Developing the role of legumes in West Africa under climate change

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West Africa is faced with significant challenges from climate change, including parts of the region becoming hotter with more variable rainfall. The Sahelian region in particular is already subject to severe droughts. To address this better adapted crop varieties (such as for cowpea) are clearly a central element, a complementary one is a greater use of resilient alternative crops especially underutilized legumes particularly Bambara groundnut, African yam bean, winged bean and Kersting's groundnut. Genetic diversity of these crops conserved in genebanks and farmer's field provides an opportunity to exploit climate resilient traits using cutting-edge genomic tools and to use genomics-assisted breeding to accelerate genetic gains in combination of rapid cycle breeding strategy to develop climate-resilient cultivars for sub-Saharan Africa.

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Introduction

Recent studies and simulation reports predict 2–4°C increase in temperature by the late 21st century [1,2] and that will reduce the global yield of all major crops [3,4]. An IPCC-2012 [5] report of summary for policymakers states that African agriculture faces rising temperature and more risky weather due to climate change. Thus, climate change is likely to have a significant negative impact on agriculture as well as on livelihoods and food security in sub-Saharan Africa. West Africa and parts of southern Africa, particularly Zambia and Zimbabwe, show rapid and statistically significant decreases in precipitation [1]. The Sahelian region, in particular, is already subject to severe drought. Top six key staple crops of SSA are rice, cassava, sorghum and grain legumes/pulses, along with maize based on production, area harvested and yield [6]. Nodulated legumes have been cultivated by indigenous peoples in Africa for centuries, but their full potential has never been realized [7]. Cowpea is the only indigenous legumes crop, which is a traded commodity and grown in large areas throughout the Africa, majority from West Africa. There are other African legumes includes Bambara groundnut, African yambean and Kersting's groundnut part of a group known as orphan legumes or underutilized legumes, which are grown by poor smallholder farmers. These are well-adapted to the many soils and climatic conditions of Africa, in particular, drought and low soil fertility [7]. However, despite its relatively high tolerance to drought, considerable reduction in cowpea yield has been reported due to prolonged drought periods in sub-Saharan Africa [8,9]. All these legume crops nodulate and fix nitrogen, with varying degrees of effectiveness and using a range of bacterial symbionts. Advanced breeding efforts to improve yield and climate resilient traits including quality are constrained by a low level of genetic diversity in breeding programmes. The Genetic Resources Center (GRC) of the International Institute of Tropical Agriculture (IITA) conserve the world's largest collection of cowpea, Bambara groundnut, African yambean and a small collection of winged bean and Kersting's groundnut. The genetic diversity of these crops has not been fully explored and utilized in active breeding programmes. With recent advances in genomics, large germplasm collection can be characterized genome-wide to identify single nucleotide polymorphism (SNP) markers and superior alleles/haplotypes through NGS based sequencing approaches and SNP markers can be used in genomics-assisted breeding (GAB) together with precise phenotyping can be deployed to improve genetic gain for complex climate resilient traits. Robust GAB approaches can be utilized in any season or any stage of plant growth [10]. Limited efforts have been made towards GAB in cowpea and any other orphan legumes compared with chickpea, pigeon pea, groundnut and soybean [11–13]. GAB approach can play an important role to accelerate genetic gain of climate resilient traits by developing improved cultivars which can mitigate climate change to meet the target demands of food production of SSA region.

In this review, we summarize the likely climate change impacts in West Africa and applications of genetic and genomic information together with precision phenotyping in the breeding of legumes for this region. We focus on genetic resources available and future production potential

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of cowpea, African yam bean, Bambara groundnut, winged bean and Kersting's groundnut.

Climate change in West Africa

Because of climate change, majority of countries in Africa will experience novel climates over at least half of their current crop area by 2050 [14]. Climate change especially temperature and precipitation have immediate effects on crop production and food security globally and in Africa [1,15–20]. Already relatively strong future climate change signal has been projected for the African continent, [17] that will highly impact this continent due to two reasons; 1) its geographical characteristics with the majority of land in warming tropics, and 2) relatively limited capacity to adapt to climate effects [1,21]. There have been few models of future climate scenarios for West African crops. However, in recent years a number of studies give insights into past trends. Girvetz et al. [1] in Coupled Model Intercomparison Project Phase 5 (CMIP5) suggested that temperature increases for Africa with the current emissions trajectory (i.e. RCP 8.5) is 1.7°C by the 2030s, 2.7°C by the 2050s, and 4.5°C by the 2080s using GCM model. Modeling of future precipitation is very difficult [22,23]. The median of the CMIP5 models indicates that by 2050, under the higher emission scenario (RCP 8.5), annual precipitation will increase across much of eastern and central Africa, while decreasing across parts of southern, western and northern Africa [1]. Sylla et al. [24] note that 'it is thus evident that in a 'business as usual' world, most countries in West Africa will have to cope with shorter rainy seasons, generalized torrid, arid and semi-arid conditions, longer dry spells and more intense extreme precipitations'. Projected climate change indicates continuous and stronger warming (1.5–6.5°C) and a wider range of precipitation uncertainty (roughly between −30 and 30%) larger in the Sahel and increasing in the farther future [24]. Barry et al. [25••] analyzed trends for the 50 years from 1980 in 14 West African countries. They found 'statistically significant increases of 0.16°C/decade and 0.28°C/decade for mean annual maximum and mean annual minimum temperatures, respectively. Moron et al. [26] also observed similar linear trends of annual mean maximum and minimum temperature equal respectively +0.021°C/year and +0.028°C/year using a network of 90 in situ observation in West Africa. Several studies conclude that benefit of elevated CO_2 will be greater for C3 crops (e.g. soybean groundnut) that accumulate more biomass and for C4 crops in arid regions with increased water use efficiency [27–29]. However, both Sultan et al. [28] and Deryng [30] also showed that it partially offsets the impacts from climate changes especially in the Western part of Africa where yield losses are expected even after accounting for CO_2 fertilization effect. A meta-database of future crop yields, built up from 16 studies database, was used to provide an overall assessment of the potential impact of climate change on yields. They found that despite a large dispersion of yield changes ranging from −50% to +90%, the median was a yield loss near −11% in thirteen major staples crops (cotton,

groundnut, maize, millet, rice, sorghum, soybean, wheat, yams, Bambara groundnut, beans, cassava, cowpea) of African continent including West Africa [31••]. Ramirez-Villegas and Thornton [32] found that humid and West African countries (including those across the Sahel) are amongst the most negatively impacted, with mean production losses between 20 ~and 40% by 2050s (RCP8.5). They also projected that the majority (∼90 %) of currently cropped maize area of African continent will experience negative impacts, with production reductions in the range 12–40%. However, Sorghum, cassava, yam and pearl millet show either little area loss or even gains in suitable area, whereas common bean, maize, banana and finger millet are projected to reduce their suitable areas significantly (30–50%). Maize cultivation across Africa could mitigate 31% of yield losses attributable to water stress [33]. West African regional average yield reductions were projected 10–20% for millet and 5–15% for sorghum in the two crop models [34]. Using time series data on rainfall, production and other weather and agronomic data for Niger, Mohamed et al. [35] and Vanduivenbooden et al. [36] argue that by 2025 climate change might lower millet yields by 13%, groundnuts by 11–25% and cowpeas by 30%, while Butt et al. [37] projected that by 2030 climate change might lower maize yields by 22–25%, groundnuts by 21–22%, sorghum by 21–24 % and cowpeas by 22–24 % in Sikasso regions (north, west and central) of Mali. Under climate change scenario GISS A2 2080, Bambara groundnut (orphan African legume), yields were almost trebled (37.1% increase above that for sowing date alone (12.9%)) due to increase length of growing period and the positive effects of higher CO_2 concentrations [38]. Overall mostly research effort in crop modeling were have been focused on the world's major food crops such as wheat, maize, rice and sorghum and the simulation of crops common in African farming systems (sorghum, millets, cassava, yam) is less well developed as well as simulations of crops grown as intercrops across Africa [39,40] including cowpea and other orphan legume crops. From these studies, it seems clear that the effects of climate changes will be marked particularly in the Sahelian region where options for smallholder farmers are already constrained. There is an estimation that over 30% of the area where maize is grown and over 60% of the area where beans are grown would need to grow entirely different crops by the end of the century [41]. New alternative crop varieties well suited to the future climatic conditions are required [14] for future food security in the SSA. Alternative crops for African continent could be approached by extending the crop diversification which is currently depending on few major crops of the world. This extended crop diversification could include enhanced the use of 'orphan crops' (also known as 'minor crops', 'underutilized plant species', 'neglected crops' and 'future foods') which are rich in vitamins, essential minerals and other micronutrients important for healthful diets [42] and also climate resilient [43–46]. Alternative legume crops could also be used as intercrop with other crops like maize, cassava, sorghum and millet to avoid complete crop failure.

So, there is an urgent need to focus on both adaptation of major crops and development of alternatives that may help develop more climate resilient and nutritious food production systems. Another dimension is the likely change in distribution and severity of pests and diseases. These are already significant causes of yield loss in the staple crops of the region particularly cowpea as shown below.

Cowpea

Cowpea (*Vigna unguiculata*) is one of the most economically important indigenous African food legume crops which provides an affordable source of essential nutrients and low-cost protein [47,48] to millions of people and also quality fodder for livestock in the dry savannas of tropical sub-Saharan Africa (SSA). This crop is widely grown in SSA with around 12.5 million hectares produced mainly in the dry savannahs to the Sahel in the fringes of the Sahara Desert with annual rainfall of about 300 mm or even less [49] due to its ability to survive in arid and semi-arid conditions with a tropical climate, low fertility soil and soil fertility enrichment using nitrogen-fixation.

Genetic resources

The Genetic Resources Center (GRC) of the International Institute of Tropical Agriculture (IITA) has the largest cowpea collection of over 15 003 accessions and 2500 accessions of wild *Vigna* species collected from about 89 countries across the globe, a key legume of the savannah and Sahelian regions of West Africa. A core collection of 2062 accessions covering most of the diversity existing in the entire collection at IITA has been defined using 28 agronomic and botanical descriptors for the grouping of accessions which covered a wide range of phenotypic variation among the collection. A mini-core collection of 370 has also been developed as well as further set of about 200 accessions derived from a Focused Identification of Germplasm Strategy (FIGS) which allows the selection of a trait based sub-set of germplasm for heat and drought tolerance. This subset will be tested by breeders in sub-Saharan Africa and elsewhere. A multi-parent advanced generation intercross (MAGIC) population of 305 lines for cowpea has been developed [50••] from eight founder parents that were genetically diverse and carried many abiotic and biotic stress resistance, seed quality and agronomic traits relevant to cowpea improvement in the United States and SSA. The MAGIC populations are an emerging type of genetic resource for dissecting the genetic structure of traits and improving breeding populations. A number of advances in cowpea genomics have been made including development of genetic linkage maps, an improved consensus genetic linkage map, MAGIC population and identification of quantitative trait loci associated with desirable traits such as resistance to *Striga*, *Macrophomina*, *Fusarium* wilt, bacterial blight, root-knot nematodes, aphids, foliar thrips and heat and drought stress [50••]. Several cowpea breeding programs have been initiated with available genetic resources at IITA to implement molecular breeding, especially for marker-assisted recurrent selection (MARS) and marker-assisted backcrossing (MABC) populations, to accelerate cowpea variety improvement in SSA region [51,52]. Recently, the cowpea reference genome has been published [53••] which will provide opportunities for improving our understanding of the history of cowpea domestication, how to link genomic information between gene to trait and to accelerate crop improvement. The combination of advanced bioinformatics tools and accessible genome-wide profiling (DNA or RNA) have greatly enhanced our understanding of crop genome and marker/gene to trait association. Both mini-core set and FIGS population of cowpea at GRC, IITA have been genotyped using high-throughput DArTseq-GBS (genotype-by-sequencing), SNP (single nucleotide polymorphism) and *in silico* markers (presence/absence) to get detailed genome-wide genetic diversity information, population structure and QTL/gene discovery with marker-trait association analysis for genomics-assisted breeding (GAB) research. Similarly, a core set of 305 lines (F8 generation) of cowpea MAGIC population also has been genotyped with 51 128 SNPs using the Illumina Cowpea Consortium Array [54] and used for marker-trait association analysis for different agronomical and morphological traits such as photoperiod sensitivity, flowering, maturity, seed size and yield. More than twenty-four IITA cowpea varieties were released from 2008 to 2017 in 13 different countries to improve yield in sub-Saharan Africa. There is need to have focus to do genotyping of cowpea core-collection as well as whole conserved collection of cowpeas at GRC-IITA to explore untapped genetic diversity which can be key factor for future breeding to develop climate resilient cultivars.

Nutrition

Cowpea is a rich source of phytonutrients which make it one of the most suitable African indigenous crops in aspects of nutritional balanced diet and solving malnutrition crisis among the resources-constrained household in SSA [55–57]. A nutritional study of 1541 cowpea germplasm lines revealed that on average cowpea has 25% protein and ca. 38 mg Zn/kg, 53 mg Fe/kg, 1.9 g Mg/kg, 0.825 g Ca/kg, 5 g P/kg, and 15 g K/kg [57]. Jemo *et al.* [58] reported that nitrogen fixation was significantly reduced in soils with low P levels and limited water supply. Cowpea can play a great role in soil fertility enrichment by adding 70–350 kg nitrogen per ha [58] through nitrogen fixation. There is limited research done for QTL discovery of nutritional traits. At the same time, it needs more attention to do genomics research for the nutrition traits of cowpea that will help sustain the nutritional security of SSA regions.

Yield constraints

Both biotic and abiotic stresses are significant yield-limiting constraints in cowpea. Africa contributed over 87% cowpea

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production in total word cowpea production 7.7 K tonnes [59] with over 80% of African production in West Africa. But the average productivity of SSA farmer's fields is less than 600 kg/ha compared with a potential grain yield over 2000 kg/ha [49]. This average yield productivity can be further reduced in climate change scenario especially in SSA regions. The integrated breeding efforts for increasing yield in SSA has been initiated by IITA through enhancing the resistance potential of cowpea for its yield constraints both biotic, abiotic stresses and for yield attributive traits using both conventional and molecular approaches. Several efforts have been made on cowpea to develop many linkage maps, recombinant inbred line (RIL) population, Multi-parent advanced generation inter-cross (MAGIC) population to identify QTLs for the desirable traits. Several efforts have been made to identify QTL for many desirable traits using bi-parental mapping population, back-cross mapping population, and natural population for genome-wide association study (GWAS) in cowpea. The detail of the identified QTLs of several traits of cowpea has been mentioned in Table 1, which could be useful for genomic-assisted breeding to develop improved cowpea under climate change.

Biotic stresses

Insects and other pest are the major limiting factor which affects cowpea yield in SSA throughout the crop cycle, among them aphids (*Aphis craccivora Koh*) at seedling stage [60] flower thrips (*Megalurothrips sjostedti Trybom*), pod borer (*Maruca vitrata Fab.*) and pod sucking pest (*Clavigralla tomentosicollis Stal*) after flowering stage are important pest in tropical Africa [60,61]. The QTL for aphid and foliar thrips tolerance have been identified in [62,63], while another new source of aphid resistance found in wild relative lines TVNu-1158 [49]. Besides pest, cowpea is also susceptible for diseases which caused by virus, fungi, bacteria and nematodes. Bacterial blight (*Xanthomonas* sps) and anthracnose and brown blotch (*Colletotrichum* sps) are main bacterial and fungi disease in cowpea, while root-knot nematodes (*Meloidogyne* sps.) damage cowpea root-system and cause yield reduction in different cowpea production area of Africa. In highly susceptible line grown in monocrops with severe disease attack can cause yield reduction of 30–50% [64]. Several viruses affect cowpea yield but among them cowpea aphid-borne mosaic potyvirus (CABMV) is most problematic and reduced yield up to 60% [65]. The candidate genes and QTL have been reported for different disease stresses in cowpea such as identify bacterial blight [66], fusarium wilt race three and race four [67,68], charcoal rot resistance [69] and cowpea golden mosaic virus [70]. *Striga gesnerioides* and *Alectra vogelii* are two parasitic weeds in which *Striga* is mainly present in the dry savannah areas of West and Central Africa while *Alectra* is found predominantly in eastern and southern Africa [49]. Yield reduction was reported from 73 to 100% by *Striga* infestations in Africa [71]. Striga resistance gene race one and race three have been mapped by molecular markers [72,73] and are in use to improve striga resistance in cowpea breeding.

Abiotic stresses

Abiotic stresses are a major cause of yield-loss to agriculture crops worldwide because different vegetative, physiological, reproductive plant attributes including the seed development process affected by these stresses from seedling to crop maturity. Vogel *et al.* [74••] found that growing season climate factors including mean climate as well as climate extremes explain 20%–49% of the variance of yield anomalies (the range describes the differences between crop types), with 18%–43% of the explained variance attributable to climate extremes, depending on crop type. It is true cowpea is relatively tolerance to drought and salt stress [75] but unpredictable 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 in SSA [49]. In cowpea, temperature about 35°C can cause yield reduction by aborting pollen in flowering stage and also by affecting seed development during grain filling period. A set of 190 drought tolerance were identified from 1200 accessions under terminal drought screening in field trial [76]. The QTL has been identified for drought-induced senescence [76] senescence [77] and heat tolerance [78] in cowpea. The QTL for early flowering [77] and maturity [69] have been detected. Lines that are early flowering and maturity can be used for escaping damage by flower/pollen abortion as well as flower/pod feeding insect and abiotic stresses namely terminal heat and drought stress. Goufo *et al.* [79] studied the mechanisms by which cowpea modifies its metabolism to meet the demands of diverse resistance functions when exposed to water deficit appear to be determined by the interplay between the shikimate and arginine/proline pathways, giving rise to three drought-responsive metabolites, namely proline, galactinol and quercetin 3-O-6''-malonylglycoside. Cowpea genomic region jointly associated with these pathways and investigating their co-localization with quantitative trait loci in a larger population may indicate promising candidate for drought tolerance. Out of nine candidate reference genes of abiotic stresses used in qPCR validation activities in cowpea, the candidate genes *UNK*, *VuACT* and *UE21D* were most stable under root dehydration stress, while the candidate genes *UNK*, *UE21D* and *FBOX* were the most stable genes for salt stress [80]. These candidate gene results may guide future research on gene expression in cowpea under other abiotic stress.

Another genomic approach known as genomic selection (GS) offers simultaneous selection of thousands of SNP genome-widely to ensure that all genes are expected to be in linkage-disequilibrium (LD) with at least some of the SNP markers [81,82]. Because GS can capture small-effect QTL which governing the majority of phenotypic variation, including epistatic interaction effects [83], it could play an important role in cowpea breeding to increase genetic gain and accelerate plant breeding cycles for complex quantitative traits of biotic and abiotic stresses.

Table 1

QTL detected by using different mapping population for cowpea traits

S. No	Traits	Population name	Type	Marker type	markers/ QTLs	Linkage group (LG)/ Chromosome (Chr)	R^2 %	References
1	Domestication-related traits	(JP81610 × JP89083) × JP81610	BC1 F1	SSR	1-11 for most traits	LG3,7,8,11	3–57%	Kongjaimun *et al.* [149]
2	Seed Pattern	One MAGIC population (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246); four RIL California Blackeye-27 x IT82E-18; California Blackeye-27 x IT97K-556-6; California Blackeye-46 x IT93K-503-1; 524B x IT84S-2049); Three F2 populations (California Blackeye-27 x Bambey 21, Bambey 21 x California Blackeye 50, Tvu-15426 x MAGIC014)	Multi-parent advanced generation inter-cross (MAGIC) population, four RIL and three F2 populations	SNP	3	Chr7, 9, 10		Herniter *et al.* [150]
3	Maturity	IT93K503–1 × CB46	RIL	AFLP	2	LG7, 8	25–29%	Muchero *et al.* [69]
4	Hastate leaf shape	Sanzi × Vita 7	RIL	SNP	1	LG15	74.70%	Pottorff *et al.* [151]
5	Flower and seed coat color	ZN016 × Zhijiang 28-2	RIL	SNP & SSR	1 each	LG8		Xu *et al.* [152]
6	Time of flower opening	524 B × 219-01	RIL	SSR	5	LG1	9–30%	Andargie *et al.* [153]
7	Days to flower	524 B × 219-01	RIL	SSR	3	LG1		Andargie *et al.* [153]
8	Days to first flowering	ZN016 × ZJ282	RIL	SNP	3	LG3,10,11	10–32%	Xu *et al.* [77]
9	Nodes to first flower	ZN016 × ZJ282	RIL	SNP	4	LG2,4,6,11	11–22%	Xu *et al.* [77]
10	Floral scent compounds	524 B × 219-01	RIL	SSR	63	LG1,2,4	60%	Andargie *et al.* [154]
11	Pod tenderness	(JP81610 × JP89083) × JP81610	BC1F1	SSR	3	LG7,8,11	6–50%	Kongjaimun *et al.* [155]
12	Pod tenderness	JP81610 × JP89083	F2	SSR	2	LG7, 8	6–45%	Kongjaimun *et al.* [155]
13	Root architecture	natural germplasm	GWAS population	SNP	32	LG1,2,3,4,5, 6,7,8,910,11		Burridge *et al.* [156]
14	Flowering time (days) under long day length at UCR-CES	inter cross of eight parents (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246)	Multi-parent advanced generation inter-cross (MAGIC)	SNP	4	Chr4,5,9,11	8.8–15.3%	Huynh *et al.* [50••]
15	Flowering time (days) under short day length at CVARS	inter cross of eight parents (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246)	Multi-parent advanced generation inter-cross (MAGIC)	SNP	4	Chr1,4,5,9	8.8–13.3%	Huynh *et al.* [50••]
16	Growth habit at UCR-CES	inter cross of eight parents (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246)	Multi-parent advanced generation inter-cross (MAGIC)	SNP	2	Chr1,9	9.4-10.1%	Huynh *et al.* [50••]
17	Growth habit at CVARS	inter cross of eight parents (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246)	Multi-parent advanced generation inter-cross (MAGIC)	SNP	1	Chr1	21.60%	Huynh *et al.* [50••]

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Table 1 (*Continued*)

S. No	Traits	Population name	Type	Marker type	markers/QTLs	Linkage group (LG)/Chromosome (Chr)	R^2 %	References
18	Maturity (days) at CVARS under normal irrigation	inter cross of eight parents (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246)	Multi-parent advanced generation inter-cross (MAGIC)	SNP	1	Chr5	11.80%	Huynh et al. [50••]
19	Maturity (days) at CVARS under restricted irrigation	inter cross of eight parents (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246)	Multi-parent advanced generation inter-cross (MAGIC)	SNP	3	Chr2,5,9	8.9–10%	Huynh et al. [50••]
20	Seed size	524B × 219-01	RIL	SSR	6	LG1, 10	9–19%	Andargie et al. [157]
21	Pod fiber layer thickness	524B × 219-01	RIL	SSR	4	LG1, 10	6–17%	Andargie et al. [157]
22	Pod length	(JP81610 × TVnu457) × JP81610	BC1 F1	SSR	9	LG1,2,3,4,5,7,8,9,11	31	Kongjaimun et al. [158]
23	Seed weight	IT2246-4 × TVNuI963	F2	RFLP	2	LG2, 6	37–53%	Fatokun et al. [159]
24	Seed weight	524B × 219-01	RIL	SSR	6	LG1,2,3,10	8–19%	Andargie et al. [157]
25	Pod number per plant	ZN016 × ZJ282	RIL	SSR	3	LG2,3,4	11–20%	Xu et al. [160]
26	Seed size	Eight different populations	RIL	SNP	10	LG2,5,67,8,10	47%	Lucas et al. [161]
27	Seed weight	Natural population	GWAS meta-analysis	SNP	13	LG3,4,5,6,8,10,11		Lo et al. [162]
28	Seed weight	Natural population	GWAS meta-analysis	SNP	1	LG3	7%	Lo et al. [162]
29	Seed weight	Natural population	GWAS meta-analysis	SNP	3	LG2,8,11	7–22%	Lo et al. [162]
30	Seed size (g/100 seeds) at CVARS	inter cross of eight parents (SuVita-2, CB27, IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, IT84S-2246)	Multi-parent advanced generation inter-cross (MAGIC)	SNP	2	CHr6,8	10.1–27%	Huynh et al. [50••]
31	Pod shattering	JP81610 × TVnu-457	F2:3	SSR	1	LG7	32.12%	Watcharatpong et al. [163]
32	Striga resistance	TVx 3236 × IT82D-849	F2	AFLP	3	LG1		Oue'draogo et al. [164]
33	Striga resistance	Tvu 14676 × IT84S-2246–4	F2	AFLP	6	LG1		Oue'draogo et al. [164]
34	Striga resistance	Tvu14676; TVx 3236 × IT82D-849	F2	SCAR (61R & 61R-M2)	2	LG1		Oue'draogo et al. [165]
35	Striga resistance	IT93 K-693-2 × IAR1696; T93K-693-2 x Kamboinse local	F2	AFLP/SCAR	4	Same linkage group		Boukar et al. [72]
36	Striga resistance	Gorom x Tvx 3236	F2	AFLP	7			Oue'draogo et al. [166]
37	Striga resistance	TVx 3236 × IT82D-849	F2	AFLP	5			Oue'draogo et al. [166]
38	Cowpea golden mosaic virus	IT97K-499-35 × Canapu T16	F2	AFLP	3	Same linkage group		Rodrigues et al. [70]
39	Cowpea bacterial blight resistance	Danlla × TVu7778	RIL	SNP	3	LG3, 5, 9	10–22%	Agbicodo et al. [66]
40	Charcoal rot resistance	IT93 K-503-1 × CB46	RIL	SNP/AFLP	9	LG2,3,5,6,11	8–40%	Muchero et al. [69]
41	Fusarium wilt resistance (For race 3)	CB27 × 24-125B-1	RIL	SNP	1	LG6	28%	Pottorff et al. [68]
42	Fusarium wilt resistance (For race 4)	IT93K-503-1 × CB46,	RIL	SNP	1	LG8	19–47%	Pottorff et al. [67]

Table 1 (*Continued*)

S. No	Traits	Population name	Type	Marker type	markers/ QTLs	Linkage group (LG)/ Chromosome (Chr)	R² %	References
43	Fusarium wilt resistance (For race 4)	CB27 × 24-125B-1	RIL	SNP	1	LG9	32–40%	Pottorff et al. [67]
44	Fusarium wilt resistance (For race 4)	CB27 × IT82E-18	RIL	SNP	1	LG3	18–27%	Pottorff et al. [67]
45	Root-knot nematodes	RIL (CB27 × 24-125B-1)	RIL	SNP	2	LG11	70.9–72.9%	Huynh et al. [167]
46	Root-knot nematodes	F2:3 (IT84S-2049 × UCR779)	F2:3	SNP	1	LG11	83.10%	Huynh et al. [167]
47	Root-knot nematodes	F2:3 (IT93 K-503-1 × UCR779)	F2:3	SNP	1	LG11	64.50%	Huynh et al. [167]
48	Root-knot nematode (root-galling) resistance (isolate Avr-M.i)	CB46-Null x FN-2-9-04	F2:3	SNP	2	Chr1,4	33.0–73.3%	Ndeve et al. [168]
49	Root-knot nematode (root-galling) resistance (isolate race M.j)	CB46-Null x FN-2-9-04	F2:3	SNP	1	Chr1	95.10%	Ndeve et al. [168]
50	Root-knot nematode (root-galling) resistance (isolate race M.j)	CB46 x FN-2-9-04	F2	SNP	2	Chr1	47.3–65.9%	Ndeve et al. [168]
51	Root-knot nematode (egg-masses per root system) resistance (isolate race M.j)	CB46 x FN-2-9-04	F2	SNP	2	Chr1	24.7–34.1%	Ndeve et al. [168]
52	Root-knot nematode (root-galling) resistance (isolate race M.j)		RIL	SNP	1	LG9	64.00%	Santos et al. [169]
53	Brown blotch resistance	KVx775-33-2 G x KN1 (Vita 7)	F2	allele-specific PCR (AS-PCR)	4	Chr2, 3, 6, 8		Ohlson et al. [170]
54	Foliar thrips	CB46 × IT93 K-503-1 and CB27 × IT82E-18	RIL	SNP	3	LG2, 4, 10	9–32%	Lucas et al. [63]
55	Foliar thrips	CB46 × IT93 K-503-1 and CB27 × IT82E-18	RIL	AFLP	3	LG5, 7	9–32%	Muchero et al. [171]
56	Fower bud thrips resistance	SANZI x VYA	F2	SNP	3	LG2,4,6	6.5–24.5%	Sobda et al. [172]
57	Drought-induced senescence	IT93K503–1 × CB46	RIL	AFLP	10	LG1,2,3,5, 6,7,9,10	5–24%	Muchero et al. [76]
58	Leaf senescence	ZN016 × ZJ282	RIL	SNP	2	LG3,7,11	11–29%	Xu et al. [77]
59	Heat tolerance	CB27 × IT82E-18	RIL	SNP	5	LG2,3,6, 7,10	12–18%	Lucas et al. [78]
60	Nitrogen utilization-related traits	BRS Marataoa x IC-1	F2	SSR	2	LG4, 6	21.4–49.3%	Ohlson et al. [170]
61	Pod fiber contents (Hemicellulose, Cellulose and lignin)	JP81610 × TVnu-457	F2:3	SSR	4	LG7	5.79 –51.32%	Watcharatpong et al. [163]
62	Pod fiber contents (Hemicellulose, Cellulose and lignin)	JP81610 × TVnu-45	F2	SSR	3	LG7	11.31–58.14%	Watcharatpong et al. [163]

R² % represents ranges of phenotypic variation of the given QTLs. Adapted and updated from Boukar et al. [52].

African yam bean

African yambean (*Sphenostylis stenocarpa* Hochst. Ex A. Rich Harms) is an indigenous underutilized legume of SSA. It has the potential to aid the development of nutritious diets under climate change in the smallholder agriculture of SSA. African yambean (AYB) is one of the neglected crops with very limited research attention and no breeding [84]. Its seed, tubers and leaves are nutritionally rich and healthy for

human consumption. AYB is mainly grown for its seeds in West Africa while the crop is grown in East and Central Africa for its tubers.

The neglect and underutilization of AYB may be due in part to some production and utilization constraints, such as long duration of cooking, low yields, anti-nutritional factors and long maturity period [85,86].

The cost of AYB and lima beans are considerably lower than other legumes such as cowpea [87]. Unlike cowpea, AYB and lima beans are neither popular nor widely accepted, despite their wide distribution and better yields [88]. AYB leaves are also cooked and eaten as vegetables [89] because of its nutritional content AYB also has the potential to serve as food supplement to most diets in the third world where there is the lack some essential nutrients resulting in malnutrition in those areas [90,91].

AYB is adaptable to and capable of growing on acid and sandy soils of the humid tropics [43] which makes it a potential climate smart crop for the future. Formation of nodules on AYB plants was recorded by Obiagwu [92] hence the contribution of AYB to soil productivity was attributed to nitrogen fixation and also to its low nitrogen harvest index hence, it is possible to grow AYB without additional supplementary nitrogenous fertilizer, Giller [93] African yam bean's ability to fix atmospheric nitrogen thus imply that large amount of nitrogenous fertilizer is not required to grow on marginal soils which makes its production economically affordable for low income farmers who has little or no resources for chemical fertilizers. The utilization of AYB and other legumes as cover crops increases soil nitrogen content and the amount of organic matter thereby maintaining high soil productivity [94]. AYB climbing habit is also useful in forming a living fence around fields of cocoyam when grown on [43].

Different type of molecular markers such as RAPD [95], AFLP [96,97], SSR [98] and ISSR [99] have been used for molecular research in AYB. There were cross-species transferability of SSRs were reported in AYB by Shitta et al. [98] where cowpea SSR showed PCR amplification and polymorphism in AYB collection. Cross-species molecular marker transferability is useful for those species which don't have any sequence information or marker available, especially in case of orphan crops where limited molecular resources available. There are very limited molecular research efforts done in AYB as compared to cowpea and Bambara groundnut. Genetic diversity of 77 and 67 different accessions was done using AFLP [96], and SSR [98] markers, respectively. The results of most of the genetic diversity study were clustered in three to four groups [96,98,99] and similar trends were also shown in population structure [97,99] analysis using principal component analysis. All these studies indicate availability of wide variation in

AYB collection which can be used for AYB crop breeding. The Alliance for Accelerated Crop Improvement in Africa (ACACIA) is currently carrying out the whole genome sequencing project of AYB [100•]. The genome sequencing of AYB will helpful for markers discovery as well as precise discovery of QTL position in AYB genome. GRC-IITA holds over 450 AYB accession, in which majority of the accessions are from Nigeria. The GRC collection of AYB has been characterized and evaluated for key traits: yield, nitrogen fixation, nutritional quality of tuber and seed and drought tolerance. Significant variation has been observed between accessions for key traits including yield, nitrogen fixation, drought tolerance and seed and tuber composition in preliminary analysis. The genetic diversity, population structure analysis and GWAS analysis for characterized traits are in progress with 250 AYB accessions using DArTseq SNP markers [101] at GRC-IITA. The SNP genotyping can also use for developing core-set of collection from total AYB collection for future breeding research. Development of bi-parental mapping population for different important traits including yield related and nutrition traits are also in progress. So far, there is no report available for the linkage map development and QTL discovery in AYB.

Bambara groundnut

Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is a hardy crop of West African origin with a growing cycle and harvest time ranging from 4 to 6 months depending on the genotype and end use. It is believed to have centers of origin/diversity in Nigeria and Cameroon and is grown in these countries as well as in the Sahelian region of West and Central Africa. It is grown at low levels of inputs very extensively throughout sub-Saharan Africa. There is variation between landraces in the growing degree days to maturity and many other physiological traits. The production of Bambara groundnut (BG) is across the Africa and has been recorded to be approximately 0.3 million tonnes annually [102,103] with Nigeria regarded as the largest producer of BG in Africa (0.1 million tonnes. Although the yield (t ha^{-1}) of BG in Africa varies between landraces and locations (0.5–3 t ha^{-1}) with yield potential of over 3 t ha^{-1} [104] the average yield of 0.85 t ha^{-1} was reported to be comparable to other legumes [105]. In spite of the useful characteristics in BG, farmers in sub-Saharan Africa obtain low yields and this requires research attention to develop improved varieties and crop management practices. It is highly nutritious and has been termed a complete food with a source of protein and fiber and as it nutritionally complements cereal crops [106]. Its seed consist of 49%–63.5% carbohydrate, 15%–25% protein, 4.5%–7.4% fat, 5.2%–6.4% fiber, 3.2%–4.4% ash and 2% mineral compared to whole fresh cow milk 88% moisture, 4.8% carbohydrate, 3.2% proteins, 3.4% fat, 0.7% ash, and 0.01% cholesterol [106]. It also provides the

minerals such as calcium, 95.5–99 mg/100 mg, iron 5.1–9 mg/100 mg, potassium 11447–14355 mg/100 mg and sodium 2.9–10.6 mg/100 mg [107]. Its chemical composition is comparable to the soybean [106], while its milk had been rated higher in acceptability than milk from other legumes like soybean and cowpea [106].

BG become neglected possibly during the introduction of Groundnut (Arachis hypogaea) to West Africa from Brazil, groundnut is seen as a crop with significant amounts of oil so it is being cultivated as an oil seed crop. In recent years, people's interest has begun to increase in BG cultivation and consumption possibly due to its potentials as a food crop that thrives in dry areas, although it still lacks proper seed systems and best agronomic practices have not been established and shared widely [102,108••]. The 'hard-to-cook' phenomenon increases the effort required to prepare seed for meals and in many countries, this means a greater fuel cost. Consequently, this trait has been often identified as one of major bottleneck for the uptake of BG [109]. Hard-to-cook also develops with seed storage condition, particularly under humid and hot conditions, and a number of theories have been developed to explain components of this storage trait [110].

BG and similar crops can be an important part of more resilient and complex systems, which provide additional nutritional and food security. BG exhibits all three drought tolerance mechanisms avoidance, escape and tolerance [111–115]. Mabhaudhi et al. [44] reported that BG has been indicated to adopt dehydration-escape mechanisms, including a reduced vegetative growth period, early flowering, a shorter duration of the reproductive stage, and early maturity date in response to water stress. Landraces Red' and 'Brown' have been shown an earlier maturity date when the plants were stressed at 30% of the crop water requirement (ETa; mean: 122.75 DAP) as compared to 100 % ETa (mean: 128 DAP) [44]. BG is held high value for its nutritional quality and ability to tolerate a range of environmental conditions and durations of stress (known as drought tolerance) by the consumers and the farmers in SSA regions, respectively. Because of the climate change, crop modeling projected [19] that common bean, maize, banana, and finger millet are projected to reduce their suitable areas significantly (30–50%). Out of these crops, common bean yield is highly sensitive to climate than other legumes and a small change in yield within ±5% of current yield levels can be expected in less than 2% of the agricultural area of the continent [19]. Thus, cowpea drought/heat tolerance improved varieties could be used as adaptive major crop and BG could also be used as alternative crop. These indigenous legumes can be promoted as climate resilient crop as a crop shifting strategy under climate change, especially in drought prone and unpredictable rainfall regions of African continent including West Africa to avoid any reduction in crop production and food security of SSA regions.

Different nature (dominant and co-dominant) of markers including advanced SNP marker are in use for genetic relationship and linkage mapping of BG [101,116–125]. The results of the genetic diversity studies showed that the majority of West African accessions were grouped with Cameroon/Nigeria accessions, while they were differentiated from East African, central African and Southeast Asian accessions by grouping in different clusters [101,125]. Both allelic and gene diversities were also higher in the West African and Cameroon/Nigeria regions than East Africa and other groups [125]. Crop breeders and geneticist has been shown their tremendous interest for genetic diversity study to use smartly the large germplasm collection for their crop improvement program. The results of integrated linkage map from Ho et al. [117] showed that the genetic linkage map of IA (IITA686 x Ankpa4) consisted 11 linkage groups from 223 markers (DArTseq SNP and DarT markers) using 263 F2 lines which covered 1395.2 cM and the genetic map of TD (Tiga Nicuru x DipC) from 71 F3 lines also gave 11 linkage groups consisting of 293 markers and covered 1376.7 cM. Different type of markers used in both linkage maps were showing synteny to their close relative legumes namely, common bean, adzuki bean and mung bean genomes [117]. The crops (like pigeon pea, chickpea, groundnut, etc.) were known as an orphan crop in the past but now they are entered in advanced era of molecular breeding and improvement after their genomes were sequenced using NGS technology [126]. The sequencing of BG has been completed [127••,128••]. The size of genome of Bambara groundnut is 550 Mbp as compared to 620 Mbp of cowpea genome. With the advancement of NGS, 236 plant genomes have been sequenced [126]. The complete sequencing of plastid genome (size 152 015 bp) of BG has also been reported by Liao et al. [129••]. A study of QTL discovery using bi-parental mapping population was conducted by Ahmad et al. [130]. They identified a total of 36 QTL in BG for different traits including internode, days to emergence, growth habit, seed weight, pod length and width. The phenotypic effect explained by a single QTL ranged from 11.6%–49.9% [130]. The stable QTL were found only for internode length [117,130] and growth habit [130]. A study focused on the analysis of the transcriptomic changes was done in two BG landraces (DipC and TN) in response to dehydration stress by Khan et al. [131]. The results were indicated that many potential dehydration-responsive genes are expressed, even under water-sufficient conditions, in both landraces, suggesting that Bambara groundnut could at least be in a partially ready state for dehydration, even in the absence of dehydration stress. The DipC genotype displayed the differential expression of some well-known dehydration-associated transcriptions factors (especially WRKY40), while TN showed the differential expression of CONSTANS-LIKE 1 and MYB60 [131].

GRC-IITA conserved over 1900 accessions which is the world largest Bambara groundnut collection. Evaluation of the GRC collection of this crop is focused on the key constraints to greater use. This includes analysis of yield, yield stability, drought tolerance, cooking time and nutritional quality including protein content. We are also studying a key attribute known as nitrogen fixation by analyzing variation in nodule number and nitrogen fixed. For all analyzed traits significant variation has been observed between accessions in preliminary analysis. We have applied SNP genotyping using DArTseq to explore the untapped genetic diversity in the collection and can now identify parents to initiate breeding programs as well as for QTL analysis using GWAS method. Core collection from total BG population will also be developed for future breeding research. However, the lack of ability to easily cross any genotype of this species remains a constraint to both breeding and linkage and QTL mapping. There are no GWAS and genomics selection (GS) study reported in BG so far. Genomic-assisted breeding can help to explore the great potential of BG by developing improved climate resilient lines to use as an alternative crop in case of crop shifting due to climate change for improving both nutritional diet and food security.

Winged bean

Winged bean (*Psophocarpus tetragonolobus* (L.) DC.) is a tropical legume; however, it belongs to the family Fabaceae and genus Psophocarpus, Winged bean (WB) is suspected to have originated from Papua New Guinea, Madagascar Mauritius and India. The genus Psophocarpus contains nine species, eight of these are wild; the cultivated winged bean is known to produce edible highly nutritious tubers and quadrangular pods, whose length could be up to 30 cm long with longitudinal wings subtended on its vegetative part and they are the most economically important. It is a perennial plant that is grown as annual, winged bean compares well with Soybean protein content (35%); the seeds contain a high percentage of crude protein content ranging between 29.8% and 42.5% [132]. Harding *et al.* [133] observed a higher capacity for nodulation and nitrogen fixation in winged bean than in any other tropical legumes such as cowpea, common bean, groundnut, soybean and so on. The high protein level in the various plant could be attributed to the high nodulation and nitrogen fixing rates [134].

The ability of WB to grow in heavy rainfall makes the species a good candidate to adequately nourish the people of tropical equatorial countries in Africa [135]. The tubers can be used as a root vegetable, similar to potato, and have a nutty flavor they are also much richer in protein than potatoes. The dried seeds can be useful as flour and also to make a coffee-like drink. WB can also be used to produce its milk made from water, WB, and emulsifier. It provides many opportunities for economic benefit. Mature winged bean seeds can command high prices NRC, [136].

Both RAPD and ISSR markers were used to characterize twenty-four accessions of WB to see the genetic relationship of the population [137], ISSR markers were more efficient in WB over RAPD markers to unravel the polymorphism. Similar results have been also seen in other crops, including legumes [138,139]. WB population was grouped in two major groups and further also grouped in seven subclusters [137]. Considerable genetic variations among winged bean genotypes were present, although the groupings of accessions were not in congruence with their geographical affiliations [137]. DArTseq GBS SNP genotyping of available 48 accessions at GRC-IITA has also been initiated for WB for genetic diversity and population structure analysis. The diversity and population structure results will help to develop crossing between diverse lines for future breeding research.

Kersting's groundnut

Kersting's groundnut also known as geocarpa groundnut or ground bean is the seed of *Macrotyloma geocarpum* [140]. Kersting's groundnut [*Macrotyloma geocarpum* (Harms) Maréchal and Baudet] is a leguminous crop cultivated on small-scale in the western part of Africa. Kersting's groundnut (KG) is drought-tolerant and well adapted to the Sudan, Guinean, savannah agro-ecological zone [141]. The crop thrives well in the savannah and rainforest-savannah zones of West tropical Africa. It requires light, sunshine and moderate rainfall and grows well on sandy loam soils. It is able to tolerate some amount of drought in the tropical dry forest zone [142]. The crop grows successfully in areas with annual rainfall of between 500–600 mm [143] but can survive under low annual rainfall of 75–150 mm. The crop can grow and fix nitrogen in drought-prone environments where any other crops can barely survive [144]. KG is less susceptible to diseases and pest attack in the field [46]. Its yield ranges from 350 to 650 kg seed/ha in farmers field, although yields up to 1500 kg seed/ha have been reported in Rhodesia (now Zimbabwe) [145]. These yields compare well with yields of pigeon pea of 500–1600 kg seed/ha. With current climate variability and the occurrence of intra-season drought in West African region [146], it may be a viable crop option for vulnerable ecosystem.

Isozyme markers was used by Pasquet *et al.* [120] for characterizing eighteen domesticated and two wild accessions of KG from Togo and Burkina Faso. The results were showing narrow genetic base of KG, which is not likely to favor genetic gain in breeding programmes [147]. The cross-species molecular marker transferability was also observed in KG [148], where twelve Simple Sequence Repeat (SSR) markers from cowpea to KG were identified. Out of 12 SSR markers, 9 SSR were showing monomorphic and three were not amplified [148]. The successful cross-genus transferability of cowpea SSR in KG is showing the existence of an

evolutionary relationship between two species. The genotyping of available KG germplasm has also been initiated at GRC-IITA using DArTseq GBS-SNP for genetic diversity and population structure analysis.

Conclusion and prospects

Strong significant future climate signals have been reported showing that there will be shorter rainy season, arid, semi-arid conditions, longer dry spells and heavy rainfall in most West African countries. Mean crop production could be reduced between 20%–40% by 2050 in humid and West African countries. Little research has been done on modeling of future climate signals for West African crops compared to the major crops of the world. Cowpea yield could reduce 22%–24% by 2030, while interestingly BG yield can increase 37.1%, under climate change scenario GISS A2 2080. More efforts are required now on modeling for West African crops including cowpea, BG and AYB. There is no climate modelling report available for AYB, WB and KG. In the case of crop failure due to climate change scenario, there should be an alternative crops strategy which can mitigate the effects of climate change. Orphan legumes particularly BG could be used as an alternative crop either directly (landrace) or as improved varieties that will derived from traditional photoperiod-sensitive landraces which are less affected by temperature increase since the photoperiod limits the reduction of the crop duration and also the positive effects of higher CO_2 concentrations. These more resilient orphan legumes could be promoted as replacement options for areas that require adaptation alongside, a shift to more drought/heat tolerance varieties of staple crops such as cowpea. Evaluation of the GRC-IITA collection (including cowpea FIGS population) of these crops is focused on exploring existing genetic diversity for climate adaptive traits yield, drought and nutritional traits for pre-breeding. We are also applying cutting-edge genomics tools in these crops for high-depth genome-wide SNP discovery using NGS, exploring genetic diversity, population structure and development of high-density genetic linkage/QTL maps. The QTL-trait discovery is in progress for adaptive traits using GWAS approach in cowpea, BG and AYB. By using reference genome, there is a great scope to apply genome-wide methods for marker-trait association studies and to select desirable genotypes via genomic selection which can increase genetic gains and accelerate rapid breeding cycles for complex quantitative traits of biotic and abiotic stresses. The reference genome is available only for cowpea and recently BG draft genome also published too. Consequently, the use of advanced genomic tools is well adapted with advanced breeding approach in cowpea and it is followed BG and AYB. GAB has the potential to increase the rate of genetic gain for complex traits including climate adaptive traits. There is also an urgent need to initiate more research efforts on nutritional traits with genomic tools of these legume crops including cowpea because of minimal molecular research of nutritional traits conducted in the past. It is unlikely that sufficient funding for genomics and advanced breeding programmes in a diverse range of orphan crops with significant unfulfilled potential will be forthcoming.

Conflict of interest statement
Nothing declared.

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Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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