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REVIEW ARTICLE

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Cowpea (*Vigna unguiculata*): Genetics, genomics and breeding

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Abstract

Cowpea, *Vigna unguiculata* (L.), is an important grain legume grown in the tropics where it constitutes a valuable source of protein in the diets of millions of people. Some abiotic and biotic stresses adversely affect its productivity. A review of the genetics, genomics and breeding of cowpea is presented in this article. Cowpea breeding programmes have studied intensively qualitative and quantitative genetics of the crop to better enhance its improvement. A number of initiatives including Tropical Legumes projects have contributed to the development of cowpea genomic resources. Recent progress in the development of consensus genetic map containing 37,372 SNPs mapped to 3,280 bins will strengthen cowpea trait discovery pipeline. Several informative markers associated with quantitative trait loci (QTL) related to desirable attributes of cowpea were generated. Cowpea genetic improvement activities aim at the development of drought tolerant, phosphorus use efficient, bacterial blight and virus resistant lines through exploiting available genetic resources as well as deployment of modern breeding tools that will enhance genetic gain when grown by sub-Saharan Africa farmers.

KEYWORDS
breeding, cowpea, genetics, genomics, productivity, *Vigna unguiculata*

1 | INTRODUCTION

Cowpea (*Vigna unguiculata* (L.) Walpers) also known as black eye pea is a herbaceous annual crop mostly grown in the dry agro-ecologies of the tropics in Latin America, Africa and south Asia. It is a legume and belongs to the family Fabacea, tribe Phaseoleae, genus *Vigna* and section *Catiang* (Marechal, Mascherpa, & Stainer, 1978). Cultivated cowpea, which is in subspecies *unguiculata*, is divided into five cultivar groups namely Unguiculata, Sesquipedalis (yard-long-bean), Textilis, Biflora and Melanophthalmus. The commonly cultivated cowpea belongs to cultivar group Unguiculata while members of cultivar group Textilis, characterized by long peduncles are grown in some parts of Nigeria for production of fibre. Cowpea is a diploid with $2n = 22$ and a genome size of about 620 million base pairs. According to Padulosi and Ng (1997), the area where maximum diversity of land races and cultivated cowpeas is present is West and Central Africa.

The bulk of cowpea production and consumption is in sub-Saharan Africa (SSA) particularly West and Central Africa. Nigeria produces the most quantity of cowpea grains annually at approximately 2.14 million metric tonnes (FAOStat, 2017) and consumes more than 3.0 million metric tonnes. The other major producers are Niger Republic and Burkina Faso with an average of 1.59 and 0.57 million metric tonnes, respectively (Table 1). Another major cowpea producing country is Brazil with an annual production of more than 491,000 tonnes on an area of about 1.5 million hectares (Singh et al., 2002).

Being drought tolerant, cowpea is grown predominantly in the dry savannahs to the Sahel in the fringes of the Sahara Desert with annual rainfall of about 300 mm or even less. Cowpea is cultivated

TABLE 1 Top 20 cowpea producing countries in the world (2014)

Rank	Country	Production (tons)	Area (ha)	Yield (Kg/ha)
1	Nigeria	2,137,900	3,701,500	578
2	Niger	1,593,166	5,325,168	299
3	Burkina Faso	573,048	1,205,162	475
4	United Republic of Tanzania	190,500	197,323	965
5	Cameroon	174,251	209,019	834
6	Mali	149,248	353,382	422
7	Kenya	138,673	281,877	492
8	Myanmar	115,200	132,000	873
9	Mozambique	103,837	377,900	275
10	Sudan	80,000	260,000	308
11	D R C	70,042	159,945	438
12	Senegal	64,088	153,142	418
13	Malawi	35,903	81,753	439
14	Haiti	29,895	41,525	720
15	United States of America	21,591	12,060	1,790
16	Peru	17,588	12,779	1,376
17	Serbia	16,189	4,777	3,389
18	Sri Lanka	15,281	11,519	1,327
19	China, mainland	13,500	13,000	1,038
20	Uganda	10,100	25,000	404

Source: FAOSTAT, 2017.

mainly for its grains, which are rich in protein with most improved varieties containing between 20 and 25 per cent protein on dry weight basis. Fresh leaves are also used as pot herb especially in East Africa. Samireddypalle et al. (2017) reported that cowpea haulm (dried leaves, stems and pod walls) could be a good source of income for farmers in the dry savannah areas where the farmers also keep livestock. In an earlier study, Duke (1990) found that cowpea fodder could contain up to 18.6 g protein per 100 g dry weight.

Depending on the region, seed coat colour and texture could be very important to consumers. For example, in northern parts of Nigeria where cowpea is generally produced because of favourable climatic conditions white-coloured grains are preferred by consumers, whereas in the southern parts of the country, preference is for brown-seeded types. Consumers also have preference for varieties with short cooking time, as less fuel is needed when cooking such varieties. This article reviews key achievements in the genetics, genomics and breeding of cowpea which contribute to the enhancement of the productivity of this crop.

2 | PRODUCTION CONSTRAINTS

2.1 | Insect pests

The productivity of cowpea in typical SSA farmers' fields is abysmally low at less than 600 kg/ha when compared with a potential grain yield of over 2,000 kg/ha. A number of abiotic and biotic factors are responsible for these low yields. The adverse effects of these yield limiting constraints can be reduced to their barest minimum through genetic improvement. Cowpea seedlings can be attacked and even killed by aphids (*Aphis craccivora*) if not controlled with insecticides or planting of resistant variety. Aphids are more devastating when drought occurs shortly after seedling emergence in the field. The single dominant gene that conferred resistance to aphid and assigned the symbol *Rac-1* by Bata, Singh, Singh, and Ladeinde (1987) has become ineffective against aphid. This is a typical example of a major resistance gene breaking down in cowpea. Ombakho, Tyagi, and Pathak (1987) and Pathak (1988) reported another dominant gene, derived from induced mutation and confers resistance to aphid, was given the gene symbol *Rac-2*. The flower bud thrips (*Megalurothrips sjostedti*) is yet another major insect pest of cowpea with devastating effects mainly on flower buds thereby inhibiting anthesis and pod formation. As no pods develop on plants attacked by this insect, they tend to remain vegetative for a longer period of time. The legume pod borer, *Maruca vitrata*, the most cosmopolitan of cowpea pests, is capable of causing extensive grain yield reduction (20%–80%) if not controlled (Singh, Jackai, Dos Santos, & Adalla, 1990). A number of pod sucking bugs (*Clavigralla tomentosicollis*, *Riptortus dentipes* and *Nezara viridula* among others) attack pods and suck sap from the seeds while still developing within the pods. Such seeds become seriously reduced in size and malformed thus making them unviable and unattractive to farmers and consumers. When cowpea seeds are placed in storage, weevils (*Callosobruchus maculatus*), which often accompany seeds from the field, cause extensive damage by the insect's larvae, that feed and develop inside with adults boring holes through which they emerge. Low levels of resistance to a few of these insect pests have been identified among some cowpea germplasm lines. Host plant resistance through incorporating desired genes in improved varieties would be the preferred approach to protect cowpea plants in the field and seeds in storage against these pests. Effective insecticides are not readily available and could be unaffordable to majority of the farmers.

2.2 | Diseases

Cowpea is also affected by several fungal, bacterial and viral diseases causing extensive yield reductions. Among fungal diseases are preemergence and postemergence damping off caused by *Pythium ultimum*, Fusarium wilt caused by *Fusarium oxysporium*, macrophomina blight caused by *Macrophomina phaseolina*, web blight and root rot caused by *Thanatephorus cucumeris (Rhizoctonia solani)*, stem rot by *Phytophthora vignae*, scab by *Sphaceloma* sp., cercospora leaf spot by *Pseudocercospora cruenta* and *Cercospora apii*. The major bacterial disease of cowpea is bacterial blight caused by (*Xanthomonas axonopodis* pv *phaseoli*). Under serious infection, bacterial blight causes stem canker, which could eventually kill the affected plant. Bacterial pustule caused by *Xanthomonas sp.* occurs sporadically and is less damaging to cowpea compared to bacterial blight. Cowpea farmers in sub-Saharan African are looking forward with great delight to the

development and deployment of improved varieties characterized by resistance to these various biotic constraints.

2.3 | Abiotic constraints

Although cowpea is known to be drought tolerant when compared to other crops, the productivity of cowpea could be hampered by erratic rainfall in the beginning and towards the end of the rainy season—a common phenomenon, in the semi-arid tropics where cowpea is mostly grown. With the current effects of climate change, the pattern of rainfall in the subregion, which either comes late or stops earlier than usual, requires that efforts be made to enhance the level of drought tolerance in currently existing improved crop varieties being grown by farmers (Fatokun, Boukar, & Muranaka, 2012). Cowpea yield can also be affected considerably by heat in sensitive varieties. When the night temperature reaches about 35°C, cowpea flowers abort due to poor pollen development, which can result in poor seed and pod set (Hall, 1993). Low soil fertility due to low organic matter and low phosphorus in the savannah soils is also a major constraint for cowpea production.

3 | GENETICS

Comprehensive reviews of cowpea genetics were published by Fery (1980, 1985), Fery and Singh (1997) and Singh (2002). These reviews covered relevant literature on cytologic, qualitative and quantitative genetics. We will cover here some more recent literature. Padi (2003) studied the inheritance of leaf node pigmentation, flower (petal) colour, immature pod colour, seed coat colour, seed eye colour and seed eye colour pattern and reported that presence of pigment was dominant over the absence of pigment and the black seed eye was dominant over brown eye. He further reported partial dominance of the very small eye pattern to the Holstein eye type.

Mustapha and Singh (2008) also reported that pod pigmentation is digenic while pigmentation in the pod tip followed two patterns of inheritance (monogenic and digenic), which agreed with Harland's (1920) findings. Cowpea seed coat colour is an important market trait of the crop in West Africa. Using six different biparental crosses, Egbadzor et al. (2014) could not classify segregating materials based on seed coat colour as chi-square goodness-of-fit test could not be conducted on them. They suspected that many genes might be involved in cowpea seed coat colour inheritance. Fery (1985) already mentioned that the complete mechanism of seed coat pigmentation was complex and not yet understood. Lachyan, Desai, and Dalvi (2016) studied also the inheritance of some traits in cowpea. The results showed monogenic inheritance for all four qualitative traits including growth habit, flower colour, seed coat colour and seed coat colour pattern. Joint segregation was observed between seed coat colour and seed coat colour pattern. Lopes, Gomes, and Filho (2003) reported that the number of genes that control 100-seed weight in cowpea is five and the high values for narrow sense heritability indicates that selection for seed size can be made in early generations. Pandey and Dhanasekar (2004) reported the presence of connate foliaceous stipules of primary leaves and their inheritance in cowpea genotype EC394736. They found the rudimentary stipules (RS) to be dominant over foliaceous stipules (FS). The F_2 segregation into 15 (RS): 1 (FS) indicated that duplicate recessive genes control the presence of the FS.

Ishiyaku, Singh, and Craufurd (2005) showed that photoperiod in the field of 13.4 hr per day was long enough to delay flowering of photoperiod-sensitive cowpea genotypes and photoperiod sensitivity was found to be partially dominant. Additive and additive × dominance interactions were the most important gene actions conditioning days to flower. Narrow sense heritability of 86% was observed while at least seven major genes with an average delay of 6 days each control time to flowering in the cross.

Cowpea aphid-borne mosaic virus (CABMV) is a major virus disease that causes substantial cowpea yield loss. Orawu, Melis, Laing, and Derera (2013) have reported that CABMV resistance is conditioned by more than one recessive gene in eight populations, single recessive genes controlled resistance in other seven populations. The continuous distribution of progeny for severity data observed in the F_2 populations suggests significance of quantitative inheritance for CABMV resistance. The general combining ability effects (59.8%) were more important than the specific combining ability effects (40.2%) in determining virus resistance in the tested cowpea varieties. In another study using genotypes KVx640 and KVx396-4-5-2D, Barro et al. (2016) found that resistance to CABMV is governed by two dominant genes, each variety contributing a resistant gene.

Three types of host reaction to bacterial pustule were observed by Patel (1981) during the screening of cowpea lines: brown hypersensitive resistant (BHR), non-hypersensitive resistant (R) and susceptible (S). Inheritance study of the BHR, R and S host reactions produced by three races of the bacterial pustule pathogen (*Xanthomonas campestris* pv. *vignae unguiculatae*) revealed that BHR reaction was dominant over R and S reactions, and R was recessive to S reaction (Patel, 1982). BHR reaction seemed to be controlled by two genes: one governing BHR reaction to race 1 and the other to races 1 and 2. Both of these genes were ineffective against race 3. The study showed that R reaction seemed to be controlled by one, two or three recessive genes that are effective against all the races.

Using six populations (Parent 1, Parent 2, F_1, F_2, BC_1 and BC_2) generated from each of four crosses involving four resistant and two susceptible cowpea varieties evaluated for resistance to Cercospora leaf spot (CLS), Booker and Umaharan (2008) found that mode of inheritance of resistance to *Pseudocercospora cruenta* can be oligogenic or polygenic depending upon the cross. This is the first report of polygenic inheritance of CLS resistance. In another study, the evaluation of CLS disease in F_2 plants and $F_{2:3}$ families derived from a cross between "CSR12906" (susceptible) and "IT90K-59-120" (resistant) revealed that the disease scores were continuously distributed, suggesting that the resistance in IT90K-59-120 is a quantitative trait (Duangsong, Kaewwongwal, Somta, Chankaew, & Srinives, 2016).

The genetics of flower thrips resistance was studied in crosses of four cowpea lines. Omo-Ikerodah, Fatokun, and Fawole (2009) found that resistance to thrips is quantitatively inherited with broad sense

heritability ranging from 56% to 73% and maternal effect. Additive, dominance and epistatic gene effects contributed significantly to thrips resistance. These authors reported that resistance to flower thrips is oligogenic with different genes involved in the control of resistance in TVu1509 and Sanzi.

4 | GENOMICS

With recent advances in molecular biology, some applications of DNA marker technologies were initiated in different cowpea research programmes. These include molecular characterization of germplasm, development of genetic and quantitative trait loci (QTL) maps.

Restriction fragment length polymorphism (RFLP) markers were used to characterize 44 accessions of different species belonging to four subgenera of the genus *Vigna* (Fatokun, Danesh, Young, & Stewart, 1993). Also, random amplified polymorphic DNA (RAPD) (Kaga, Tomooka, Egawa, Hosaka, & Kamijima, 1996; Simon, Benko-Iseppon, Resende, Winter, & Kahl, 2007), inter-simple sequence repeat (ISSR) (Ajibade, Weeden, & Chite, 2000), amplified fragment length polymorphisms (AFLPs) (Fang, Chao, Roberts, & Ehlers, 2007) and simple sequence repeat (SSR) (Gupta & Gopalakrishna, 2010; Ogunkanmi, Ogundipe, Ng, & Fatokun, 2008) have been used to study genetic diversity within both cultivated and wild relatives of cowpea. Huynh et al. (2013) used more than 1,200 single nucleotide polymorphism (SNP) markers to genotype a world collection of landraces and African ancestral wild cowpea. Their study revealed the presence of two major gene pools in cultivated cowpea in Africa: gene pool 1 with landraces mostly distributed in Western Africa, while the majority of gene pool 2 are found in Eastern Africa. Each gene pool is most closely related to wild cowpea in the same geographical region. More recently, genotyping by sequencing (GBS) was applied to discover SNPs in cowpea, which were used to estimate genetic diversity, population structure and phylogenetic relationships (Xiong et al., 2016).

Cowpea has a relatively small genome size estimated at 620 Mbp. Genome sequencing and analysis of the hypomethylated portion of the cowpea genome selectively cloned by methylation filtration (MF) technology were carried out by Timko et al. (2008). Over 250,000 genespace sequence reads (GSRs) with an average length of 610 bp were generated, yielding ~160 Mb of sequence information. About 74% of cowpea expressed sequence tags (ESTs) and 70% of all legume ESTs were represented in the GSR data set. Given that 12% of all GSRs contain an identifiable SSR, the data set is a powerful resource for the design of microsatellite markers. The identification of informative markers for marker-assisted trait selection and map-based gene isolation necessary for cowpea improvement could be possible. The longer-term goal of the Cowpea Genomics Initiative (CGI) project is to conduct transcriptomic, proteomic and metabolomic analyses to understand the basic biology of host and non-host resistance to *Striga* and *Alectra* parasitism, and the control of key agronomic characteristics such as drought tolerance, photoperiodic control of flowering and seed nutritional quality.

Munoz-Amatriain et al. (2017) recently reported a whole-genome shotgun (WGS) assembly, a bacterial artificial chromosome (BAC) physical map, and assembled sequences from 4,355 BACs using cowpea line IT97K-499-35. In addition, WGS sequences of 36 other diverse cowpea accessions supported the development of a genotyping assay, Illumina Cowpea iSelect Consortium Array for 51,128 SNPs. This assay was used to support linkage mapping, synteny analysis and evaluation of materials currently in use in three West African breeding programmes (Institut National de l'Environnement et des Recherches Agricoles (INERA—Burkina Faso), Savanna Agricultural Research Institute (SARI- Ghana), Institut Senegalais de Recherches Agronomiques (ISRA-Senegal) and IITA. The platform was applied to five biparental RIL populations to produce a consensus genetic map containing 37,372 SNPs mapped to 3,280 bins. The marker density of this map and its resolution over an earlier consensus map (Lucas et al., 2011) are 34-fold and fourfold increases, respectively. The map spans 837.11 cM at an average density of one bin per 0.26 cM and 11.4 SNPs per bin. All 11 cowpea LGs are densely covered with 1.85 cM on LG1 being the largest gap. The authors have investigated genetic diversity along each linkage group and explained macrosynteny between cowpea and common bean. The annotated reference genome assembly was recently made accessible through Phytozome (www.phytozome.net).

Through early efforts of generating putative markers for cowpea, about 41,949 EST sequences were produced from stressed and non-stressed drought susceptible and tolerant cowpea materials representing 16,954 unigenes. This resource was merged with the available genespace sequences (GSS) data to create a larger unigene set that has been mined to generate 4,958 molecular markers utilized to generate a microarray chip for expression analysis in cowpea.

The development of cowpea genomic resources was initiated under the CGIAR Generation Challenge Program (GCP) led Tropical Legumes One project. The University of California, Riverside, (UCR) played an important role in elaborating these resources. LGC Genomics provided outsourcing facilities for the conversion of SNPs to KASP based on the design/sequence information provided by UCR. Early activities using the established genotyping platform were the implementation of marker-assisted backcross (MABC) and marker-assisted recurrent selection (MARS) strategies in NARS and IITA cowpea breeding programmes through the use of 100 to 400 customized SNP markers (Boukar, Fatokun, Huynh, Roberts, & Close, 2016). Informative markers associated with quantitative trait loci related to biotic and abiotic stresses resistances were generated while QTLs for drought tolerance and stay green (Muchero, Ehlers, Close, & Roberts, 2009; Muchero et al., 2013) and for heat tolerance (reproductive stage) (Lucas et al., 2013) were identified. QTLs related to aphid resistance (Huynh et al., 2015), bacterial blight resistance (Agbicodo et al., 2010), Fusarium resistance (Pottorff et al., 2012), foliar thrips resistance (Muchero et al., 2010; Lucas, Ehlers, Roberts, & Close, 2012), Macrophomina resistance (Muchero, Ehlers, Close, & Roberts, 2011), nematode resistance (Huynh et al., 2016) and virus resistance (Gioi, Boora, & Chaudhary, 2012) have been reported. QTLs for leaf shape, maturity time, grain weight (seed size), seed

coat colour and patterns have also been identified. Detailed information on QTLs was provided in recent review (Boukar et al., 2016).

Several informatics application tools were developed to manage the different genomic resources for cowpea improvement. HarvEST:Web (http://harve st-web.org/) and HarvEST:Cowpea (Windows software HarvEST:Cowpea (download from http://harvest.ucr.edu) allow easy access to available cowpea genome resources. BreedIt SNP Selector was created to facilitate the identification of SNP sets for customized genotyping in cowpea genetic studies. This online application (http://breedit.org/) produces different polymorphic marker subsets according to the marker genome coverage specified. ParentChecker is another user-friendly tool to automate inference of parental genotypes for assisting in QTL mapping in cowpea and other crops. It is used to develop recombinant inbred line (RIL) populations particularly for cases where precise parental genotypic information of parents is not available. KBio converter is a conversion tool that allows the user to input a standard LGC Genomics SNP Viewer input file and output an equivalent file in which each SNP has been converted to a reference strand.

5 | BREEDING

5.1 | Historical trends

Cowpea research has been underway in some African countries for many years. In Nigeria, the Federal Department of Agricultural Research, the Institute for Agricultural Research and Training (IAR&T) at Ibadan, the University of Ife and the Institute of Agricultural Research (IAR) started cowpea research in early 1960s. The Centre National de Recherches Agronomiques (CNRA) in Senegal initiated cowpea breeding as early as 1961 (Sene & N'Diaye, 1973). Makerere University in Uganda started cowpea improvement programme in 1965 (Rubaihayo et al., 1973), while in Tanzania, work on cowpea began in 1959 (Rai & Utkhede, 1973). Cowpea research was boosted in 1977 with the involvement of two organizations: Canada's International Development Research Centre (IDRC) and IITA-SAFGRAD (Semi-Arid Food Grains Research and Development). Cowpea research program in Mali received IDRC's support in 1980. Many other African countries (Togo, Botswana, Kenya, Malawi, Rwanda, DRC, Central African Republic, Niger, Benin, Ghana, Ethiopia and Zimbabwe) started their cowpea research activities around 1980 (Singh & Ntare, 1985).

Early breeding activities in sub-Saharan Africa involved germplasm collection, evaluation and maintenance, followed by screening for disease resistance. Efforts were directed to breeding for insect resistance, early maturity, improved plant types and desired seed quality. Pure line and mass selection were initially conducted to identify the lines with high yield potential, meanwhile followed by activities involving hybridization, population advance and selection. Seed quality, high grain yield potential, early maturity, insensitivity to day length, erect growth habit, lodging resistance and best fitting to intercropping were among the initial key desired traits. Some level of work on disease resistance was initiated in Tanzania with technical support from IITA. Mass selection, conventional bulk method and pedigree of bulk-progeny test were among the main breeding methods. Lines developed by IITA were evaluated and seeds of promising lines multiplied and released for general cultivation by national partners (Singh & Ntare, 1985). So far, more than 80 varieties from IITA breeding nursery have been released in over 60 countries.

The priorities for cowpea improvement at IITA were reviewed and modified regularly. In the 1970s, the focus was on diseases which resulted in the identification of lines with high potential: TVu 201(S), TVu 1190, TVu 1977 and TVu 4557 (Singh & Ntare, 1985). In the 1980s, focus shifted to cowpea improvement for insect and multiple disease resistances and white rough seed coat characteristics. In the 1990s to early 2000s, the IITA cowpea breeding programme embarked on the development of (1) extra-early-maturing (60–70 days) photo-insensitive grain type, mainly used in sole crop and short rainy seasons, (2) medium-maturing (75–90 days) photo-insensitive grain type, fitting to sole crop and intercrop, (3) late-maturing (85–120 days) photo-insensitive dual-purpose (grain + leaf) types, for use as sole crop and intercrop, (4) photosensitive early-maturing (70–80 days) grain types, for intercropping, (5) photosensitive medium-maturing (75–90 days) dual-purpose (grain + fodder) types, for intercropping, (6) photosensitive late-maturing (85–120 days) fodder type, for intercropping and (7) high-yielding, bush-type vegetable varieties (Singh, Chambliss, & Sharma, 1997). Over the years, systematic incorporation of desirable genes for resistance in improved breeding lines as well as some selected varieties as recurrent parents was also carried out.

A number of improved lines were developed and released by national programs in Africa. In Nigeria, landraces/breeding lines released for cultivation by farmers included Westbred, Prima, Dinner (vegetable cowpea variety), Ife brown, IAR 339-1, IAR 341, IAR 345 and IAR 355. In Senegal, there were Ndambour, Mougne, Bambey 21 and 23, while in Tanzania and Burkina Faso, there were TK-1, TK-5, TKx133-16D-2 and Cross 1-6E-2 and Suvita-2, KN-1 (Vita 7) and TVx3236, respectively.

5.2 | Current status

From 2007, IITA's cowpea breeding programme placed emphasis on building on progress recorded from previous work. Activities were initiated on the identification of additional sources of resistance to abiotic (drought, heat) and biotic (aphid, flower thrips, striga and alectra) stresses by exploiting the germplasm collections. Being a self-pollinated crop, breeding methods such as pure line selection, mass selection, pedigree, backcross and single seed descent have been employed successfully in cowpea genetic improvement. In view of recent developments in modern breeding, some molecular breeding tools have been generated for cowpea, which are now being deployed through marker-assisted selection (marker-assisted recurrent selection and marker-assisted backcrossing).

5.3 | Genetic resources

A total of 15,003 cultivated cowpea from 89 countries are maintained in IITA's genebank. Based on geographical, agronomical and botanical descriptors, a core collection of 2062 accessions was

established. The diversity in the core collection was similar to that of the entire collection and correlated traits that may be linked were also preserved in the core collection (Mahalakshmi, Ng, Lawson, & Ortiz, 2007). A reference set, also called mini core, composed of 370 accessions representing the entirety of the genetic diversity of the core was constituted. The minicore is a critical resource for scientists to study new adaptive traits, conduct comparative genomics studies, and discover new favourable alleles and new lines for prebreeding activities.

In addition to the cowpea minicore, the first eight-parent cowpea multiparent advanced generation intercross (MAGIC) population was developed recently as an important genomic community resource for trait discovery and breeding. The eight founder parents were selected based on abiotic and biotic stress tolerance or resistance and agro-morphological trait variability (Huynh et al., 2017). The eight parents were intercrossed using structured matings as described by Cavanagh, Morell, Mackay, and Powell (2008) with some modifications. Pairwise crosses (AxB; CxD; ExF; GxH) were performed followed by 600 double crosses producing F_1 seeds (300 ABxCD; 300 EFxGH). A total of 300 four-way random pair crosses were made (ABCD x EFGH). Three hundred and sixty-five (365) F_1s were generated from the crosses and advanced by single seed descent (SSD) till F8 generation (Huynh et al., 2017). Prior to the advancement of the population through SSD, each of 365 eight-way individuals was genotyped using SNP genotyping with the cowpea Illumina 60K iSelect BeadArray to confirm each individual was derived from an eight-way cross.

6 | COWPEA BREEDING UNDER TLII

Cowpea is grown mostly in the dry northern guinea savannah, Soudan Savannah and Sahel agro-ecologies characterized by low annual rainfall. In recent times, the amount of rainfall received in these areas is declining and the distribution of the rains is irregular especially during early or late stages of the cropping seasons. These predispose cowpea to drought while also undermining yield in farmers' fields. The development and release of cowpea varieties with enhanced levels of drought tolerance to farmers in drought prone areas of SSA was the main plank of objective three of Tropical Legumes II project. However, most of these varieties remain on shelves of various breeding programmes. Following the inauguration of the Tropical Legumes project which aims to improve livelihoods of peoples by enhancing cowpea productivity and production in drought prone areas of sub-Saharan Africa, it was possible to disseminate some of the shelved cowpea varieties. Farmer participatory variety selection (FPVS) was employed to help facilitate uptake of the improved breeding lines by farmers in various communities.

In Mozambique, farmers showed interest in adopting the following breeding lines, IT00K-1263, IT97K-1069-6 and IT82E-16 because of their high yield performance and drought tolerance while the following cowpea breeding lines IT00K-1263 and IT99K-1122 were released in Tanzania. During FPVS, we observed that the best lines in terms of grain yield in some locations were not necessarily the most preferred by farmers. Attributes such as striga resistance was a very important selection criterion coupled with grain and fodder yields by farmers in West Africa hence they selected IT97K-499-35 in Mali, Niger and Mali whereas farmers in Mozambique preferred IT00K-1263 because of its high grain yield ability (Fatokun, Boukar, Kamara, et al., 2012). More than 24 IITA breeding lines were released during the last 10 years in 13 different countries in sub-Saharan Africa (Table 2).

6.1 | Sustenance of the breeding pipeline

In order to identify sources of new genes to use in the development of better performing breeding lines, some germplasm and improved breeding lines available at IITA were screened for different desirable traits under the Tropical Legumes Project.

6.2 | Screening for drought tolerance

About 1,200 germplasm lines from the Genetic Resources Center at IITA were evaluated in the field for their responses to drought conditions. The evaluation was carried out under irrigation during the dry season. Drought stressed plants were exposed to terminal drought following withdrawal of irrigation at 5 weeks after sowing. It was observed that drought depressed grain yield in all the germplasm lines tested. However, there were significant differences in the extent of grain yield reduction due to drought among the lines. Most of the lines flowered and matured earlier under drought. A number of lines remained green at 7 weeks after irrigation water

TABLE 2 List of released cowpea varieties from 2008 to 2017

Year of release	Variety	Country
2008	IT97K-499-35	Nigeria
2009	IT89KD-288, IT89KD-391	Nigeria
	IT97K-499-35, IT97K-499-38, IT98K-205-8	Niger
2010	IT97K-499-35, IT93K-876-30	Mali
	IT99K-573-1-1	Niger
2011	IT82E-16, IT00K-1263, IT97K-1069-6	Mozambique
	IT99K-494-6	Malawi
	IT99K-573-1-1, IT99K-573-2-1	Nigeria
2012	IT99K-7-21-2-2-1, IT99K-573-1-1	Tanzania
2013	IT99K-573-2-1, IT98K-205-8	Burkina Faso
	IT95K-193-12	Benin
2015	IT00K-1263, IT99K-1122	Tanzania
	IT07K-292-10, IT07K-318-33	Nigeria
	IT05K-321-2, IT97K-390-2, IT82E-16, IT-82E-18, IT99K-494-4	Swaziland
	IT99K-573-2-1, IT99K-573-1-1	Sierra Leone
2016	IT90K-277-2, IT07K- 211-1-8	South Sudan
	IT99K-573-2-1, IT99K-573-1-1	Ghana

was suspended. Some of these stay-green type had delayed flowering under drought (Fatokun, Boukar, & Muranaka, 2012). A total of 190 lines were found to show enhanced levels of drought tolerance as proportions of grain yield reduction due to drought were relatively lower among them. These were further evaluated, and the best 10 were selected for use in making crosses aimed at developing populations segregating for drought and from where selections have been carried out for breeding lines with superior drought tolerance.

6.3 | Screening for phosphorus use efficiency

The marginal soils in which cowpea is mostly grown in the Sahel and Soudan savannah agro-ecologies are generally sandy with very low levels of organic matter. The soils are also deficient in minerals needed by plants for good growth. Cowpea is a legume, which can fix atmospheric nitrogen in the crop's root nodules. It can therefore obtain some of its needed nitrogen from the root nodules while also leaving some in the soil for crops that follow in rotation. For good nodulation to occur phosphorus is an essential mineral that is generally lacking in the marginal soils where most cowpea is grown. Fifty improved breeding lines from IITA cowpea breeding nursery were evaluated in pots placed on benches in the glass house for their responses to phosphorus applications (0, 30, 60 and 90 kg/ha). Nodulation was highest in a dual-purpose breeding line IT98K-166-44. Response to added phosphorus was higher in IT89KD-288 than in IT98K-166-44. Line IT89KD-288 was superior to all others in terms of efficiency in the utilization of P, while line IT99K-7-21-2-2 was found to be least efficient under low P application. The study showed that the application of 90 kg P per hectare could adversely affect cowpea's performance; hence, application of P between 30 and 60 kg per hectare would be most beneficial to many lines. It is possible, from this work, to develop cowpea breeding lines that can utilize efficiently low amounts of phosphorus application.

6.4 | Screening for resistance to aphid

Aphid *(Aphis craccivora)* is a major insect pest of cowpea especially during the crop's seedling stage in the field. Aphid attack on cowpea is most devastating when drought occurs in the seedling stage. Entire crop can be wiped out in such situations. The single dominant gene that confers resistance to this pest and which had been incorporated in several improved breeding lines and varieties has now become ineffective as such plants now succumb to the pest. There is need for identification of new sources of resistance. A number of germplasm lines and some cross compatible wild relatives were screened for resistance to aphid in the seedling stage. A wild cowpea relative, line TVNu 1158, was found to be resistant to aphid, and this has been crossed to some improved breeding lines with the aim of transferring the resistance gene to good background through backcrossing. A set of about 210 recombinant inbred lines (RILs) has been generated from the cross which has been used to produce a genetic linkage map of cowpea comprising about 17,739 SNP markers. The RILs have also been phenotyped for aphid resistance, and the data will be used for QTL analysis.

6.5 | Screening for resistance to bacterial blight

Bacterial blight, caused by *Xanthomonas axonopolis* pv. *vignicola*, is one of the major diseases of cowpea. It causes considerable yield losses in susceptible lines. Fifty improved cowpea breeding lines (Table 3) were inoculated by spraying a suspension containing the bacterium obtained from a culture maintained in IITA's pathology laboratory. The results showed that fourteen of the 50 improved breeding lines tested were resistant to bacterial blight. These breeding lines are good sources of genes for resistance to bacterial blight.

6.6 | Screening for resistance to bean common mosaic virus in cowpea

The bean common mosaic virus (BCMV) is one of the important viruses affecting cowpea in SSA. About 100 germplasm lines were screened for resistance to this virus, and two showed good levels of resistance using both visual scores and enzyme-linked immunosorbent assay (ELISA) test. An evaluation of F_{1s} from a diallel cross involving 10 (both resistant, tolerant and susceptible) lines revealed that both additive and non-additive genetic variability are important which suggests that integrated breeding strategies can be adopted to efficiently utilize the

TABLE 3 Severity of bacterial blight on 50 cowpea accessions 4 weeks after inoculation with *Xanthomonas axonopolis* pv *vignicola*

Variety	Disease severity	Group
IT98-692, IT04K-405-5, IT99K-573-2-1, TVu-7778	3–3.67	HS
IT89KD-288, IT03K-378-4, IT97K-1069-6, IT97K-1042-3, IT04K-227-4, IT98K-1103-13, IT98K-128-3, IT99K-573-1-1, IT99K-377-1, IT00K-1207, IT98K-412-13, IT03K-316-1, IT99K-494-6, IT98K-589-2, IT99K-216-24-2, IT98K-205-8, IT99K-529-2, IT96D-610, IT97K-390-2, IT97K-568-18, IT00K-901-5, IT98D-1399, IT98K-1092-1, IT97K-499-35,	2–2.83	S
IT93K-452-1, IT03K-351-1, IT98K-131-2, IT00K-898-5, IT99K-216-44, IT99K-7-21-2-2, IT98K-503-1, IT98K-628, IT98K-491-4, IT98K-506-1,	1.13–1.92	MR
DANILA, IT00K-1263, IT03K-324-9, IT97K-819-118, IT98K-1092-2, IT98K-1111-1, IT98K-1263, IT98K-133-1-1, IT98K-166_4, IT98K-311-8-2, IT99K-1060, IT99K-1122, IT99K-529-1, IT00K-835-45	1	R
Mean	1.92	
SE	0.13	

HS, Highly susceptible; S, susceptible; MR, moderately resistant; R, resistant.

additive as well as non-additive genetic variability (Inegbenose, 2016) in the development of BCMV resistant cowpea breeding lines.

7 | CONCLUSION

Although cowpea has for some time now been regarded as an orphan crop in view of the relatively low level of research attention given to the crop, modest progress has been made in the assemblage and conservation of its germplasm, generation of genomic tools for more effective breeding and development of improved varieties some of which are already available in SSA farmers' fields. The challenge of striga to cowpea production especially in the dry savannah agro-ecologies is being effectively contained with the development of varieties that show immunity to this parasitic weed. There is however room for the development of better performing varieties that will be characterized by high stable grain yield, good amount of protein, large seed size, white or brown seed coat colour, resistance to some insect pests which presently creating huge losses to the crop. The over 15,000 and 2,000 accessions of cultivated and wild compatible wild relatives in the gene bank at IITA, respectively, need to be systematically screened for adaptive genes that control the abiotic and biotic stresses still limiting its productivity. In addition, cowpea breeding programmes at IITA and NARS are currently engaged in the implementation of modern breeding practices that will improve their efficiency. With the development of various platforms such as phenotyping, genotyping and data management coupled with necessary resources now being committed to cowpea research, more impacts in term of variety development and integrated crop management practices will be achieved.

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