation	47	Days to 50% flowering
18	Basal color of variegated seeds	48	Peduncle length
19	Pattern of testa variegation	49	Petiole length
20	Testa texture	50	Terminal leaf length
21	Brilliance of seeds	51	Terminal leaf width
22	Eye color of white seeds	52	Tuber production
23	Eye color pattern	53	Shapes of tubers
24	Seed weight per pod	54	Tuber skin color
25	Seeds per pod	55	Tuber yield
26	100 seed weight	56	Tuber weight
27	Seed volume	57	Tubers per plant
28	Seed thickness	58	Tuber length
29	Seed width	59	Tuber width
30	Seed length	60	Length/width ratio of tubers

TABLE 2 List of the descriptors established at GRC, IITA used for the African yam bean characterization

Fogliano, Chidewe, Bakker, & Linnemann, 2018). Nigeria is the largest producer of Bambara groundnut in Africa with an average of 0.1 million tonnes. Bambara groundnut yield ($t\ ha^{-1}$) in Africa varies between land races and locations ($0.5\text{--}3\ t\ ha^{-1}$) with yield potential of above $3\ t\ ha^{-1}$ (Massawe, Roberts, Azam-Ali, & Davey, 2003). The crop has an average yield of $0.85\ t\ ha^{-1}$, which is comparable to some other legume (Begemann, 1988). It is a source of protein and fiber and nutritionally complements cereal crops (Massawe, Mwale, Azam-Ali, & Roberts, 2005). Adu-Dapaah, Berchie, Amoah, Addo, and Akuamoah-Boateng (2016) reported that Bambara groundnut milk has 15%–16% more protein than soymilk. In recent years, interest has begun to increase in Bambara cultivation and consumption, possibly due to its potential as a food crop that thrives in dry areas, although Bambara still lacks adequate seed systems and best agronomic practices (Mubaiwa et al., 2018). The effort required to prepare Bambara groundnut seeds for meals in many countries is increased by the long cooking time required, which translates into increased cost of cooking

fuel. Consequently, this is one of the major bottlenecks identified for the consumption of Bambara groundnut (Adzawla et al., 2016). The “hard-to-cook” phenomenon can also be influenced by seed storage conditions, particularly heat and humidity. Several other theories have been put forward to explain components of this storage trait (Mubaiwa, Fogliano, Chidewe, & Linnemann, 2017). Many of these constraints can be ameliorated by increased attention to developing improved varieties and implementing best crop management practices.

All of the drought tolerance mechanisms are exhibited by Bambara groundnut: escape, avoidance, and tolerance (Collinson, Azam-Ali, Chavula, & Hodson, 1995; Collinson, Clawson, Azam-Ali, & Black, 1997; Halimi et al., 2019; Jorgensen et al., 2010). Bambara groundnut has the ability to tolerate drought and provide reasonable yields (Adzawla, Donkoh, Nyarko, O'Reilly, & Mayes, 2016; Olayide et al., 2018), which make it an ideal crop to grow in a wide range of environmental conditions.



FIGURE 2 Bambara groundnut (a) field plants, (b) nut formation, and (c) seed coat color. Image source: Genetic Resources Centre, International Institute of Tropical Agriculture, Ibadan, Nigeria

Morphological traits and various molecular markers have been used to assess the genetic diversity of Bambara groundnut, but reports have been on limited numbers of genotypes (Aliyu & Massawe, 2013; Ho et al., 2017; Olukolu et al., 2012; Massawe, Dickinson, Roberts, & Azam-Ali, 2003; Massawe, Roberts, et al., 2003). GRC conserves a total of 1913 accessions, which is the largest collection of Bambara groundnut in the world. International Plant Genetic Resources Institute (IPGRI) Bambara groundnut descriptors have been used to characterize all of the accessions. Recently, in late 2019, exploration of Bambara groundnut was carried out in Cameroon to collect Bambara groundnut landraces to fill some gaps in the GRC collection. Bambara groundnut is reported to have its center of diversity from plateau state and Yola in Nigeria to Garoua in Cameroon (Goli & E., 1997; Olukolu et al. (2012), which justifies the choice of country of this exploration. Various prebreeding activities have begun on this crop in GRC. Field research is being carried out on the genetic diversity associated with yield, nitrogen fixation, seed longevity, drought tolerance, cooking time (Mubaiwa et al., 2017), and cross compatibility within and across landraces.

GRC has embarked on a large-scale screening and evaluation of hundreds of Bambara groundnut accessions for yield in the northern part of Nigeria. Assessment of genetic diversity of Bambara groundnut with the aid of molecular tools and field assessment is an on-going joint project on between GRC and Crops For the Future Research Centre (CFFRC) for the development of drought tolerant lines. This project is being supported by the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA).

4 | KERSTING'S GROUNDNUT

Kersting's groundnut (*Macrotyloma geocarpum* [Harms] Marechal and Baudet) belongs to the Fabaceae family of the Phaseoleae tribe (Amuti, 1980), and it is grown as an annual herbaceous and geocarpic legume crop (Figure 3). It is also known as Hausa groundnut or ground bean. It is predominantly cultivated in the arid and semi-arid regions of West Africa (Aremu, Olaofe, & Akintayo, 2006). Kersting's groundnut has a very high adaptation to dry areas as it can thrive with rainfall as low as 500–600 mm, well distributed over 4–5 months (Mergeai, 1993). Dako and Vodouhe (2006) reported that Kersting's groundnut originated from either Northern Togo or central Benin. Cultivation spans countries in West Africa including Burkina Faso, Nigeria, Ghana, Mali, Togo, and Benin. The crop is also cultivated outside West Africa in Tanzania, Mauritius, and Fiji (Dako & Vodouhe, 2006). The morphological diversity of the seed is reflected in seed color variation (Pasquet, Mergeai, & Baudoin, 2002). Kersting's groundnut cultivation is being carried out on a small scale for home consumption by few farmers despite its potential importance as a protein source, with better adaptation to local climatic conditions and lower production costs than cowpea. Despite the minimal cultivation of Kersting's groundnut, there is a long history of cultivation by local farmers (Mergeai, 1993), but information about its agronomic and genetic potential is very scarce (Chivenge, Mabhaudhi, Modi, & Mafongoya, 2015; Padulosi, Hoeschle-Zeledon, & Bordoni, 2007; Will, 2008). The West African savanna zone, Tchad, and Cameroon



FIGURE 3 Kersting's groundnut (a) field plant and (b) seed coat color. Image source: Genetic Resources Centre, International Institute of Tropical Agriculture, Ibadan, Nigeria

are reported as a cultivation belt of Kersting's groundnut (Mergeai, 1993). There are no available statistics on the global harvested area, yield, and production of the crop.

The major factors affecting cultivation of underutilized crops in general also have a negative impact on Kersting's groundnut, including low seed yield, small grain size, labor-intensive cultivation and harvesting, low market value, and lack of improved cultivars. There has been a reduction in cultivation of this crop in many growing areas (Amujoyegbe, Obisesan, Ajayi, & Aderanti, 2010; Tamini, 1995). Gradual extinction of this crop from production systems was observed in Ghana (Bampuori, 2007), Togo (Mergeai, 1993), Burkina Faso (Tamini, 1995), and more recently Nigeria (Amujoyegbe et al., 2010) and Benin (Assogba et al., 2015). It is becoming necessary to consider defining and including the current status of this legume species in the International Union for Conservation of Nature (IUCN) red list. The traditional utilization of this food crop and its inclusion in various ceremonies by some ethnic groups could be an advantage that will help its conservation and prevent its total neglect in such areas.

A total of 22 accessions of Kersting's groundnut were collected from Nigeria and conserved at GRC. It shows a geographical diversity gap and need to collect additional material from other African countries including Northern Togo or Central Benin to provide adequate representation of the geographical distribution of genetic diversity and to prevent genetic erosion.

5 | CHALLENGES OF EXPLOITING ORPHAN LEGUMES FOR SSA

Up to now, around 240 whole plant genomes have been sequenced with varying quality (Chen et al., 2018). Single genome sequencing is not adequate to capture complete genetic diversity within a species constrains exploration of genetic variation for crop improvement (Tao, Zhao, Mace, Henry, & Jordan, 2019). Resequencing of genome of several accessions have recently been sequenced in rice (3000 rice genome; Li, Wang, & Zeigler, 2014), chickpea (3000 chickpea genome sequencing initiative; Varshney, 2016), pigeonpea (Varshney et al., 2017), and maize (Tao et al., 2019). This resequencing of genomes facilitates opportunities to identify structural variation and genetic dissection for critical agronomical traits (Yang et al., 2019).

Resequencing of genomes of multiple accessions would help develop the high-quality pangenome of the crops, which refers to the union of genome sequence from representative individuals in a biological clade (Tao et al., 2019). Orphan legumes in general have attracted some research interest in breeding and application of molecular tools. International research collaborations have been developed, and significant progress has been made by partners including the International Institute of Tropical Agriculture (IITA), International Crops Research Institute for Semi-Arid Tropics (ICRISAT), and the African Orphan Crops Consortium (AOCC) in providing platforms for crop improvement programs. A few of the legume crops (chickpea, groundnut, pigeon pea, and cowpea) were considered as orphan crops in the last century and have now entered in the advanced era of breeding through the utilization of molecular breeding tools together with their genome sequencing information, for example, chickpea (Li et al., 2018; Varshney et al., 2012 & Varshney et al., 2013), groundnut (Bertioli et al., 2016; Janila et al., 2016; Varshney, 2016), pigeon pea (Varshney et al., 2017), and cowpea (Boukar et al., 2019; Huynh et al., 2018; Lonardi et al., 2019). In the context of orphan legumes, it is essential to use genome sequencing information, molecular breeding tools, and precise phenotyping of a large number of germplasm of orphan crops. It will speedup trait mapping in orphan crops to mine essential agronomical genes and incorporate important genes to develop improved lines for harsh and extreme climate conditions.

In many parts of SSA, climate change has led to severe consequences with respect to food security and income generation for smallholder farmers with little or no mitigation measures (Edgerton, 2009; Fisheries, 2014). In general, SSA is considered to be vulnerable without a strong capacity to manage the impacts of extreme weather conditions (Chauvin, Mulangu, & Porto, 2012; Edgerton, 2009).

According to Wezel et al. (2009), the impacts of climate change will include effects on water supplies to agricultural farms. Currently, the available water resources are not sufficient to boost food and income security for smallholder farmers. The use of orphan legumes as drought-tolerant crops is being advocated as one part of adaptation measures (Altieri, Funes-Monzote, & Petersen, 2012; Mabhaudhi, Chibarabada, & Modi, 2016; Rosegrant et al., 2014).

Dawson et al. (2018) evaluated the significance of developing research investment programs for orphan legumes. The authors made

suggestions including the use of genomic tools in crop improvement. Modern breeding programs with the latest tools that are different from traditional or conventional breeding techniques could go a long way in developing the desired traits (Hickey, Chiurugwi, Mackay, & Powell, 2017). The African Plant Breeding Academy of the University of California (http://pba.ucdavis.edu/PBA_in_Africa/; with activities in SSA) and other partners, including IITA, ICRISAT, Kirkhouse Trust are supporting efforts at developing breeding and training programs for orphan legumes and African scientists.

6 | GENOMICS OF UNDERUTILIZED CROPS

Conventional breeding and biotechnology and their application have resulted in numerous critical advances in crop molecular biology, crop genetics, and breeding to increase food production. The past decade, in particular, has seen revolutionary advances in the application of next-generation sequencing from SNP marker discovery to the whole genome-sequencing that is likely to deliver breakthroughs for crop research, especially for underutilized crops. Molecular markers give precise and reproducible information about genetic variation in the whole genome at the DNA level. Such studies in major crops have had a significant impact on crop improvement and description of genetic diversity. However, limited efforts have been made regarding the genomics and breeding of underutilized crops. Because of limited awareness concerning the potential of underutilized crops, limited research funds from governmental and international agencies have been invested and these crops have been largely overlooked (Heller, Begemann, & Mushonga, 1997; Massawe et al., 2005; Oyeyinka, Singh, Adebola, Gerrano, & Amonsou, 2015; Will, 2008; Williams & Haq, 2002). However, the high nutritional value and, tolerance of abiotic stresses and potential role under climate change make support for these crops important in the future (Jaenicke & Höschele-Zeledon, 2006; Massawe, Mayes, & Cheng, 2016; Will, 2008). Detailed information on genetic diversity and relationships among germplasm accessions is an important prerequisite for crop improvement. However, detailed information of the genetic relationships between landraces of these underutilized crops is not well developed. This limits the possibility of utilizing conserved germplasm by researchers, breeders, and farmers. The underutilized crops widely exist as landraces, but few cultivars have been developed using breeding efforts (Basu, Roberts, Azam-Ali, & Mayes, 2007; Massawe, Dickinson, Roberts, & Azam-Ali, 2002; Massawe, Mwale, Azam-Ali, & Roberts, 2007).

Modern sequencing technologies have the potential to be used effectively in genetic improvement of underutilized crops including (1) exploring genetic diversity and genetic relationships within and between landraces; (2) developing core collections or trait based subsets; (3) discovering genes for important traits using marker-trait association; (4) supporting marker-assisted selection (MAS); (5) enabling genomic selection (GS) for prediction of breeding values; (6) facilitating global exchange of molecular information, sequence data, and DNA of

accessions; and (7) identifying gaps in current underutilized crop collections and guiding new exploration missions and exchange of germplasm. A further long-term goal is carrying out transcriptomic, proteomics, and metabolomic analyses to elucidate the molecular mechanism of complex traits including stress tolerance, yield, flowering, crop maturity, and nutritional value. In the future, precise genetic information of underutilized crops will encourage and attract the attention of crop researchers.

Genetic diversity in underutilized crops has been evaluated using different types of molecular markers, for example, isozymes (Howell, 1990; Pasquet, Schwedes, & Gepts, 1999), random amplified polymorphism DNA (RAPD; Amadou, Bebeli, & Kaltsikes, 2001; Massawe, Roberts, et al., 2003; Moyib, Gbadegesin, Aina, & Odunola, 2008; Rungnoi, Suwanprasert, Somta, & Srinives, 2012), amplified fragment length polymorphism (AFLP) (Massawe et al., 2002; Ntundu, Bach, Christiansen, & Andersen, 2004), simple sequence repeats (SSR; Adewale et al., 2015; Aliyu & Massawe, 2013; Basu, Roberts, Azam-Ali, & Mays, 2007; Mohammed, Sanjay, Elias, Sowley, & Felix, 2018; Shitta, Abberton, Adesoye, & Adewale, 2015; Somta, Chankaew, Rungnoi, & Srinives, 2011) and intersimple sequence repeats (ISSR; Nnamani et al., 2019; Rungnoi et al., 2012), DArT markers (Ho et al., 2017; Olukolu et al., 2012), and single nucleotide polymorphism (SNP; Ho et al., 2017; Paliwal, Oyatomi, Faloye, & Abberton, 2019) have been developed more recently. Out of all these kinds of markers, SSRs and SNPs are the most popular due to their abundance in the genome, reproducibility, and the codominant nature of polymorphisms (Collard, Jahufer, Brouwer, & Pang, 2005). Because of recent advances in technology, reduced representation sequencing has become more common as a means of genotyping. A popular type of this is referred to as genotype-by-sequencing (GBS; Poland & Rife, 2012; Torkamaneh, Laroche, & Belzile, 2016). This provides a large number of genome-wide SNP markers from multiplexed samples. Single locus markers like SNPs have an advantage over multilocus markers (Comadran et al., 2009; Jin et al., 2010; Stich et al., 2005) because they can be assigned to a particular genomic position, avoiding difficulties arising from paralogous genes, or homeologs in the case of polyploids (Chen, Nelson, Ghamkhar, Fu, & Cowling, 2008; Li et al., 2013). Genome-wide GBS-SNP and silicoDArT markers (score as presence and absence; <https://www.diversityarrays.com/technology-and-resources/dartseq/dartseq-data-types/>) genotyping have been initiated in Bambara groundnut, African yam bean, and Kersting's groundnut in GRC, using high depth DArTseq GBS (<https://www.diversityarrays.com/>). All three of these underutilized crops in this study are diploid (<http://africanorphan crops.org/meet-the-crops/>) which simplifies the genotyping.

Draft genome sequencing of underutilized crops has been initiated by the African Orphan Crops Consortium (AOCC; <http://www.africanorphan crops.org>) for sequencing, assembling, and annotating the genomes of 101 orphan crops including Bambara groundnut and Kersting's groundnut (Prasad et al., 2019). The draft-genome sequencing of the Bambara groundnut has been completed (Chang et al., 2018a, 2018b). Kersting's groundnut is in the pipeline and yet

to be begun by AOCC, whereas the Alliance for Accelerated Crop Improvement in Africa (ACACIA, 2019) is currently carrying out whole genome sequencing of African yam bean.

Resequencing of underutilized crops is also in progress (Prasad et al., 2019). The Bambara groundnut genome was sequenced using high-density Illumina short-read data, which means that complete pseudochromosomes are not yet available. There are also plans to sequence the Bambara groundnut genome using long-read sequence data (Gregory et al., 2019). The total genome size of Bambara groundnut is 550 Mb as compared to 640.6 Mb of the cowpea genome (Lonardi et al., 2019). The number of protein-coding genes identified was 31,707, which is higher than mung bean (22,427) and lower than adzuki bean (34,183; Chang et al., 2018b). In total, 98.0% of the Bambara groundnut genome was functionally annotated (Chang et al., 2018a). A total of 605 gene families were identified in Bambara groundnut and its paralogs linked mainly with glyoxylate and dicarboxylate metabolism, zeathin biosynthesis, and carbon fixation (Chang et al., 2018a, 2018b). Gene ontology (GO) analysis revealed that the paralogous genes of Bambara groundnut were enriched in ion binding (Chang et al., 2018a).

Complete sequencing of the plastid genome has also been reported (Liao, Yang, & Huan, 2019). It has a typical quadripartite structure with two inverted repeats (IRs) and both large and small types of single-copy regions. The size of the plastid genome was reported to be 152,015 bp, with two IRs (26,259 bp), a large single-copy (82,157 bp; LSC) and a small single-copy (17,540 bp; SSC) region. The plastid genome encodes 71 protein-coding genes, 33 tRNA and 4 rRNA genes in Bambara groundnut. There were 12 genes (*trnM-CAU*, *trnN-GUU*, *trnV-GAC*, *trnL-CAA*, *trnA-UGC*, *trnR-AGC*, *rps7*, *rps12*, *rps19*, *rpl2*, *rpl23*, *ycf2*, and *ndhB*) that were duplicated in inverted repeat regions (Liao et al., 2019).

Molecular markers including SNPs are in use for genetic diversity analysis in underutilized crops (Aliyu & Massawe, 2013; Ho et al., 2017; Olukolu et al., 2012; Paliwal et al., 2019; Pasquet et al., 1999 & 2002; Massawe, Dickinson, et al., 2003; Massawe, Roberts, et al., 2003; Ntundu et al., 2004; Rungnoi et al., 2012; Somta et al., 2011). A total of 240 landraces of Bambara groundnut from different geographical regions (including South-East Asia, East Africa, Central Africa, West Africa, Cameroon/Nigeria) were analyzed with 22 SSR markers (Somta et al., 2011). Somta et al. (2011) reported that West African accessions clustered together with Cameroon accessions but were separately grouped from East African, Central African, and Southeast Asian accessions. They also found higher allelic and gene diversity in West African and Cameroon/Nigeria accessions as compared to East African and other groups. Population structure analysis showed two major subpopulations, one in West and Central Africa and one in South-East Africa, using both SSR markers (Molosiwa, Aliyu, & Stadler, 2015; Somta et al., 2011) and DArT markers (Stadler, 2009). The population structure results of these studies suggested two separate diverse gene pools of Bambara groundnut. A diversity analysis of Bambara groundnut accessions from different African geographical groups (East Africa, West Africa, Central Africa and South Africa) was carried out at GRC, using SNP

markers. The diversity grouped in seven different clusters in which the majority of lines were grouped according to their geographical regions (Paliwal et al., 2019). Three distinct population groups from West Africa, Central Africa, and East Africa were found using principal component analysis (Paliwal et al., 2019). The majority of wild relatives were grouped with West African accessions (Paliwal et al., 2019), confirming that it is an indigenous West African crop. A genetic relationship study was carried out for 56 Indonesian Bambara Groundnut with 114 diverse accessions from Africa to investigate their origin with SSR and SNP markers by Redjeki et al. (2020). They suggested East Java Bambara groundnut lines could be introduced from West Java materials. The current Indonesian accessions, most probably introduced from South Africa, showed a small fraction of the genetic variability within the species (Redjeki et al., 2020). The narrow genetic base of Indonesian lines could be extended by introducing lines from other geographical regions like West Africa and East Africa. They reported three major distinct subpopulations, which coincided with their geographical regions (Central and Western Africa, Southern and Eastern Africa, and Indonesian collection). The genetic diversity study of Bambara groundnut indicates geographical-specific selection and founder effect, which could play a significant role in influencing its genetic diversity (Redjeki et al., 2020). The extensive degrees of allelic diversity of different geographical population could be potentially used for developing improved cultivars. With this available diverse regional genetic collection from across Africa, and its wild relatives, GRC has an excellent resource for future crop improvement.

Different types of molecular markers, namely, RAPD (Moyib et al., 2008), AFLP (Adewale et al., 2015; Ojuederie, Morufat, Iyiola, David, & Mercy, 2014), SSR (Shitta et al., 2015), and ISSR (Nnamani et al., 2019) have been utilized in African yam bean crop research. Shitta et al. (2015) reported cross-species transferability using SSR markers, where cowpea's SSR markers showed PCR amplification and polymorphism in an African yam bean collection. The cross transferability of markers among different species is useful for species that do not have sequence information or other markers, especially in underutilized crops where limited molecular resources available. Genetic diversity of 77 and 67 different accessions was analyzed using AFLP (Adewale et al., 2015) and SSR (Shitta et al., 2015) markers. The accessions used in these studies were grouped in three to four clusters in both genetic diversity (Adewale et al., 2015; Nnamani et al., 2019; Shitta et al., 2015) and population structure (Ojuederie et al., 2014; Nnamani et al., 2019; Ojuederie et al., 2014). These studies showed wide variation is available in the African yam bean collection and can be useful for future breeding research. A genetic diversity study of over 250 accessions of African yam bean was carried out using DArTseq SNP markers (Paliwal et al., 2019) at GRC, IITA. The proportion of heterozygosity was higher in the less grown landraces than in the most popular ones (Paliwal et al., 2019). All accessions were grouped into six different clusters (Paliwal et al., 2019) which revealed the existing genetic diversity of the collection and can be use by breeders to select diverse lines.

Genetic diversity research on Kersting's groundnut has been reported with isozyme markers that were used for the characterization

of eighteen domesticated and two wild accessions from Togo and Burkina Faso by Pasquet et al. (2002). They found a narrow genetic base, which is not a favorable sign to increase genetic gain in breeding programs (Spillane & Gepts, 2001). The transferability of 12 SSR markers of cowpea to Kersting's groundnut was reported, with nine SSR monomorphic (Mohammed et al., 2018), but the aligned sequence of three nonamplified SSR indicated the availability of genetic variation among the landraces, with single nucleotide polymorphisms found at different positions. The successful cross-species transferability between cowpea and Kersting's groundnut is consistent with a close evolutionary relationship. A population of 281 Kersting's groundnut accessions from Benin was genotyped with 493 SNPs using the DArTseqTM method (Akohe, Achigan-Dako, Sneller, van Deynze, & Sibiyi, 2020). A total of 10.6% of these SNPs were aligned on the reference genomes of adzuki bean and mung bean, indicating an evolutionary relationship of Kersting's groundnut with adzuki bean and mung bean (Akohe et al., 2020). The population of Kersting's groundnut was grouped into four distinct clusters based on seed coat color (white-seed, red-seed, black-seed, and white with black eye seed color) using the unrooted neighbor-joining tree method. In contrast, it was grouped only into two populations ($K = 2$) in admixture-model based clustering method (Akohe et al., 2020). The expected heterozygosity (H_e) ranged from 0.01 to 0.09 within the clusters, indicating narrow genetic diversity between within clusters (Akohe et al., 2020). DArTseq GBS-SNP genotyping has also been initiated for Kersting's groundnut at GRC and will be used for genetic diversity and population structure analysis. With these results, parental lines can be selected for crossing to develop transgressive segregation lines for desired traits and for the development of linkage maps and QTL discovery.

Genetic linkage mapping and QTL discovery for important traits are valuable for any genomic assisted breeding program (Collard et al., 2005). Biparental mapping populations have been used for linkage mapping, which is a classical method for discovery of QTL discovery (Collard & Mackill, 2008). Many QTL discovery studies on different traits using this method have been reported, including on legumes (Emebiri et al., 2017; Hong et al., 2010; Saxena et al., 2012). However, little research has been carried out for linkage mapping and QTL discovery in underutilized crops. No linkage maps or other QTL discovery research has become available in African yam bean or Kersting's groundnut, and in Bambara groundnut development of linkage mapping and QTL discovery research was only recently initiated (Ahmad et al., 2016; Ho et al., 2017). In the first report, Ahmad et al. (2016) reported linkage mapping of Bambara groundnut with a small mapping population of 73 F3 lines using a 238 marker DArT array and SSR markers. This linkage map consisted of 21 linkage groups (LGs), with a total genetic distance of 608.3 cm. Another integrated linkage map of two mapping populations was reported in by Ho et al. (2017). This genetic linkage map of IITA686 × Ankpa4 population generated 11 LGs of total genetic length 1995.2 cm from 223 markers (DArTseq and DArT markers) using 263 F2 lines. Another linkage map of TD population (Toga Nicuru × DipC) of 71 F3 lines generated 11 LGs with 293 markers and covered 1376.7 cm genetic distance (Ho et al., 2017). Both linkage maps showed synteny with

common bean, adzuki bean, and mung bean (Ho et al., 2017). A total of 36 QTL have been discovered in Bambara groundnut for different traits, including internal node, days to emergence, growth habit, seed weight, pod length, and width (Ahmad et al., 2016). The phenotypic variation of these 36 QTLs ranged from 11.6% to 49.9% (Ahmad et al., 2016). There were only two stable QTL discovered for growth habit (Ahmad et al., 2016) and internode length (Ahmad et al., 2016; Ho et al., 2017). The development of biparental mapping populations of Bambara groundnut, African yam bean, and Kersting's groundnut is in progress for QTL discovery of different traits in GRC. However, the lack of ability to easily cross between Bambara groundnut genotypes remains a constraint to both breeding and linkage mapping.

With the advancement in NGS and computational technology, genome-wide association studies (GWAS) have been utilized as a robust tool for QTL discovery in different crops (Buckler et al., 2009; Schlappi et al., 2017; Yan, Warburton, & Crouch, 2011; Zhou et al., 2015). GWAS can access marker-trait association for QTL discovery in thousands of genotypes using millions of genome-wide SNP markers that provide high genetic resolution in the kilobase range. The accessibility of large SNP marker datasets of reference or non-reference genome crops has opened another way for QTL discovery using natural populations with the GWAS approach. Biparental mapping needs time and considerable expense. High-density SNP data have been generated in underutilized crops populations in GRC, and its use for GWAS is in progress. By combining phenotypic and high-density genotypic data, GWAS can overcome several of the limitations of linkage mapping and provide a powerful complementary strategy to discover QTL for complex traits (Schlappi et al., 2017; Yan et al., 2011). In Kersting's groundnut, a GWAS study reported a significant marker-trait association of 10 SNP markers with six different agronomical traits (grain yield/plant, 100 seed weight, days to 50% flowering, days to maturity, number of seeds/plant, and number of pods/plant). The marker M1 was significantly associated in two locations with 100 seed weight and contributed to over 24% of the phenotypic variation (Akohe et al., 2020). Identification of QTL for phenotypic traits of underutilized crops can play an important role in increasing the speed and efficiency of developing improved climate-resilient cultivars of underutilized crops using MAS. A population of 420 accessions of Bambara groundnut was developed from indigenous farmers, breeder seed, and genebanks by crop for future (CFF) and is being characterized for both phenotypically and genotypically to use for GWAS analysis of important agronomical traits (Muhammad et al., 2020). Bambara groundnut and African yam bean at GRC have been characterized and evaluated for morphophysiological traits, yield, nitrogen fixation, the nutritional quality of tuber and seed, and drought tolerance. GWAS of these traits in Bambara groundnut and African yam bean are in progress.

Knowledge of genetic changes that occurred during both biotic and abiotic stresses in underutilized crops at the RNA level is limited. With the advancement of NGS, transcriptome analysis using RNA-sequencing can characterize genes for complex traits, including differentially expressed genes (Wang, Gerstein, & Snyder, 2009). For functional genomics studies, gene expression analysis under specific

stress conditions can be used, especially in underutilized crops, with limited information available for the genomes (Afzal et al., 2020). SSR markers developed from expressed sequence tags (EST) known as genic SSR markers are not as abundant and as polymorphic as genomic SSR. Genic SSRs are highly conserved, which provides a high degree of transferability across related species (Mathi Thumilan et al., 2016; Xiao et al., 2016). Genic-SSR markers may provide a higher probability of marker-trait association with functional candidate gene (Ukoskit et al., 2019) than other SSRs. In cowpea, the total RNA of stems, roots, and leaves of five seedlings was sequenced to identify differentially expressed genes and develop SSR markers (Chen et al., 2017). Thus, RNA sequencing can establish genic-SSR markers which could be useful for genetic diversity and QTL identification. By using high density SNP markers, a significant QTL (QRk-vu9.1) was identified for root-knot nematode resistance in cowpea by Santos, Ndeve, Huynh, Matthews, and Roberts (2018). Further sequencing of the transcriptome of a near-isogenic line (NIL) population found that four genes positioned under QRk-vu9.1 QTL were expressing under nematode infection.

About 59 transcription factor families were reported in soybean, papaya, *Medicago truncatula*, *C. sinensis*, *P. vulgaris*, and five more underutilized crops, including Bambara groundnut (Chang et al., 2018a). Out of 59 transcription factors families, 20 (GATA, HSF, M-type MADS, LBD, Trihelix, G2-like, MIKC-MADS, GRAS, HD-ZIP, bZIP, MYB, FARI, C3H, NAC, bHLH, ERF, B3, C2H2, MYB-related, and WRKY) were in abundance in five orphan crops including Bambara groundnut (Chang et al., 2018a). High-throughput sequencing of pooled cDNA of Bambara groundnut was carried out for expression profile analysis of transcripts tags under reduced irrigation by Stadler (2009) using massively parallel signature sequencing (MPSS). The transcription factors “MYC, WRKY protein, and DREB” which have a role in water-deficit response in crops (Bartels & Sunkar, 2005; Chen et al., 2002) were absent in the Bambara groundnut dataset (Stadler, 2009).

Another recently developed powerful approach aiding precision breeding is genome-editing, through TALENs (transcription activator-like effector nucleases), or CRISPR-Cas9 (clustered regulatory interspaced short palindromic repeats-CAS systems). These have been adapted as a significant drive forward in improved stress-resistant plants (Nejat, Ramalingam, & Mantri, 2018; Zhang et al., 2016). Genome-editing offers to look beyond traditional and molecular plant breeding and can play a significant role in mitigating the adverse effects of yield constraints of crops, especially under climate change scenarios.

Genomic selection (GS) is a genomic-assisted breeding method in which a large dataset of SNP markers is used. The use of molecular markers in different genomic-assisted breeding approaches to select the desired traits has been a popular area of crop research in past decades, but their utility in the genetic dissection of complex quantitative traits has been limited (Bernardo, 2008; Harris et al., 2015). In the marker-assisted selection (MAS) method, introgression of few major QTL is straightforward. However, as the number of QTL increases for introgression, the deployment of MAS in crop improvement becomes complicated and costly, which limits the expected achievement of MAS. An advantage of GS is that it enables selection based on a large

marker dataset that can densely cover the whole genome to assure that all relevant genes are expected to be in LD (linkage disequilibrium) with at least a few of the markers (Bhat et al., 2016; Heslot, Jannink, & Sorrells, 2015). GS uses a prediction model to minimize the effects of biased markers (Heffner, Sorrells, & Jannink, 2009) by using all associated markers to estimate the breeding values for a trait. The majority of complex traits are quantitative and governed by minor QTLs (Desta & Ortiz, 2014), which govern the majority of phenotypic variation of a trait, including epistatic effects (Deshmukh et al., 2014).

Because GS can capture both small effects of QTL and epistatic interaction effects, it could play an important role in enhancing genetic gain. This approach has been used for improving different complex traits like forage yield data (Li et al., 2015), quality traits (Biazzi et al., 2017) in alfalfa, and cyst nematode resistance (Bao et al., 2014), grain yield (Jarquin et al., 2014), and seed weight (Zhang, Song, Cregan, & Jiang, 2016) in soybean. In Kersting's groundnut, Akohoue et al. (2020) explored genomic selection with ridge regression analysis using a population of 281 accessions with 493 SNPs. They observed both moderate (0.42 to 0.44) and high (0.62 to 0.79) prediction accuracy for days to 50% flowering, days to maturity, seed length, seed weight, and 100 seed weight, using the stratified cross-validation sampling method. There has been so far no GS study reported for Bambara groundnut and African yam bean crops.

7 | POTENTIAL REWARDS

The promotion of orphan legumes could help in managing the drought situation in most parts of SSA. Three main factors that threatens food security in the region are rapid population increase, scarcity of water and climate change (Initiatives, O.W., 2006; Madzivhandila, Sibanda, Yamdjeu, Moalosi, & Gwelo, 2016). The crops described here can tolerate harsh environmental conditions after years of neglect of farmers and the research community (Leakey et al., 2009).

Orphan legumes possess significant attributes in contributing to the generation of income for smallholder farmers and supporting food security. If utilized, they can support low input agricultural systems of farming and respond adequately to biotic and abiotic shocks (Vanlauwe et al., 2014). Orphan legumes are being intercropped in some areas as they have been identified to play special roles in vulnerable regions in SSA (Snapp, Jones, Minja, Rusike, & Silim, 2003).

An element of strategies for technology delivery and increasing support to small holder farmers is increasing the availability and quality of seeds (Shiferaw, Kebede, & You, 2008). Several countries in SSA have developed policies that ensure the safe distribution and use of only approved seeds for sales to farmers. Notwithstanding, as in the case of Tanzania, the community has also been involved in the sales and distribution of seeds to reduce the challenge of acute shortages (Abate et al., 2012).

Overall, the public and private sectors must join together to ensure adequate crop improvement plans, while also emphasizing management and distribution of plant genetic materials to end users (Minot et al., 2007).

8 | CONCLUSIONS

In this review, we identify challenges and rewards associated with the exploitation of orphan legumes for SSA. The potential of these underutilized indigenous legumes is still largely untapped but could become a valuable element of enhanced food and nutrition security in SSA. The available diverse genetic resources for these legumes provide an opportunity for research to explore their potential for food security, employment and income generation, particularly for smallholder farmers of SSA. Sustained research investments, nutritional awareness, and genetic characterization of these underutilized indigenous legumes are prerequisites for exploring their full potential to ameliorate climate impacts.

Some of these legumes still require an expansion of available genetic resources to avoid genetic erosion of their diversity. For example, the majority of African yam bean and Kersting's groundnut in the collection come from Nigeria, which indicates gaps in the GRC collections of these two legumes. It will be necessary to broaden genetic diversity and geographical representation of these collections. Awareness of these crops and traditional knowledge about their use and cultivation still lie in aged farmers' hands in most rural areas where the crops are grown.

Advanced breeding research on these underutilized crops is far behind other legumes crops, such as soybean, groundnut, chickpea, cowpea, and pigeon pea, but the breeding efforts for important and complex traits of these legume crops can be hastened by applying cutting edge genomics and phenotyping tools. The use of genomic-assisted breeding can help unravel the genetic potential of these legumes for their improvement and open up further research opportunities.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Writing—original draft and review and editing: MA, RP, and TTA. Writing—review and editing: BF and OO. All authors read and approved the final manuscript.

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ORCID

Rajneesh Paliwal  <https://orcid.org/0000-0001-6493-3289>

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SUPPORTING INFORMATION

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