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REVIEW ARTICLE

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Public sector soybean (*Glycine max*) breeding: Advances in cultivar development in the African tropics

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Abstract

Formal public sector soybean breeding in Africa spans over four decades, and it was initiated by the International Institute of Tropical Agricultural (IITA). As the demand of soybean continues to outstrip production, strategic projects such the Tropical Legume (TL) were initiated, in which the main goal was to enhance the productivity of soybean in the farmers' fields in Sub-Saharan Africa. One of the strategies to enhance the productivity of soybean in the farmers' fields is through developing and deploying improved soybean varieties in the target countries. Through the TL I and TL II projects, a number of varieties were released in the target countries, Kenya, Nigeria, Malawi and Mozambique by employing participatory variety selection (PVS). This review provides highlights of the achievements made by IITA breeding programme and insights of what needs to be done to enhance yield improvement for soybean in Africa using demand-driven breeding approaches.

1 | INTRODUCTION: SOYBEAN PRODUCTION AND DEMAND TRENDS IN AFRICA

Cultivated soybean (*Glycine max* [L.] Merr.) accounts for about 84.5% of the world grain legume trade (Abate et al., 2011), and it is the number one oil and protein supplier for animal and human nutrition (FAOSTAT, 2014). United States, Brazil, Argentina, China and India are the major producers of soybean and account for more than 90% of the annual average global production of 340 million metric tons for the past decade (Global Soybean Production, 2017; http://www.globalsoybeanproduction.com/). Although Africa accounts for <2% of the global production with major producers being South Africa and Nigeria (Global Soybean Production, 2017; http://www.globalsoybeanproduction.com/), soybean constitutes an important component in the smallholder cropping systems and its advantages are well-documented. Some of the advantages of soybean under the smallholder cropping systems in Africa include but not limited to (a) soil fertility improvement and pest control as a rotational crop with cereals, soybean-maize rotation can increase maize yield by more than 20% (Yusuf, Iwuafor, Abaidoo, Olufajo, & Sanginga, 2009), and rice grain yield following soybean was 75%–146% higher than 2-year continuous cropping of rice in Benin (Oikeh et al., 2010). (b) Increased household food and nutrition security, for example, soy milk and maize–soy-blended products, and (c) increased rural incomes and employment opportunities especially for women farmers and the youth. Compared to other legumes, cost of production and storage of soybean are relatively low and it is the only legume that has shown an enormous worldwide expansion in production during the last two decades (FAOSTAT, 2014).

Across Sub-Saharan Africa (SSA), average soybean yields increased from <1.0 ton/ha before 2000 to about 1.2 tons/ha in 2011–2013. In addition, both area expansion and yield growth have made roughly comparable contribution to the observed growth in soybean production in SSA with annual growth rates of 3.0% in area and 3.5% in yield (Figure 1). Despite these positive trends, the average soybean yields in Africa (1.2 tons/ha) are much lower than the global average yields of nearly 2.5 tons/ha. The low yields are due to a number of production constraints and low adoption of improved varieties and agronomic practices. This provides an overview of soybean breeding in sub-Saharan Africa and update of the accomplishments of the IITA breeding soybean programme.

2 | GERMPLASM AND GENETIC DIVERSITY STUDIES

Soybeans *Glycine max* (L.) [Merr.] and *Glycine soja* (Seib. et Zucc.) are annuals and the two species of the subgenus Soja. *Glycine max* is the cultivated soybean while *Glycine soja* is the wild annual progenitor found naturally in China, Japan, Korea, Russia and Taiwan (Hymowitz & Shurtleff, 2005). Both the cultivated soybean *G. max* and its annual wild progenitor, *G. soja*, are cross-compatible and have 2n = 40 chromosomes. Cultivated soybean exhibits wide phenotypic variability in terms of seed shape, size, colour and chemical composition; plant morphology; and maturity, as well as resistance to a broad range of biotic and abiotic stresses. Random amplified polymorphic DNA (RAPD) data by Chen and Nelson (2004) found that *G. soja* was more diverse than *G. max*. *G. soja* has been found to be a potential good source of resistance to a number of diseases and pests such as soybean mosaic virus (SMV), soybean cyst nematode (SCN) and aphids (Campbell, 2013). Available estimates of nucleotide diversity of cultivated soybean, *G. max* relative to the wild soybean, *G. soja* indicate wide genetic diversity in *G. soja* (Table 1).

Genetic studies and formal soybean breeding in Africa span over four decades with the International Institute of Tropical Agriculture (IITA) spearheading public sector research with initial focus on West Africa. Germplasm was acquired from various regions notably from the USA, Canada and Indonesia. In Africa, IITA is considered to have the largest germplasm collection of *G. max* with approximately 1,800 accessions. In 1977 and 1978 seasons, IITA screened 400 germplasm accessions from the USA and Asia for nodulation without inoculation in five diverse environments in Nigeria on soils low in nitrogen and only 10 accessions from Asia were capable of effective symbiosis at all testing sites while USA germplasm did not nodulate at all sites (Kueneman, Root, & Dashiell, 1984). The ten accessions which nodulated in nitrogen deficient soils across all sites included "Malayan" (a local variety grown in Nigeria then), "M-351." Tropical Glycine max (TGm accessions) "TGm 120," "TGm 119" and the Indonesian origin accessions, "Obo," "Indo 216," "Indo 180," "Orba," "Indo 243" and "Indo 226" (Kueneman et al., 1984). Additional sources of germplasm for nodulation were also obtained from the wild sprawling soybean accessions TGm 737, TGm 719, TGm 579 and TGm 577 from Indonesia, and these have been widely used in the IITA soybean breeding programme with their derivatives the TGx series cultivars synonymous to promiscuous nodulation in a wide range of environments (Pulver, Kueneman, & Ranga-Rao, 1985).

Diversity studies, using 37 simple sequence repeats (SSRs) and 1,223 single nucleotide polymorphisms' (SNPs) markers on 68 IITA soybean genotypes which comprised of 13 released genotypes and 55 breeding lines, showed that polymorphic information content (PIC) values for SSRs ranged from 0.09 to 0.75 with an average of 0.43, while SNP markers had PIC values ranging from 0.02 to 0.38 with an average of 0.25. The observed PIC values compared to other studies in tropical soybean in Brazil and India by Mulato et al. (2010) and Bhat et al. (2012), respectively, show that the diversity of the IITA materials used in the study is comparable low and therefore the

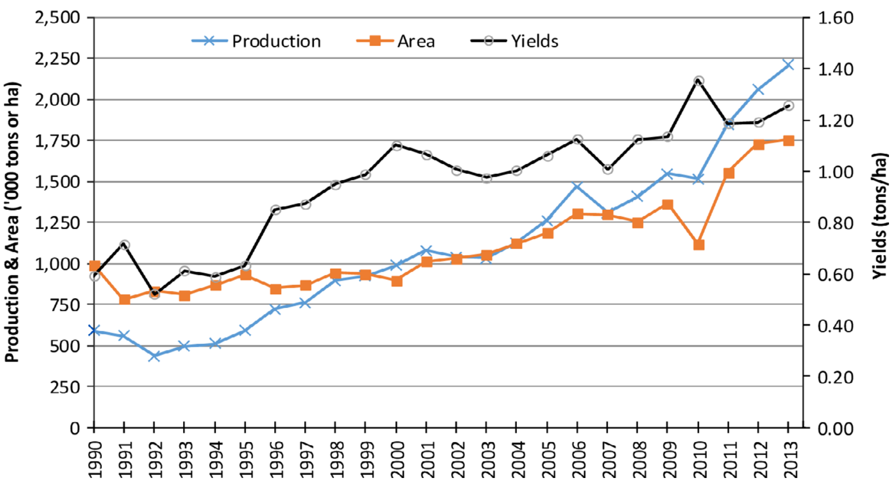

FIGURE 1 Trends in soybean production, area and yields in Sub-Saharan Africa, 1990–2013 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Estimates of nucleotide diversity of cultivated soybean (*G. max*) relative to the wild soybean (*G. soja*), data were obtained from various sources between 1996 and 2009

Data source	Genetic diversity estimate		Proportion of diversity retained after domestication
	G. max	*G. soja*	*G. max*/*G. soja*
Powell, Doyle, McNicol, Tingey, and Rafalski (2010)	0.538	0.830	0.650
Li and Nelson (2009)	0.400	0.460	0.870
Xu and Gai (1985)	0.188	0.285	0.660
Hyten et al. (2005)	0.001	0.002	0.490
Kuroda, Tomooka, Kaga, Wanigadeva, and Vaughan (1984)	0.496	0.870	0.570
Mean	0.325	0.489	0.650

need to introgress new germplasm in the breeding pools. Genetic relatedness utilizing the dendrogram grouped the genotypes into five major clusters with both markers (Figure 2). Of the 13 varieties, half of them (TGx 1485-1D, TGx 1448-2E, TGx 1440-1E, TGx 1740-2F, TGx 1019-2EN, TGx 1830-20E) coalesce in one cluster with another six breeding lines. Another four varieties (TGx 1895-33F, TGx 1835-10E, TGx 1019-2EB and TGx 923-2E) clustered closer to one another, but far away from other varieties. The remaining varieties (TGx 1904-6F, TGx 1987-62F, TGx 536-02D) spread out far apart from one another and from the rest of the varieties.

Analysis of molecular variance (AMOVA) and principal coordinate analysis (PCoA) indicated that maximum diversity was partitioned within rather than between the rust-resistant and rust susceptible groups for both molecular marker types. The estimated fixation index (FST) over 1,223 SNP loci was 0.32 and 0.22 for SSR loci, indicating a high level of genetic differentiation among the genotypes. The study laid foundation for selecting diverse parental lines carrying priority target traits (foliar disease resistance, resistance to pod shattering, early flowering, reduced plant height, efficient natural nodulation, lodging resistance, improved seed longevity, low phosphorus tolerance and yield improvement) for recombination.

3 | BREEDING OBJECTIVES, TARGET PRODUCTION ENVIRONMENTS AND SELECTION METHODOLOGIES

3.1 | Breeding objectives

Breeding objectives as defined by IITA and its partners in soybean are centred on the principle of economically increasing production and productivity through the use of appropriate varieties accompanied by good agricultural practices as a management tool. Focus is on narrowing down the yield gap or exploitable yield which is the difference between the average farm yield and the yield potential. Several, biotic and abiotic factors lead to a wide yield gap in soybean productivity, and these include drought, poor soil fertility, shattering, diseases and pests. Breeding objectives are therefore classified according to traits conferring resistance or tolerance to a biotic or abiotic stress which limits productivity and production. The breeding objectives broadly cover four primary areas:

1. Developing high yielding, drought tolerant soybean varieties with a wide range of maturity to fit different agro-ecologies in the era of climate change.
2. Developing nutrient efficient soybean varieties focusing on low phosphorus tolerance.
3. Developing disease resistance/tolerant soybean varieties focusing on rust resistance/tolerance.
4. Developing high biological nitrogen-fixing soybean lines.

In addition to the breeding objectives, availability of quality basic seeds to collaborating partners is a fundamental aspect in the IITA soybean breeding goals and hence one of the objectives of Tropical Legume project.

The evolution of priority target traits for each decade and genetic potential to improve the trait is given in Table 2. With change in climate and expansion of soybean production into the drier savanna regions, abiotic stresses such as drought become more important. Compared to the past decades, more traits are now important hence selection criteria should be re-designed to meet the never-ending challenge of developing high yielding, stable and farmer preferred soybean varieties.

3.2 | Breeding pipelines target product concepts/profiles

In order to meet continental and regional needs in soybean improvement, the breeding pipelines are structured to ensure that varieties developed meet the specific demands as per the product concepts addressing target production systems prioritized in the regional and country strategies. The crossing programme is centralized, and all the crosses are currently being done at the Ibadan station, Nigeria, as growing of the soybean crop is possible throughout the year and its possible to have three generations in a year. The crosses are classified based on the product concept, and currently, the IITA breeding pipelines are based on the regions: West Africa (medium to late maturing varieties); East and Central Africa (medium maturing) and Southern Africa (medium to early maturing). Table 3 summarises the product concept or profiles for the target regions. Evaluation and screening of major diseases such as rust *Phakopsora pachyrhizi* are done at two hot spot sites, Ibadan, Nigeria, and Bvumbwe research station in Malawi with the use of spreader rows to increase field infestation.

3.3 | Breeding methods

Soybean plant is a naturally self-pollinating crop with very little of out-crossing; hence, breeders use the breeding procedures developed to improve self-pollinated plant species (Fehr, 1991a, 1991b).

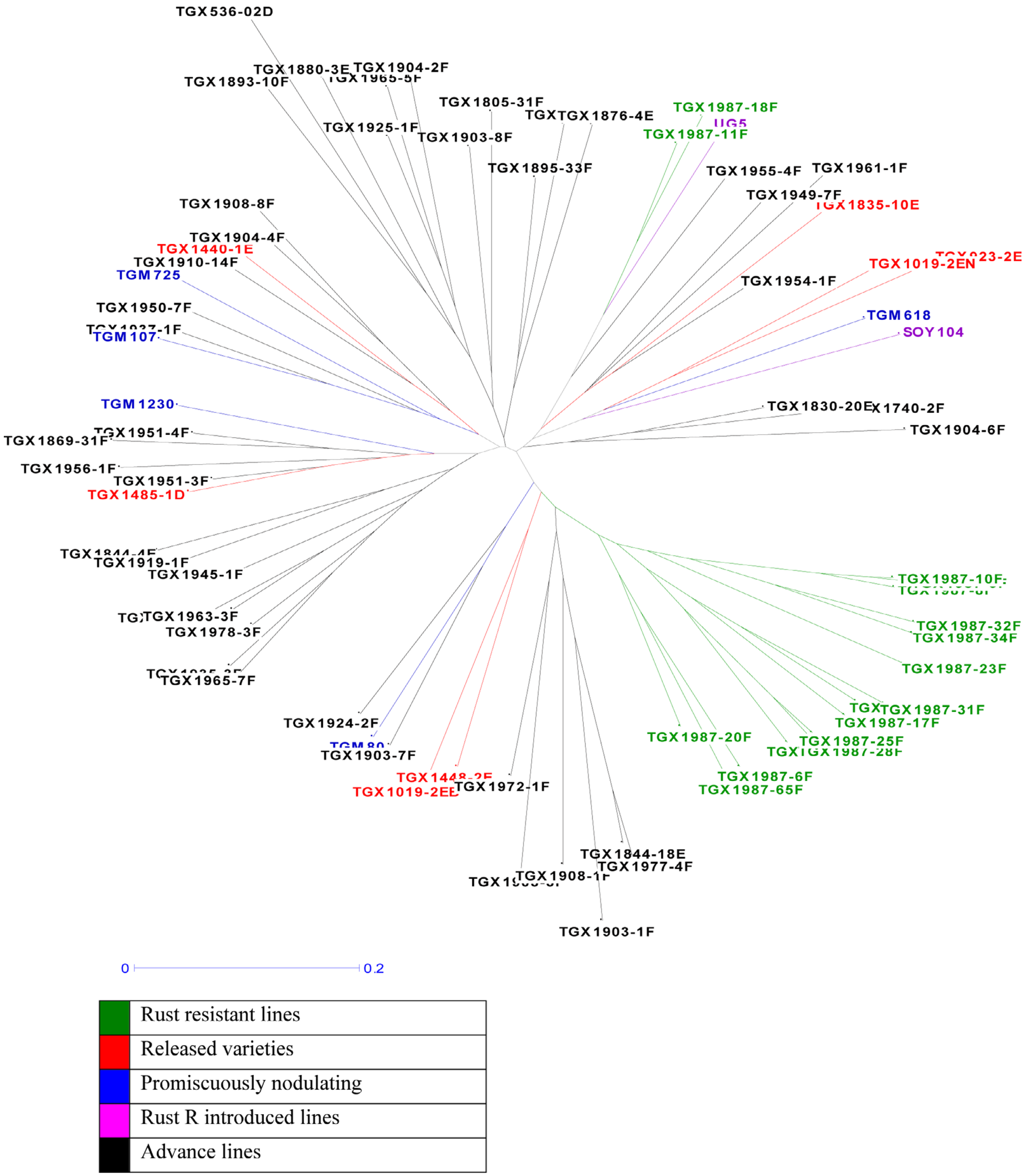

FIGURE 2 Phylogenetic relationships of 68 IITA soybean genotypes assessed with SSR markers

In the IITA soybean breeding programme, the pedigree breeding method has been used in the past resulting in very small populations as single plant selection was initiated at F_2 level. A common method used by soybean breeders in the USA is the modified single seed descent (mSSD), commonly referred to as single pod descent (SPD), which is currently being used. This procedure ensures genotypic variation, and adequate population size is not influenced by seed viability. A small number of seeds, usually two to four, are taken from each individual in the F_2 population and bulked, and a similar number of seeds are taken in subsequent generations of inbreeding, and

TABLE 2 Decadal evolution of target priority traits in soybean improvement in response to climate change and expansion of soybean production in Africa

Trait	1980–1990	1991–2000	2001–2010	2011–2020	Genetic potential for improvement (1-high; 4-poor)
Grain yield	1	1	1	1	3
Yield stability	1	1	1	1	3
Fodder yield	4	1	2	2	2
Maturity (medium-early)	3	3	2	1	1
Promiscuous nodulation	1	1	2	2	3
Seed longevity/Viability	1	1	2	2	3
Resistance pod shattering	1	1	2	2	2
Seed colour	4	2	2	2	2
Seed size	4	3	2	1	3
Lodging resistant	3	2	2	1	2
Pod clearance	4	3	3	1	2
Cercospora leaf spot	1	1	2	3	2
Red leaf blotch	4	4	3	3	3
Bacterial pastula	2	3	3	3	3
Bacterial blight	4	4	4	3	2
Rust resistance	3	3	1	1	2
Drought tolerance	4	3	2	1	3
Nutrient use efficient—low P	4	3	3	2	3
Protein content	3	4	3	3	2
Oil content	2	3	3	3	2

Note. 1-high priority; 2-medium priority; 3-low priority; 4-not breeding objective.

individual plants within the population are selected at the desired inbreeding stage (Fehr, 1991a, 1991b).

Once lines have been developed to $F_{4:5}$ stages, agronomic evaluations of the lines are done in the target production environments (TPEs). There are four basic considerations for testing breeding lines namely number of sites, field design, the plot size and the number of years/seasons of testing before releasing a variety. The sites to be used must be a sample of the soybean growing environments so that inferences are made for the right environment. In general variety testing, the number of sites depends on the types of environments available. Where there is only one type of environment, it is logical to use only one site and only duplicating for security reasons. Where genotype–environment interaction (gei) is suspected, the number of sites and number of seasons/years must be more than one to effectively estimate the ***gei***. Though not much work has been done regarding **gei** in soybean, soybean is highly photoperiod sensitive hence the need to widely test it in the production environments. Some of the documented works available include the ***gei*** influence reported on grain yields and nodulation traits in Uganda (Agoyi et al., 2017; Agoyi, Tumuhairwe, Afutu, Odong, & Tukamuhabwa, 2016; Tukamuhabwa, Assiimwe, Nabasirye, Kabayi, & Maphosa, 2012). These studies reported wide variation in the performance of the accessions from site to site for all the traits studied. Season/year to season/year variations were also reported. Agoyi et al. (2017) found the same site belonging to different mega environments depending on the season under consideration while assessing ***gei*** on various nodulation traits. The same trend was reported on grain yields by Agoyi et al. (2016). It is important that on top of locational variation, seasonal variation be catered for while testing varieties.

The current focal point for IITA soybean breeding in Southern Africa is the Chinyanja Triangle, which extends between Malawi, Mozambique and Zambia (Figure 3). In West Africa, the TPEs include the Northern parts of Nigeria specifically Kaduna and Kano States though limited trials are also done in Benue state. In East Africa, the Western part of Uganda, surrounding Kasese District, and the East Central Uganda, Jinja District, have been reported as ideal environments for variety testing in the second rainy season.

4 | ACHIEVEMENTS IN ENHANCING SOYBEAN PRODUCTIVITY AND PRODUCTION IN SUB-SAHARAN AFRICA: TROPICAL LEGUME I AND II INITIATIVES

Decentralized breeding approaches were employed in Tropical Legume I and II projects between 2007 and 2012, with the aim of fast track testing and release of soybean elite lines through farmer participatory variety selection (PVS) in the project countries Malawi, Mozambique, Nigeria, Kenya and Tanzania. Rust resistance, maturity

TABLE 3 IITA soybean product concept/profiles

Product concept	Estimated area (ha)	% area/ effort	Target and spillover agro-ecologies	Maturity (days)	Resistance/ tolerance required	Other criteria	Product development goals
(1) Early to medium maturity varieties with resistance to rust, escapes/ tolerance to drought and promiscuous nodulating	1.0 M	60%	Target: Ghana, Nigeria, Mozambique, Malawi, Zambia; Spillover: Cameroon, Kenya, Tanzania, Uganda, Democratic Republic of Congo, Rwanda, Zimbabwe, South Africa, Angola, Mali, Ethiopia, South Sudan	90–105	Biotic: rust, leaf blight, frogeye, shattering, lodging. Abiotic: drought, heat, low P	Must have traits: seed size > 16 g per 100 grains; high protein >38%, Oil >20%, high biomass for West Africa, Medium tall >50 cm <70 cm Nice to have traits: herbicide tolerant, high oleic acid content, high biomass for Southern Africa	Yield: at least 5% increase over checks (TGx 1740-2F, Jenguma, and/or recently released varieties in maturity group). Maturity: ±3 day check. Resistant to rust, frogeye, leaf blight, shattering, lodging
(2) Medium-late maturing varieties with resistance to rust, tolerance to drought and promiscuous nodulating	0.8 M	40%	Target: Ghana, Nigeria, Mozambique, Malawi, Zambia; spillover: Cameroon, Kenya, Tanzania, Uganda, Democratic Republic of Congo, Rwanda, Zimbabwe, South Africa, Angola, Mali, Ethiopia, South Sudan, Cote d'ivoire	110–120	Biotic: rust, leaf blight, frogeye, shattering, lodging. Abiotic: drought, heat, low P	Must have traits: seed size > 16 g per 100 grains; high protein >38%, Oil >20%, high biomass for West Africa. Height >60 < 90 cm, good pod clearance. Nice to have traits: herbicide tolerant, high oleic acid content, high biomass for Southern Africa	Yield: at least 5% increase over checks (SC Saga, Safari, Square, Dina, Makwacha, TGx 1951-3F and/or recently released varieties in maturity group). Maturity:±3 day check, Resistant to rust frogeye, leaf blight, shattering, lodging

and grain yield were the major traits which formed the basis of variety released in the project countries.

TGx 1835-10E was the first variety to be released on the project in Nigeria in 2008, in one season PVS trials, due to its superior performance, particularly for rust resistance. The Nigerian Plant Variety Release Committee in its meeting in December 2008 approved the registration and release of TGx 1835-10E for general cultivation. TGx 1835-10E was the first released rust-resistant variety in West and Central African countries, as well as the first release of a soybean variety in Nigeria since 1992. In an on-farm trial carried out at 13 locations in eight states, TGx 1835-10E showed a yield advantage of 25% over a rust susceptible variety TGx 1485-1D used for a long time. Subsequently, a new medium maturing variety, TGx 1904-6F, with high grain and fodder yields was released at the end of 2009 in Nigeria. TGx 1904-6F is adapted to northern Nigeria where both crop and livestock farming are practiced. The variety has a high biological nitrogen fixation capacity. TGx 1904-6F is resistant to lodging, pod shattering, Cercospora leaf spot and bacterial pustule. In Borno State, the mean grain yield of TGx 1904-6F was 3,034 kg/ha whereas the previously popular variety TGx 1448-2E released in 1992 gave 2,441 kg/ha.

Two other rust-resistant varieties (TGx 1987-62F and TGx 1987-10F) were released in Nigeria through the approval of the Nigerian Variety Release Committee in December 2010. TGx 1987-62F and TGx 1987-10F gave an average grain yield of 1,670 and 1,630 kg/ha, respectively, in a two-year multi-location on-station trials in Nigeria. TGx 1987-62F and TGx 1987-10F gave 58% and 54% more grain yield, respectively, as compared to an early maturing variety TGx 1485-1D in a 2-year average performance. They also surpassed TGx 1835-10E by 22% to 33% in grain yield in the 2009 on-station trials. The maturity of these varieties range from 96 to 97 days on average and are capable of producing 2.6 MT/ha fodder under on-station trials condition. Besides giving high grain yield, these varieties were resistant to soybean rust and other foliar diseases. In the 2009 multi-location trials, rust incidence was only 1.3%–1.6% as compared to the susceptible variety TGx 1485-1D that showed a 22.3% incidence in the same trial. On-farm trials in four states (Kaduna, Benue, Kano and Niger) of Nigeria by 175 farmers showed that TGx 1987-10F and TGx 1987-62F averaged 1,626 and 1,567 kg/ha, respectively. These new varieties surpassed TGx 1485-1D by 5%–9% in terms of grain yield. These varieties are preferred by many farmers because they smother weeds and reduce the cost of weeding, mature early, give high yield and the seed colours are attractive.

In Malawi, TGx 1740-2F was officially released on 18 January 2011 through the approval of the Malawi Agricultural Technology Clearing Committee (ATCC). TGx 1740-2F outperformed the popular varieties both on-station and on-farm trials and was released under the commercial name 'Tikolore' meaning let us harvest in local language and now covers more than 40% of the area under soybean production in Malawi. Five high yielding varieties with a range of maturity were released and popularized in Mozambique, TGx 1740-2F ('Wamini'), TGx 1904-6F ('Zamboane'), TGx 1908-8F ('Wima'), TGx 1937-1F ('Olima') and TGx 1485-1D ('Sana'). These varieties currently

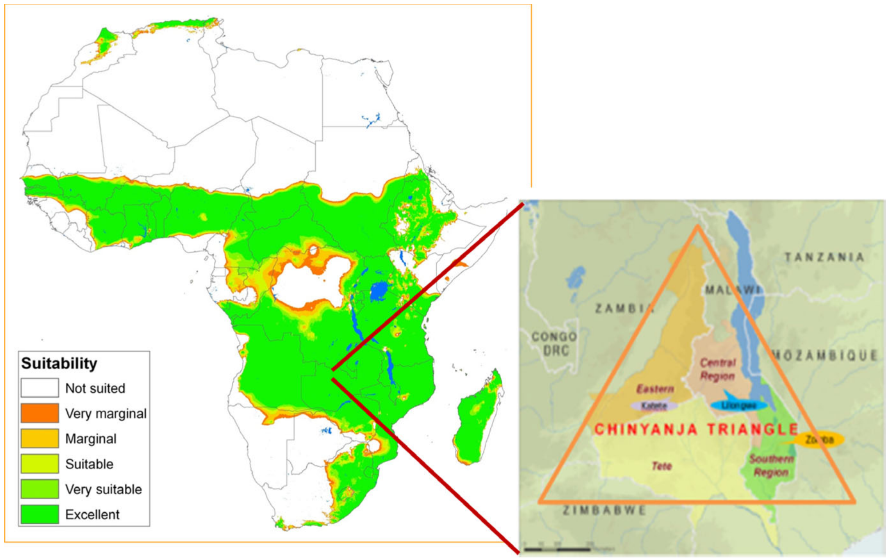

FIGURE 3 Soybean suitability map showing the Chinyanja Triangle, the Target Production environment for Southern Africa [Colour figure can be viewed at wileyonlinelibrary.com]

are occupying more than 50% of area under soybean production in Mozambique.

In Kenya under Tropical Legume II, five soybean varieties including varieties from the private sector, 'Nyala', 'Hill', 'Black Hawk', 'Gazelle' and 'EAI 3600' that have been used in the country for a long time were officially released and registered in 2009 by KEPHIS. In 2010, two dual-purpose for grain yield and fodder yield IITA promiscuous varieties (TGx 1740-2F and TGx 1895-33F) were released as SB19 and SB8, respectively.

Spillover countries which benefitted directly from TLI and TLII include Zambia where TGx 1740-2F and TGx 1937-1F were released as 'Kafue' and 'Mwembeshi' respectively in 2015. TGx 1740-2F is now one of the widely adapted soybean varieties having registered and released commercially in eight African countries which include Benin, Cote d'ivoire, Kenya, Malawi, Mozambique, Nigeria, Togo and Zambia.

Another major achievement of the TLII project was the production and dissemination of seeds of newly released soybean varieties in the project countries to enhance adoption. Several partnerships were established with seed companies, community seed producers, farmers' associations, agro-dealers and other legume seed value chain actors to facilitate seed production and delivery to farmers in remote locations. An innovative soybean seed system was developed to strengthen the knowledge and skills of seed producers, establish linkages among seed value chain actors, create awareness on new varieties through various channels including demonstration plots, field days, user-friendly bulletins and fact sheets, and radio and television programmes. Through the project, breeder and foundation seeds were produced and made available to seed producers to produce certified or quality declared seeds which were sold to farmers. This significantly increased seed production in the project countries which enhanced access to improved soybean seeds by farmers. During its implementation 2008 to 2014, the project and partners produced a total of 12,556 tons of soybean seeds in Nigeria, 5,170 tons in Mozambique, 443 tons in Kenya and 150 tons of seeds in Malawi (Monyo & Varshney, 2016).

5 | GERMPLASM EXCHANGE AND COLLABORATIONS

IITA in collaboration with National Agricultural Research systems (NARs) in Nigeria and Ghana initiated comprehensive soybean international trials (SIT) in the early 1980s and today this has expanded to include a number of African countries and a total of 112 trials were sent out between 2013 and 2016 with 60% being early maturing variety trials (Table 4). The trials have been an important testing platform for partnerships for germplasm exchange and information resource for the different stakeholders in the soybean industry who have specific requirements in order to overcome their production constraints and improve profitability. Survey carried out by Alene and Mwalughali (2012) on the adoption of improved soybean varieties and varietal catalogues from participating countries indicate that in total, over 100 IITA varieties were released in more than 15 countries with Nigeria, Cote d'ivoire, Benin and Ghana having the highest number of varieties (Figure 4). In Ghana, the replacement of old soybean varieties that were susceptible to pod shattering with new pod shattering resistant varieties 'Jenguma' (TGX 1448-2E), released in 2003 and 'Afayak' (TGX 1834-5E), released in 2012 boosted production by small-scale farmers who previously suffered significant yield losses due to late harvesting from 50,000 metric tonnes in 2005 to 142,000 metric tonnes in 2015 (MoFA-SRID, 2007; 2015). Participation in the soybean international trials is free, and contact information can be forwarded on IITA web pages http://www.iita.org/research/our-research-themes/improving-crops/soybean-crop-improvement/.

6 | PERSPECTIVE ON FUTURE BREEDING APPROACHES

In order to clearly identify and engage collaborators at various stages of the breeding programme, the stage-gate approach commonly used by private sectors has been adopted by the IITA soybean breeding

TABLE 4 Number of soybean international trials' summary of SIT sent out by IITA between 2013 and 2016

Year	No. countries participating	No. institutes participating	Number of genotypes/trial	Early	Medium	Total trials per year
2013	7	13	32	20	16	36
2014	10	12	32	16	15	31
2015	9	10	26	11	8	19
2016	6	11	17	21	5	26
Total trials				68	44	112

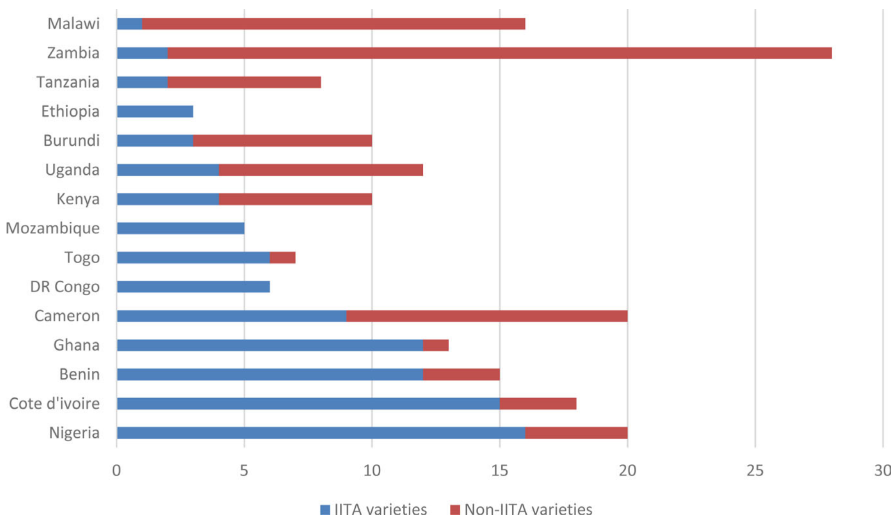

FIGURE 4 Number of IITA varieties released in 15 African countries with the Soybean International Trials (SIT) as the main source of germplasm [Colour figure can be viewed at wileyonlinelibrary.com]

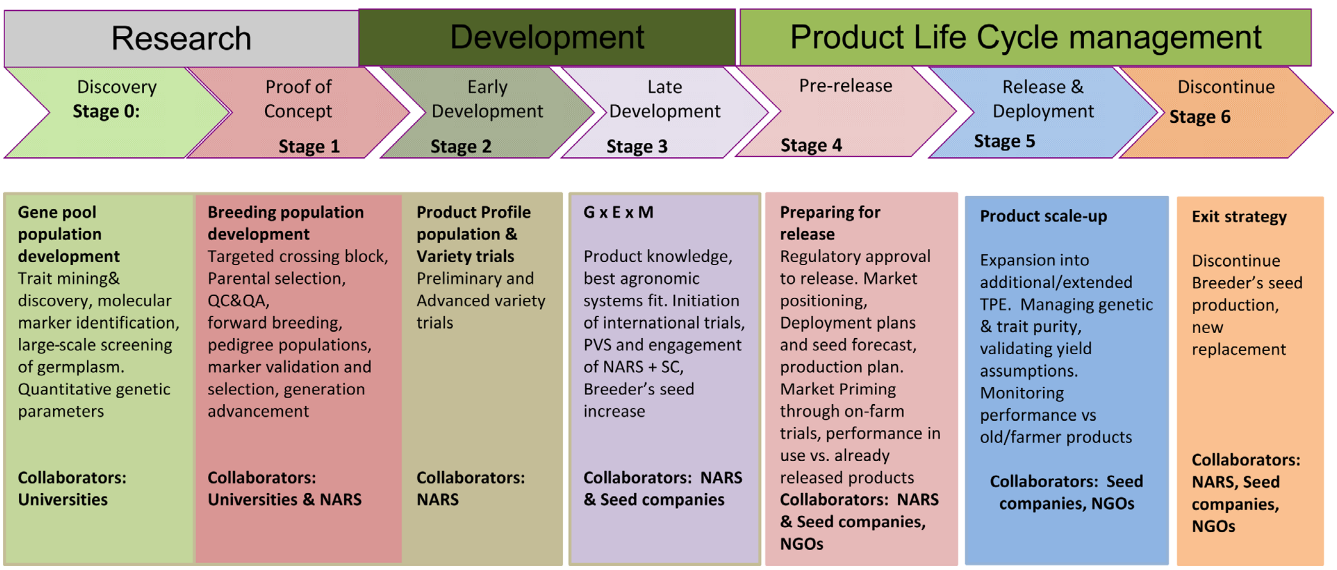

FIGURE 5 Collaborative breeding and selection strategy in the IITA soybean breeding program following the stage-gate approach commonly used by the large private sector seed companies [Colour figure can be viewed at wileyonlinelibrary.com]

programme. The stage-gate approach permits resource allocation for continuity of breeding operations and genetic gain per unit time; so that the generation interval and delays in bringing improved varieties into hands of farmers are minimized. It also allows the leverage germplasm in gene pools and breeding populations to increase and preserve genetic diversity for the long-term as well as avoid dilution of genetic gain by managing the product life cycle (Figure 5).

In the discovery and proof of concept, stages 0 and 1 respectively, sometimes also referred to as pre-breeding stage, collaborations with universities will be key to the success of this strategy as this will require the evaluation of large populations to elucidate the genetic architecture of the traits before selection begins. The use of molecular markers at these stages is also vital for quantitative trait loci (QTL) identification, validation and gene pyramiding. Selecting parental genotypes using molecular markers for initiating targeted crossings in the breeding pipelines based on defined target product profiles to form bi-parental breeding population starts and MAGIC populations is still in its infant stage at IITA. Currently, markers are only used for quality control (QC) and quality assurance (QA) of F_1 progenies using SSR markers is routinely being carried out to eliminate selfs or contaminations at early stages in the IITA breeding programme. Stages 2 to 6 are self-explanatory as outlined in Figure 5. IITA is currently implementing stages 2 to 6 in collaboration with a number of institution including the Soybean Innovation Laboratory (SIL), the Syngenta Foundation through the Pan African Variety Trials, NARs in Cameroon, Ghana, Ethiopia, Malawi and Zambia through the Soybean International Trials (SIT) which resulted in the release and commercialization of over 100 soybean varieties since its inception in the 1980s (Chiona, Chigeza, & Ntawuruhunga, 2017).

Despite the abundance of genomic resources, the application of genomics-assisted breeding in soybean is dismally low in the public sector breeding but high in the private sector in countries such as the USA. There are wide array of DNA marker resources available for soybean improvement worldwide in a form of breeders tool kit (Grant, Nelson, Cannon, & Shoemaker, 2010; https://www.soybase.org/). Numerous molecular genomic resources, including SSR, single nucleotide polymorphism (SNP) and targeting induced local lesions in genome (TILLING) resources, are available in public databases. Some of the notable databases and tools that are relevant to soybean include the following: SoyBase and the Soybean Breeder's Toolbox (Grant et al., 2010; https://www.soybase.org/) where resources such as physical and genetic maps, genome sequences, expression data, analysis tools are freely accessible and downloadable. Likewise, the Soybean Knowledge Base (SoyKB): a web resource for soybean translational genomics is freely available (Joshi et al., 2012; http://soykb.org/). Other useful resources include the LIS—Legume Information System: Information about legume traits for crop improvement—A collaborative, community resource to facilitate crop improvement by integrating genetic, genomic and trait data across legume species (Dash et al., 2015; https://legumeinfo.org/). Phytozome (https://phytozome.jgi.doe.gov/pz/portal.html) and Plant genome database (http://www.plantgdb.org/) also have resources for mapping SNP markers to the reference genome and other genomic analysis including similarity search, annotation, multiple sequence alignment, and comparative genomics. Such resources are crucial in genomics discovery research aimed at developing functional predictive markers for use in accelerated breeding of economically important agronomic traits.

7 | CONCLUSIONS

Soybean is a crop with high potential for expansion in Africa. Remarkable progress by IITA and its partners has been achieved in the varietal release front especially in West Africa. Replicating this success story in Southern Africa while maintaining the momentum in West Africa remains the challenge of the current and future IITA breeding programme. Breeding strategies to pyramid unmet market traits such as seed size, rust resistance, heat and drought tolerance on the pillar lines is in progress. The advent of next-generation technologies and availability of a plethora of genomic resources, genotyping platforms, paves the way for accelerated, genomics-driven improvement of soybean. Such genomics-assisted breeding pipelines are easily adoptable by NARS in developing countries to enhance soybean productivity by developing high yielding varieties. Equally important for the future is portfolio management which includes maintaining genetic and trait purity for the released varieties.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interests.

AUTHOR CONTRIBUTION

Godfree Chigeza (GC) and Eric Agoyi (EA) coordinated the manuscript layout and wrote the manuscript; Malaku Gedil (MG) did the genetic diversity studies on 68 IITA soybean lines and wrote the section on soybean diversity; Steve Boahen (SB) and Alpha Kamara (AK) wrote the section on achievements of Tropical Legumes I and II in Mozambique and Nigeria, respectively; Emmanuel Alamu (EA) and Therese Gondwe (TG) provided inputs and data on variety release in Malawi and Zambia; Nicholas Denwar (ND) provided data and contributed to soybean release and registration in Ghana. Abush Tesfaye (AT), Hapson Mushoriwa (HM) and David Chikoye (DC) improved the manuscript and provided revisions to the different sections of the manuscript.

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