INTRODUCTION

Yam is a multi-species monocotyledonous crop extensively disseminated in Africa, Asia, Oceania and South America. The genus Dioscorea to which yam belongs encompasses about 600 species (Burkill, 1960); however, a few are cultivated for food and income. Dioscorea alata, D. cayenensis and D. rotundata are by far the major cultivated species worldwide, while D. bulbifera, D. esculenta, D. opposita, D. japonica, D. nummularia, D. pentaphylla, D. transversa, D. trifida and D. dumetorum are also economically important (Lebot, 2009; Sonibare, Asiedu, & Albach, 2010). Many wild yam species serve as sources of food in West Africa especially in times of food scarcity (Bahuchet, Mckey, & Garine, 1991; Sato, 2001). Dioscorea rotundata is indigenous to West Africa and represents the most important species in terms of volume of production while D. alata, which was introduced to Africa from Asia, is the most widely cultivated species globally (Abang, Winter, Mignouna, Green, & Asiedu, 2003).

Yam is an important staple source of carbohydrates (starch, sugars and fibres), proteins, minerals, vitamins and small amounts of lipids in the diets of millions of people in the tropics and subtropics. Yam is not only cultivated for consumption and as a source of income, but it is a highly esteemed food crop integrated into the social, cultural, economic and religious aspects of life of West Africans (Zannou et al., 2004). The rituals, ceremonies and superstitions

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often associated with yam cultivation and utilization in West Africa is a strong indication of the antiquity of use of this crop (Norman, Pearson, & Searle, 1995). The new yam festival, which symbolizes the beginning of yam harvesting, is an outstanding social event almost everywhere in the yam-growing belt of West Africa (Coursey & Coursey, 1971). Dioscorea species are also recognized for their secondary metabolites aside their food value. They contain steroidal saponins, diterpenoids and alkaloids, which have been exploited for making poisons (Neuwinger, 1996) and pharmaceutical products (Chu & Figueiredo-Ribeiro, 1991).

Although Africa accounted for over 97% of the total yam production worldwide in 2017, only two countries in Africa are among the top five countries recording the highest yields per hectare (FAOSTAT, 2017). The top five countries producing high yield per unit area are Ethiopia, Mali, Japan, Papua New Guinea, and Portugal, while Nigeria, Cote d’Ivoire, Ghana, Benin and Togo are the top five countries in the world in terms of total area under yam cultivation (FAOSTAT, 2017). A number of constraints including high cost of planting materials, high labour costs, poor soil fertility, low yield potential of local varieties, pests and diseases (yam anthracnose, virus and nematodes), and shortage of quality seed yam of popular landraces and released varieties have been identified as the major constraints of yam production in Africa (Aidoo et al., 2011; Baimey, Coyne, & Labuschagne, 2006; Lopez-Montes, Bhattacharjee, & Tessema, 2012). The presence of virus in yam tubers not only causes yield loss but also hinders the international exchange of yam planting materials and germplasm (Asala et al., 2012; Kumar, 2015). The increase in yam production in Africa over the years is mainly due to the rapid increase in the area of yam fields planted into marginal lands and into non-traditional yam-growing areas (Mignouna, Abang, & Asiedu, 2008) rather than resulting from increased yield per unit land area. The current trend of area expansion with reduced fallow period will soon reach the limit. The need to provide farmers with improved varieties that combine high and stable yields with pest and disease resistance and acceptable tuber quality for processed and fresh tuber consumption markets can therefore not be over-emphasized.

A number of improved yam varieties having multiple pest and disease resistance, wide adaptability and good organoleptic attributes have been developed with empirical breeding methods in Africa and Asia by collaborative efforts of the international institutes and national yam breeding programmes. This progress with selection based on phenotypic expression of the crop for the traits of interest has however been challenging and slow due to inherent biological constraints that impede the elucidation of the genetics of important traits in yam (Mignouna et al., 2008). Although empirical breeding approaches have led to crucial achievements, contemporary tools and resources must be developed and applied to create the paradigm shift necessary to contribute significantly to feeding the rapidly increasing global population amidst climate change, dwindling resources and dynamics of consumer preferences.

The decreasing cost and rapid advancement in next-generation sequencing procedures, together with high-performance computational methodologies, have led to extensive discovery of advanced genomic resources in numerous model and non-model plants. Significant genetic gains have been recorded in several crops such as rice, soya bean, maize and wheat, and more recently cassava through the application of DNA-driven breeding techniques such as genomic selection and marker-assisted breeding. The wealth of knowledge emanating from genomes, metabolomes, transcriptomes, phenomes and gene expression profiles will immensely contribute to our understanding of underlying gene regulatory networks to enable systematic improvement of crop breeding. The deployment of these contemporary methods will therefore expedite yam breeding efforts. However, much information is needed before full deployment of molecular breeding in yam as most of the information currently available for the crop is on diversity studies and few QTL detections with less emphasis on the validation and development of informative markers for direct use in breeding.

Earlier efforts in genomics research in yam were mainly focused on the development of polymorphic molecular markers and evaluation of their potential applications for investigating genetic diversity, demarcation and identification of relationships among the various species. Quantitative trait loci (QTLs) controlling the resistance of yam to anthracnose and yam mosaic virus disease have also been identified (Bhattacharjee et al., 2018; Mignouna et al., 2002b; Petro, Onyeka, Etienne, & Rubens, 2011; Saski, Bhattacharjee, Scheffler, & Asiedu, 2015). Significant efforts have been made recently to develop more genetic tools and genomic resources to transform yam breeding. This paper reviews the advancements achieved in empirical yam breeding endeavours and the development, status and application of emerging breeding tools and methodologies for the genetic improvement of yam.

2 | GERMPLASM RESOURCES FOR YAM IMPROVEMENT

Availability and access to smart germplasm resource is vital for the development of improved crop varieties that possess superior agronomic and food quality traits. Yam germplasm collections conserved in the field and in vitro genebanks constitute a huge gene pool for yam improvement activities in order to achieve its optimum potential for food and income for farmers. By 2010, a total of 15,903 yam accessions were conserved in genebanks across the globe with IITA accounting for 21% (3,319) (FAO, 2010). Other institutions including National University of Ivory Coast, University of Abomey Calavi (Benin), Plant Genetic Resources Research Institute (Ghana), Dodo Creek Research Station, Ministry of Home Affairs and Natural Development (Solomon islands) and Peradeniya University (Sri Lanka) also hold 10, 7, 5, 3 and 3% of the global yam collections, respectively, while 93 other institutions accounted for the remaining 51% (FAO, 2010). Institutions such as CTCRI (Central Tuber Crops Research Institute) in India, PRC (Plant Resource Center) in Vietnam, PhilRootCrops in the Philippines, CRB-PT (Centre de Ressources Biologiques Plantes Tropicales) INRA-CIRAD (Institut National de la Recherche Agronomique—Centre de Coopération Internationale
en Recherche Agronomique pour le Développement), Guadeloupe, France, VARTC (Vanuatu Agricultural Research and Training Centre) in Vanuatu, South Pacific islands (Papua New Guinea, Fiji, and New Caledonia islands), and Ethiopian Biodiversity Institute and National Research System in Ethiopia maintain a substantial number of Dioscorea species under ex situ collections (Arnau et al., 2017; Chi, Hue, & Trinh, 2007; Lebot, 2009; Lebot, Malapa, & Abraham, 2017; Mekbib & Deressa, 2015). IITA has increased tremendously its yam germplasm collections from the 3,319 in 2010 to 5,788 in 2018 (IITA, 2018). The IITA collections encompass ten species: D. rotundata (68%), D. alata (21.8%), D. burkiliana (6.2%), D. abyssinica (1.6%), D. cayenensis (1.5%), D. dumetorum (1.3%), D. bulbifera (1.2%), D. esculenta (0.4%), D. preussii (0.17%) and D. mangenotiana (0.14%).

The yam germplasm collections are rich in rare alleles for target traits from which breeders source genetic materials to expedite genetic gain in a sustainable way. However, the systematic use of genebank accessions has not progressed very far in yam breeding programmes. The development of core collections representing the diversity of the entire germplasm (Frankel & Brown, 1984) facilitates easy access and enhances the utilization of the main collection for fast evaluation in crop improvement programmes. The first core collection (391 accessions) from the IITA yam germplasm represented 75% of the morphological diversity of the entire collection using data on 77 morphological descriptors and country of origin (Mahalakshmi et al., 2007). This core collection represented 13% of the entire collection. With the inclusion of new germplasm and availability of information, the yam core collection at IITA was revisited and updated using 56 morphological traits (Girma et al., 2018). The updated core collection comprised 843 accessions and represented about 20% of the whole collection. Delineation of core collections and diversity studies in general has often been based on morphological traits rather than molecular markers. The high phenotypic plasticity of yam is a limitation to morphological characterization, hence, the need to enhance “omic” resources.

Phenotypic characterization and assessment of germplasm for morphological and agronomic traits, tuber quality, ploidy status, and flowering ability have resulted in the identification of accessions as parents with attributes pertinent to the objectives of the breeding programme (Lopez-Montes et al., 2012). To explore the use of aerial tubers of D. alata as alternative planting materials owing to the high cost and supply shortage of seed yam propagules, over 800 accessions from the IITA germplasm collection were evaluated for aerial tuber production and a set of accessions bearing aerial tubers were identified (Girma, Gedil, & Spillane, 2015). A number of studies have successfully assessed the IITA’s and other institution’s yam diversity represented by different genebank accessions, landraces and breeding lines for host–plant resistance and quality traits and have shown a rich base of germplasm resource that can inform breeding strategies for resistance to major yam pests such as nematodes, anthracnose and virus diseases, and genetic enhancement for quality traits including various secondary metabolites, tuber carotenoids and other food quality traits (Mohandas, Ramakrishnan, & Sheela, 1996; Plowright & Kwoseh, 2000; Mignouna, Abang, Green, & Asiedu, 2001; Mignouna, Njukeng, Abang, & Asiedu, 2001; Abang et al., 2003; Onyeka, Petro, Ane, Etienne, & Rubens, 2006; Arnau, Maledon, & Nemorin, 2007; Egesi, Odu, Ogungyemi, Asiedu, & Hughes, 2007; Kwousch, Plowright, Bridge, & Asiedu, 2007; Asiedu & Sartie, 2010; Kwon et al., 2015; Price, Wilkin, Sarasan, & Fraser, 2016; Lebot et al., 2018; Price, Bhattacharjee, Lopez-Montes, & Fraser, 2018). There is also an ongoing initiative at IITA to sequence all the genebank yam collections to expedite its use for breeding. This effort shall be intensified by systematically arranging the trait-specific core sets to identify and utilize useful genetic variability that exists in wild and cultivated gene pools for long-term use in yam breeding. Extensive phenotyping of large set of genetically diverse yam germplasm for different traits and developing trait-specific mini-core sets such as biotic stress resistance, quality and abiotic stress tolerance could provide an opportunity to mine novel alleles from underutilized germplasm resources for breeding next generation of yam varieties.

## 3 | GENETIC IMPROVEMENT OF YAM WITH EMPIRICAL BREEDING

### 3.1 | Yam breeding targets and challenges

The breeding programmes in many countries focus on a few Dioscorea species, most specifically the dominantly cultivated yams such as D. rotundata and D. alata. The primary focus of yam breeding is the development and deployment of robust varieties with unique combinations of preferred traits required for production and consumption. The programmes generally target traits related to increasing intrinsic tuber yield potential as well as increasing tolerance for, and resistance to, yield-limiting and quality-reducing factors. Still, the specific breeding targets varied according to the region and species involved (Mignouna, Abang, & Asiedu, 2007). The breeding targets have, however, evolved over the years to meet the changing needs and preferences of farmers and other end-users. From the inception of formal yam breeding since the 1970s, the breeding targets have been gradually adding new traits along with the primary focus on high and stable tuber yield, higher dry matter, resistance to economically significant diseases (e.g. anthracnose, viruses, tuber rots) and pests (e.g. nematodes), tuber characteristics cherished by consumers (e.g. size, shape, and culinary quality), and plant architecture (e.g. dwarf genes) that reduces the need for staking (Asiedu, Ng, Bai, Ekanyayake, & Wanyera, 1998; Mignouna et al., 2007). Additionally, traits such as colour of tuber flesh, tuber oxidation, starch properties and sugar contents are now routinely measured in breeding programmes as they influence the acceptability of newly developed yam varieties (Arnau, Maledon, Nudol, & Marie-Claire, 2016; De Koeyer et al., 2017). However, high-level resistance genes to viruses, anthracnose and nematodes; shrub-like or dwarf plant architecture with stiff or stout vine base and early branching; early maturity or tuber bulking; tubers less susceptible to deformation in the soil; tolerance for low soil fertility, drought and heat; long shelf life of fresh tubers or processed food products; and
high levels of culinary attributes suited to consumer needs for fresh and processed yam are among the missing traits in current advanced breeding lines and released cultivars.

The breeding efforts over the last five decades have resulted in the identification of trait progenitors and commercial release of improved cultivars. However, the local farmers’ varieties are still the leading and dominant cultivars in the yam cultivation and consumption systems (Alene, Abdoulaye, Rusike, Manyong, & Walker, 2015). While this low market penetration of improved varieties could be attributed in part to the limited dissemination efforts, limited exposure of the customers to the released varieties or lack of preferred attributes in the varieties meeting the needs and demands of farmers and market, the setting of breeding goals or specifications for new varieties was refocused and restructured to raise the market penetration potential of future releases with correct product profile. The breeding targets have been transformed from undifferentiated product portfolio to a differentiated product concept where customer needs are profiled and translated to product specifications. Clients/customer needs are now the main focus of the variety development plan of yam breeding programmes in Africa. Accordingly, three key breeding product profiles have been carefully framed for targeting (Table S1) by IITA and its national partner breeding programmes in West Africa. The product concept where the right features or traits for the varieties that the clients (growers, processors, retailers and consumers) require or demand is identified and prioritized with a clear roadmap to achieve the target product in a specified timeframe: five years to replace the current market-leading varieties with improved features to drive adoption in short term (current product profile) and ten years to develop parental lines feeding the variety development pipeline in medium term (future product profile). The yam breeding programme, therefore, envisions implementing a product concept that can drive rapid and successful uptake of new varieties in the production and consumption system.

Making breeding progress in yam has been challenging. Many factors such as unpredictable or no flowering, non-synchronous flowering of elite genotypes, lengthy growth cycle, low multiplication ratio, polyploidy and high heterozygosity negatively influence the genetic improvement of yam (Asiedu et al., 1998). Additionally, the dioecious nature of yam, cross-incompatibility of inter- and intra-species hybridization, and the enormous phenotypic plasticity make the evaluation and stacking of several interdependent characters a problematic process (Price, Bhattacharjee, Lopez-Montes, & Fraser, 2017). Limited understanding of the genetics of main and component traits contributing to enhanced productivity under current production challenges and limited breeding enabling technologies that can contribute to its accelerated improvement have also thwarted yam breeding efforts. The influence of biochemical composition on organoleptic properties of yam is not well understood and, therefore, a significant hindrance to detecting genetic/biochemical trait markers effectively translating the genetic diversity to end-user preferred genetic gain (Price et al., 2017).

Furthermore, the existing yam germplasm has not been well characterized, limiting the efficient utilization of available diversity in genetic improvement for the agronomic and food quality traits. Transfer of genes of interest from the secondary gene pool of wild relatives to the cultivated primary gene pool is still challenging in several crops, including yam (Lebot, Abraham, Kaoh, Rogers, & Molisalé, 2019; Spillane & Gepts, 2001). Nevertheless, the wild relatives of yam could harbour essential genes and genetic variability useful in breeding endeavours to enhance the performance of yam for various economically important traits. Yam germplasm conservation has predominantly focused on the main cultivated species with little emphasis on wild relatives; hence, future studies can be limited if conservation efforts are not increased. Basal species with diverse traits are also lacking (Price et al., 2016), although they could be especially useful for genome editing. Several wild relatives of yam recently appeared on the International Union for Conservation of Nature (IUCN) red data list and have been declared threatened and may further compound the problem of the availability of genetic diversity for utilization in the breeding of this valuable staple crop.

3.2 | Conventional hybridization and selection

Traditionally, yam breeding is a two-step process that utilizes both sexual and asexual reproduction. Different breeding schemes are followed by the breeding programmes depending on the type of trait/s targeted for improvement. The general breeding outline for developing superior yam genotypes involves artificial hand or natural open pollination for the generation of full-sib or half-sib progenies segregating for desired traits and subsequent selection of their clonal derivatives for performance reproducibility and stability over seasons and locations. Yam species are mostly dioecious, and they produce male and female flowers on separate plants. Hence, separate crossing blocks of male and female parents are established with multiple planting dates to enhance synchronization of the flowering in crossing blocks. The female flowers are bagged for two to seven days before the flower opens, depending on the spike length. The pollinated flowers are then kept bagged for two weeks to ensure the purity of offspring from crosses. It usually takes one to two days for a flower bud to show a sign of crack to open fully, and the stigma of the open flower remains receptive for six to seven days. Fruit setting usually takes place in about ten days after pollination, and in about 12 weeks, the fruits start showing signs of maturity (yellowing). The botanical seeds from the controlled bi-parental crosses or the natural open pollination are collected from dried fruits before they disperse from the capsules. The seeds are then processed and stored under room temperature until the end of dormancy which is three to four months in the case of D. rotundata, or until the desired time of planting as in D. alata, which has no seed dormancy (Abraham, 1992).

The botanical seeds are sown in nursery beds or seedling trays filled with suitable growing media such as carbonized rice husk and coco peat. Seed germination starts in ten days after sowing and continues for one month. The seedlings are then transplanted to the pots under screenhouse or nursery beds in the field for single plant selections at seedling and tuber progeny nurseries and the
subsequent annual advancement of the clonal derivatives through early clonal generation evaluation nursery, preliminary performance trial, advanced multi-location and multi-season performance trial to on-farm variety validation trial for an official release and commercial deployment (Asiedu et al., 1998; Table 1). Crossing and selection have been used as a prime tool to develop improved varieties in yams. Table 2 summarizes the artificial cross-pollination and seedling production at IITA for the last five years (from 2014 to 2018). At IITA, an average of 29,191 flowers of *D. rotundata* involving 30 female and 25 male parents in 97 cross-combinations and 27,031 flowers of *D. alata* involving 22 female and 16 male parents in 85 cross-combinations were hand cross-pollinated per year over the previous five years. On average, the percentage fruit and seed sets were 20.3% and 10.5% in *D. rotundata* and 28% and 9.3% in *D. alata* crossing blocks, respectively. The artificial cross-pollination efforts over the five years have resulted in the production of 10,181 seedlings and 2,763 tuber progenies in *D. rotundata* and 6,461 seedlings and 3,434 tuber progenies in *D. alata* breeding pipelines per year for subsequent phenotypic selection. The success of cross-pollination and hybrid progeny generation for phenotypic selection was generally low compared to the pollination efficiency and seed set reported in Lebot, Abraham, et al. (2019) and has shown a lot of inter-year variances (Table 2). Lebot, Abraham, et al. (2019) reported variation in pollination efficiency, seed set and seedling survival in crosses involving diploid × diploid, diploid × tetraploid, and the same pollen parent in different cross-combinations. Sparse to non-flowering, flower asynchrony, pollen viability, the receptiveness of stigma, pollen-stigma compatibility, pollinators' efficiency in loading sufficient pollen on the stigma, embryo abortion, low seed germination, low seedling survival rate, and differential cross-fertility of parents are severely impacting the success rates of yam cross-pollination efforts. Improved techniques with flowering induction and pollen storage would increase the success rates in crosses. Moreover, ploidy determination, screening accessions for specific or general cross-compatibility for fruit and seed set, seed germination and seedling survival rate and identification of compatibility groups, development of functional molecular markers for flower sex, flowering intensity and cross-compatibility prediction, and confirmation of hybridity in progeny will contribute to overcome the low success rate and improve the efficiency of hybridization in yam breeding.

The choice of the right parents for use in the crossing scheme is a stepping stone towards success in yam breeding effort and entails the use of per se phenotypic performance for the trait of interest, estimation of breeding values, and dissection of genetic relatedness using pedigree and molecular marker information. Per se performance has been widely utilized but not always effective in producing heterotic progenies. Joining per se performance along with their combining ability is an important tool for the selection of parents for hybridization. The use of such classical breeding technique alone is slow to achieve the anticipated breeding gain. Interspecific hybridization has been less exploited due to cross-incompatibility and non-synchronization of flowering. Successful interspecific hybridization was reported between *D. japonica* and *D. opposita* under natural open pollination (Araki, Harada, & Yakuwa, 1983) and between *D. alata* and *D. nummularia* under artificial hand pollination (Lebot, Abraham, et al., 2019). *Dioscorea rotundata* has been successfully crossed with *D. cayenensis* at IITA but hybridizing either of the two to *D. alata* has not been successful (Lopez-Montes et al., 2012). The unsuccessful interspecific hybridization between *D. alata* and other yam species was also reported by Rao, Bammi, and Randhawa (1973).
| Year | No. of parents | No. of cross-combinations | Flowers pollinated | Fruit set | Seed set | Number of seeds germinated | Number of seed tubers produced |
|------|----------------|--------------------------|--------------------|-----------|----------|---------------------------|-------------------------------|
|      | Female | Male |                    |          |          |                           |                               |
|      | 2014   | 22   | 16                  | 97       | 26,190   | 7,709 (29.4)             | 15,405 (9.8)                 | 5,694 (29.4)                 | 2,384 (29.4)               |
|      | 2015   | 17   | 13                  | 54       | 22,429   | 5,091 (22.6)             | 13,684 (10.1)               | 8,527 (22.6)                | 1674 (22.6)               |
|      | 2016   | 49   | 36                  | 117      | 53,567   | 9,643 (18.0)             | 30,469 (9.5)                | 18,768 (18.0)               | 4,571 (18.0)               |
|      | 2017   | 32   | 35                  | 124      | 22,753   | 4,957 (21.8)             | 21,181 (15.5)               | 8,212 (21.8)                | 2,423 (21.8)               |
|      | 2018   | 29   | 26                  | 91       | 20,953   | 2015 (9.6)               | 9,703 (7.7)                 | 9,703 (9.6)                 | -a                        |
|      | Average| 30   | 25                  | 97       | 29,191   | 4,943 (20.3)             | 18,080 (10.5)               | 10,181 (20.3)              | 2,763 (20.3)               |
| D. rotundata | 2014   | 21   | 10                  | 76       | 22,889   | 9,209 (40.2)             | 15,192 (11.1)               | 8,206 (40.2)                | 9,385 (40.2)               |
|      | 2015   | 11   | 10                  | 48       | 23,710   | 6,591 (27.8)             | 11,820 (8.3)                | 8,968 (27.8)                | 1,536 (27.8)               |
|      | 2016   | 28   | 24                  | 113      | 35,251   | 5,641 (16.0)             | 15,344 (7.3)                | 5,851 (16.0)                | 1,949 (16.0)               |
|      | 2017   | 26   | 21                  | 104      | 26,273   | 7,364 (28.0)             | 16,441 (10.4)               | 2,817 (28.0)                | 867 (28.0)                 |
|      | Average| 22   | 16                  | 85       | 27,031   | 7,721 (28.0)             | 14,699 (9.3)                | 6,461 (28.0)                | 3,434 (28.0)               |

*aPlanted in the screenhouse in 2019 and data yet not collected.

*bCrossing block was not established for D.alata in 2018.

Source: Compiled by authors from IITA pollination and seedling generation data record for the years.
interspecific hybridization attempt at IITA has specifically targeted introgression of supposed unique traits such as high carotenoid content from *D. cayenensis* accessions, and aerial bulbil production from the *D. alata* accessions into the agronomically preferred background of the *D. rotundata* cultivars (Lopez-Montes et al., 2012). However, this effort has not progressed well due to the natural cross barrier among the different species. The failure/discontinuation of interspecific hybridization of *D. rotundata* and *D. cayenensis* was mainly because *D. cayenensis* was wrongly believed to have a higher level of carotenoids (Price et al., 2018).

Phenotypic selection of the variants within natural barriers is a core yam breeding effort by different programmes. Three to four clonal selection and testing cycles (from tuber family evaluation to advanced performance trial) are often attempted to identify superior recombinants for further assessment under a wider range of environments and user preferences (Table 1). At seedling and first clonal generation, selections are based mainly on reaction to a natural infestation of anthracnose in *D. alata* and viruses in *D. rotundata*, along with tuber appearance. At subsequent clonal derive stages, from the second clonal generation onwards, selection is made, among other things, for tuber shape and appearance (uniform, globular to cylindrical or round shape with smooth skin), tuber dry matter (>25%), tuber enzymatic oxidation (non-oxidizing white or cream flesh after peeling or cutting the tubers for at least 180 minutes), tuber yield and stability (>5% yield advantage over best check), yam mosaic virus and yam anthracnose tolerance (>2.5 severity score under field natural infestation) and plant architecture or type for adaptation to no or minimal staking. At advanced clonal stages (advanced performance or multi-environment trials), the genotypes are subjected to series of food quality analysis, most specifically boiled and pounded yam quality test in participatory trial setup engaging end-users. The most promising two to three clones from multi-environment testing then enter the final wide-scale on-farm validation or verification assessment for commercial deployment.

The current breeding scheme for yam is lengthy and slow. Setting testing and selection trials with the needed replications at scale is a challenge due to the difficulty to obtain sufficient quantity of uniform clonal planting materials. Propagules for planting from different position of the same mother tuber (proximal, central and distal parts) often produce heterogeneous sprouting and cause a high interplant variability within a clone in field trials (Cornet, Sierra, Tournebize, & Ney, 2014). With technological advancements, present-day yam breeders should increasingly be able to select superior recombinants accurately in breeding populations with reduced breeding cycles, manipulate game-changing plant attributes beyond the natural barriers and also produce sufficient quality planting materials to expedite the genetic gain.

### 3.3 Pattern of inheritance for key traits

Nature of trait heritability is essential for the design of an optimal breeding strategy. Traits can be classified as either qualitative or quantitative based on the pattern of their variation in a population. Variation is discrete for qualitative traits which are often controlled by one or a few genes whereas it is continuous for the quantitative traits which are mostly controlled by several genes with each having a minor effect. Few studies have dissected the nature of trait heritability in yam crop. Single dominant gene in a simple or major recessive gene in duplex condition controls the inheritance for yam mosaic virus (YMV) resistance in *D. rotundata* (Mignouna, Njukeng, et al., 2001). Genetic inheritance for reaction to anthracnose disease in *D. alata*, caused by *Colletotrichum gloeosporioides*, was reported as dominant gene action with quantitative inheritance (Mignouna, Abang, et al., 2001). Sartie and Asiedu (2014) assessed segregation for vegetative and reproductive traits related with tuber yield and quality in *D. alata* genetic population and reported transgressive segregation for traits like flowering intensity, tuber shape, bulbil formation, tuber flesh oxidation and reaction to anthracnose disease. Assessment of morphological and biochemical traits in *D. alata* cultivars showed high heritability coupled with high genetic advance for internode length, petiole length, days to sprout emergence, total phenol and total sugar suggesting a predominance of additive gene control on the expression of these traits (Alam, Shylla, Bora, & Saud, 2014). Broad-sense heritability for several traits in *D. rotundata* and *D. alata* breeding trials at IITA has shown a lot of intertrial variabilities (Figure 1). For majority of tuber yield-related traits assessed in trials such as fresh tuber yield per unit area (t/ha), tuber yield per plant (kg/plant), tuber number per plant, average tuber weight (g) and tuber dry matter content, heritability estimate on average was high (>50%). Phenotypic coefficient of variation reported was higher than the genotypic coefficient of variation for tuber yield-related traits such as tuber width, tuber weight, tuber yield per plant, number of tubers per plant and tuber dry matter in *D. alata* and *D. rotundata* types indicating the influence of environment on the heritability of the traits (Alam et al., 2014; Nwankwo & Bassey, 2013). The estimate for genetic parameters reported was much lower in seedling-derived plants compared to the clonal-derived plants (Akoroda, 1983) making reproducibility for the phenotypic selection at early generation stage a challenging task in yam breeding. Genes controlling essential traits such as tuber yield, tuber quality, resistance to pests, and diseases are quantitatively inherited and less likely linked, making their improvement through empirical breeding a challenging task. The efficiency and effectiveness of breeding for essential traits in yam would significantly improve with the use of genomic and genetic assisted breeding.

### 3.4 Envirotyping

Accurate examination of complex environmental factors for both target environments and specific genotypes provides a unique avenue for management and optimization of environmental variables for enhanced genetic improvement and efficient crop production in an era of global climate change. All environmental factors that influence plant growth and yield are defined as envirotypes, and the process for determination and measurement of all the environmental factors is envirotyping (Xu, 2015, 2016). The concept “envirotyping” as suggested by Xu (2015) is another “typing” technique supporting...
phenotyping and genotyping to elucidate environmental effects on crops. Through its efficient mechanisms such as integrative phenotyping, genotype-by-environment interaction, genes responsive to environmental signals and biotic and abiotic stresses, envirotyping facilitates crop modelling and phenotype prediction (Xu, 2016).

The partitioning of yam production environments into similar mega-environments will have functional implications for variety testing and performance prediction for final product recommendation thereby enabling a broader impact of breeding products. Alabi et al. (2019) mapped the yam production environment in four West African countries (Nigeria, Benin, Ghana and Cote d’Ivoire) that account for 92% of global yam production, using 23 bioclimatic variables, 21 soil properties layers, 18 remote sensing vegetation layers and five topographic variables derived from digital elevation model data. Seven different yam mega-environments were identified, four of which were country-specific while three (representing 70% of the current yam production in the four countries) were featured across the four countries, indicating their usefulness in the distribution and testing of elite yam varieties in West Africa. Characterization of the yam production environments further revealed the existence of other potential areas that have received less attention, and therefore, yam cultivar testing and development could assign varieties onto target environments through upscaling of research outputs for extensive impact.

The practice of ennoblement by farmers contributes to the broad phenotypic plasticity and ecological adaptations retained in yam, as a result of which envirotyping is comparably more crucial in yam breeding than other domesticated crops. The partitioning of the yam production environments comes with additional cost implications for enhanced multi-environment/localized breeding.

### 3.5 Variety release

A number of organizations such as IITA and its national partner breeding programmes in Sub-Saharan African (SSA) countries, INRA and CIRAD in Guadeloupe and Vanuatu, CTCRI in India (Lebot, 2009), and EIAR (Ethiopian Institute of Agricultural Research) in Ethiopia are involved in yam breeding. These breeding programmes have developed and released more resilient, productive and end-user preferred varieties of the dominant yam species that are used for commercial cultivation. The IITA and its national partner breeding programmes in SSA countries have developed and released improved varieties of the two dominant yam species: white yam (*D. rotundata*) and water/winged yam (*D. alata*). So far, 89 yam varieties have been identified and/or listed for commercial production in Africa (Alene et al., 2015; http://africayam.org/released-varieties-yam-2/) of which 25 were IITA bred lines (14 varieties of *D. rotundata* and 11 varieties of *D. alata*) officially released in Ghana and Nigeria. The varieties mentioned for Benin, Togo and Côte d’Ivoire by Alene et al. (2015) are recommended...
varieties by breeding programmes after testing for adaptation and suitability for consumption needs. Additionally, five farmer varieties with preferred culinary and agronomic features have been recognized and registered for commercial distribution in Nigeria in 2016 (http://africayam.org/released-varieties-yam-2/). There are also more candidate improved varieties in the pipeline to be released in Nigeria, Ghana, Benin and Côte d’Ivoire. The cultivar testing and release mechanisms are not uniform across countries in West Africa. Ghana and Nigeria have testing and release mechanisms for official release and registration of new varieties, but the other countries in West Africa do not have this for yam. In addition, national programmes in Ethiopia and India also released a number of improved varieties. In India, CTCRI has released 11 improved yam varieties (http://www.aicrptc.in/introduction.php). In Ethiopia, EiAR and its local research institutions have released three yam varieties (http://www.eiar.gov.et/index.php/crop-research). The French institutes, INRA and CIRAD have also released improved varieties of D. alata and D. rotundata in Guadeloupe and Vanuatu (https://ziyanmannou.cirad.fr/app_index).

3.6 | Enabling seed technologies to expedite genetic gain

The low multiplication ratio of yam has significant effects on yam production, breeding and dissemination of released varieties to farmers. The regular replacement of stocks of seed yams infested by pests and diseases is usually not possible due to short supply of quality seed tubers at affordable prices thereby forcing farmers to recycle poor quality seed yams with the risk of low yields (Aighewi, Asiedu, Maroya, & Balogun, 2015). Farmers produce quality seed yams through traditional approaches such as selection of small whole tubers from crop harvest; stimulating the development of seed tubers by “milking” ware tubers while the leaves of the plant are still green (double harvest system); cutting ware tubers into setts about the same sizes as normal seed tubers; and the “Anambra” system where seed tubers are produced from smaller setts (Aighewi et al., 2015). However, low multiplication ratio, high cost and high risk of exposure of seed tubers to contamination with pests and pathogens often characterize the traditional systems of seed yam production (Nweke, Ugwu, Asadu, & Ay, 1991).

New methods such as the minisett, microsetts/microtubers, tissue culture, vine cuttings, aeroponics and bioreactor systems, and the recently adopted semi-autotrophic hydroponics (SAH) technology have been developed to address the challenges of quantity and quality of seed tubers. A detailed review of these new methods (excluding the SAH technology), as well as the traditional techniques, has been provided by Aighewi et al. (2015). Semi-autotrophic hydroponics is a novel, low-cost, licensed technology for high-ratio propagation of true-to-type (genetic) virus-free clonal plants. Semi-autotrophic hydroponics facility for yam was initiated at IITA-Ibadan in 2017 with the capacity to produce 1,000,000 plants cumulatively per year within an area of 39.5 m² (Pelemo et al., 2018). Virus-free tissue culture plantlets, as well as botanical seeds from crossing blocks, are utilized as the starter materials for SAH. Semi-autotrophic hydroponics has the potential to facilitate large-scale early generation testing (up to 30 locations), in that, multi-location selection can be initiated within 2 years, instead of at least two locations within 4 years with the conventional breeding scheme (Pelemo et al., 2019). The SAH technique could help with extensive on-farm testing to create demand for new varieties which is a key step missing with current public yam breeding efforts. The SAH technique can therefore reduce the breeding cycle and scale testing schemes to accelerate the yam breeding gain.

4 | GENOMIC TOOLS AND RESOURCES FOR YAM IMPROVEMENT

4.1 | 4.1 Reference genome sequence

The genomes of many important crops have been sequenced with the advent of next-generation DNA sequencing technologies. It is particularly valuable for understanding the underlying genetics of complex traits in plants for their subsequent manipulation in crop improvement programmes. DNA sequence information is extremely relevant in identifying key genes regulating important agronomic characters and for detecting genetic variability among cultivars (Edwards & Batley, 2010; Thottathil, Jayasekaran, & Othman, 2016). Advances in genome sequencing through next-generation sequencing (NGS) technologies have made it possible to generate millions of novel markers and high-density genetic maps. The availability of the reference genome sequence of a species also helps to replace the conventional quantitative trait loci (QTL) mapping with association mapping. Quantitative trait loci mapping offers a wide genome range within which the gene is located while association maps mark traits with high resolution (Thottathil et al., 2016).

Tamiru et al. (2017) have developed and released the reference genome sequence of D. rotundata accession TDr96_F1 with a genome size of 594 Mb, out of which 76.4% is distributed among 21 linkage groups. The D. rotundata reference genome is available at http://genome-e.ibrc.or.jp/home/bioinformatics-team/yam. Similarly, Bredeson et al. (2018) have also developed and released an early draft assembly of the second most important species, D. alata reference genome (https://www.ncbi.nlm.nih.gov/nuccore/CZHE0000000.2). The breeding line TDa95/00328 was used as the reference accession for D. alata. This sequence accounts for nearly 50% of the total genome but an estimated 80%-90% of protein-coding loci while long-read PacBio sequencing of the reference accession is currently ongoing along with the development of a dense genetic map from eight map-crosses (Bredeson et al., 2018). The development and release of the reference genome sequences of the two most economically important species of yam have opened a new avenue for exploitation and in-depth understanding of the genetics,
genomics and domestication of this crop (Scarcelli et al., 2019). These data also facilitate the detection of allelic variations and candidate genes modulating key agronomic and quality traits, which is essential for the success of yam breeding.

4.2 Molecular markers and genotyping systems

Molecular markers are relevant tools for applications such as assessing genetic diversity and phylogenetic relationships, cultivar identification, mapping of major effect genes and QTLs, estimating population structure, identification of elite genotypes in crop improvement programmes, and for validation of progenies emanating from genetic hybridizations (Tamiru et al., 2015). Many marker systems have been developed and routinely applied to yam improvement activities (Table 3). Some of these marker systems applied in yam are listed below.

4.2.1 Isozyme markers

Isozymes were the first molecular markers to be established which showed Mendelian inheritance, co-dominant expression, complete penetrance and non-existence of pleiotropic and epistatic interactions (Weeden & Wendel, 1989). The potential of isozyme markers for molecular characterization within and between various Dioscorea species has been well established (Table 3).

4.2.2 Random Amplified Polymorphic DNA markers (RAPD)

Many RAPD markers were developed and predominantly applied for genetic diversity studies of the several Dioscorea species (Table 3). Asemota, Ramser, Lopez-Peralta, Weising, and Kahl (1995) characterized cultivars of D. alata, D. cayenensis, D. rotundata and D. trifida from Jamaica using RAPD markers. Substantial genetic variation was also detected among and between accessions of D. alata using RAPD markers (Cheng & Liu, 1996). Random amplified polymorphic DNA primers were employed to assess cultivars of D. cayenensis and D. rotundata originating from Benin Republic that could not be distinguished using isozyme markers (Dansi, Mignouna, Zoundjihékpon, et al., 2000; Zannou et al., 2009). The intraspecific diversity of D. bulbifera collections that originated from Africa, Asia and Polynesia was examined with RAPD primers (Ramser, Weising, Kahl, López-Peralta, & Wetzel, 1996).

4.2.3 Restriction Fragment Length Polymorphism (RFLP)

Terauchi, Chikaleke, Thottappilly, and Hahn (1992) exploited heterologous DNA sequences as a source of RFLP markers and developed the first RFLP markers for yam. Restriction fragment length polymorphism markers were successfully used to study the phylogeny and origin of Guinea yam (Terauchi et al., 1992) and genetic diversity of D. bulbifera accessions originating from Asia and Africa (Terauchi, Terauchi, & Tsunewaki, 1991).

4.2.4 Amplified Fragment Length Polymorphism (AFLP)

Amplified fragment length polymorphism markers were successfully used to explore the genetic variation of D. alata, D. rotundata, D. bulbifera, D. dumetorum, D. pentaphylla, D. cayenensis, D. abyssinica, D. esculenta, D. nummularia, D. persimilis, D. trifida and D. transversa (Table 3). The comparative evaluation of three molecular marker systems (RAPD, AFLP and SSR) for characterization of D. rotundata revealed that AFLPs had the highest efficiency in discovering polymorphism and detected genetic relationships very similar to morphological classification (Mignouna, Abang, & Fagbemi, 2003). Scarcelli et al. (2006) studied the practice of ennoblement of D. cayenensis, D. rotundata, D. abyssinica and D. praehensilis by farmers in Benin Republic using 91 AFLP markers. Their study established that farmers generated new cultivars with novel genetic combinations through sexual hybridization of wild and cultivated yam.

4.2.5 Simple Sequence Repeats markers (SSRs)

Microsatellites or SSR, due to their co-dominant nature, high level of polymorphism, high abundance and even distribution across the genome were necessary as yam genomics progressed. Terauchi and Konuma (1994) detected microsatellite polymorphisms in a natural population of D. tokoro. Even though the D. tokoro microsatellite primers failed to amplify any DNA when applied to other Dioscorea species, the study revealed the potential usefulness of these markers in yam. Further advancements in yam genomics resulted in the development of 10 SSR markers in D. japonica (Mizuki, Tani, Ishida, & Tsumura, 2005). Tostain et al. (2006) generated and characterized 16 microsatellite markers in different Dioscorea species (D. alata, D. abyssinica and D. praehensilis) and discovered that many of the markers were transferable to other Dioscorea species in the Enantiophyllum section. Siqueira, Marconi, Bonatelli, Zucchi, and Veasey (2011) developed 14 polymorphic SSR markers for D. alata by means of a microsatellite-enriched genomic library methodology. Additionally, six microsatellite markers with high cross-species amplification involving five Dioscorea species (D. alata, D. cayenensis, D. rotundata, D. praehensilis and D. abyssinica) were developed in American yam, D. trifida (Hochu, Santoni, & Bousalem, 2006). Silva et al. (2014) isolated and characterized nine SSR markers from an enriched genomic library of D. cayenensis. Tamiru et al. (2015) developed 90 SSR markers from an enriched genomic library of D. cayenensis and found 94.4% and 56.7% of these SSRs transferable to D. rotundata and D. alata, respectively. Saski et al. (2015) developed 1,152 EST-SSRs from EST sequences.
| Marker type | No of accessions studied | Number of markers | Application | Species | Source |
|-------------|-------------------------|-------------------|-------------|---------|--------|
| Isozyme     | -                       | -                 | Genetic diversity studies | D. alata, D. cayenensis/D. rotundata, D. esculenta and D. bulbifera | Twyford, Viana, James, and Mantell (1990) |
|             | 269                     | 4                 | Genetic diversity studies | D. alata | Lebot, Trilles, Noyer, and Modesto (1998) |
|             | 16                      | 6                 | Genetic diversity studies | D. alata | Bressan, Briner Neto, Zucchi, Rabello, and Veasey (2011) |
|             | 453                     | 5                 | Genetic diversity studies | D. cayenensis/D. rotundata | Hamon & Toure, 1990 |
|             | 156                     | 6                 | Parentage analysis | D. cayenensis/D. rotundata | Zoundjihekpon et al. (1994) |
|             | 467                     | 7                 | Genetic diversity studies | D. cayenensis/D. rotundata | Dansi, Mignouna, Zoundjihekpon, et al. (2000) |
|             | 45                      | 6                 | Genetic diversity studies | D. cayenensis/D. rotundata | Hamon & Toure, 1990 |
|             | 21                      | 7                 | Genetic diversity studies | D. cayenensis/D. rotundata | Bressan, Briner Neto, Zucchi, Rabello, and Veasey (2014) |
|             | 25                      | 7                 | Genetic diversity studies | D. trifida | Veasey et al. (2012) |
| RAPD        | 11                      | 9                 | Genetic diversity studies | D. alata, D. cayenensis, D. rotundata and D. trifida | Asemota et al. (1995) |
|             | 12                      | 14                | Genetic diversity studies | D. alata | Cheng and Liu (1996) |
|             | 20                      | 6                 | Genetic diversity studies | D. alata | Zannou et al. (2009) |
|             | 70                      | 6                 | Genetic diversity studies | D. cayenensis/D. rotundata | Zannou et al. (2009) |
|             | 23                      | 12                | Genetic diversity studies | D. cayenensis/D. rotundata | Dansi, Mignouna, Zoundjihekpon, et al. (2000) |
|             | 232                     | 10                | Genetic diversity studies | D. bulbifera | Ramser et al. (1996) |
| RFLP        | 15                      | 9                 | Genetic diversity studies | D. bulbifera | Terauchi et al. (1991) |
|             | 23                      | 7                 | Origin and phylogenetic studies | D. rotundata, D. cayenensis | Terauchi et al. (1992) |
| AFLP        | 53                      | 3                 | Genetic diversity studies | D. alata | Egesi, Asiedu, Ude, Ogunyemi, and Egunjobi (2006) |
|             | 179                     | 11                | Genetic diversity studies | D. alata, D. abyssinica, D. bulbifera, D. cayenensis/D. rotundata, D. esculenta, D. nummularia, D. pentaphylla, D. persimilis, D. transversa and D. trifida | Malapa, Amau, Noyer, and Lebot (2005) |
|             | 20                      | 64                | Genetic diversity studies | D. rotundata | Mignouna, Ellis, Knox, Asiedu, and Ng (1998) |
|             | 213                     | 91                | Genetic diversity studies | D. cayenensis/D. rotundata, D. abyssinica and D. praehensils | Scarcelli et al. (2006) |
|             | 53                      | 10                | Genetic diversity studies | D. bulbifera, D. alata, D. cayenensis and D. rotundata | Tamiru, Becker, and Maass (2007) |
|             | 53                      | 12                | Genetic diversity studies | D. dumetorum | Sonibare et al. (2010) |

(Continues)
| Marker type | No of accessions studied | Number of markers | Application | Species | Source |
|-------------|-------------------------|------------------|-------------|---------|--------|
| SSR         | 95                      | 8                | Cytogenetic studies | D. trifida | Bousalem et al. (2006) |
|             | 42                      | 10               | Genetic diversity studies | D. bulbifera | Silva et al. (2016) |
|             | 125                     | 6                | Cytogenetic studies | D. alata | Arnau, Nèmorin, Maledon, and Abraham (2009) |
|             | 89                      | 13               | Genetic diversity studies | D. alata | Obidiegwu, Asiedu, Ene-Obong, Muoneke, and Kolesnikova-Allen (2009) |
|             | 219                     | 15               | Genetic diversity studies | D. rotundata | Obidiegwu, Kolesnikova-Allen, Ene-Obong, Muoneke, and Asiedu (2009) |
|             | 56                      | 9                | Parentage analysis | D. rotundata; D. alata | Sartie & Asiedu, 2011 |
|             | 36                      | 9                | Genetic diversity studies | D. alata | Siqueira, Dequigiovanni, Corazon-Guivin, Feltran, and Veasey (2012) |
|             | 384                     | 24               | genetic diversity studies | D. alata | Arnau et al. (2017) |
|             | 146                     | 10               | Genetic diversity studies | D. rotundata | Tostain et al. (2007) |
|             | 2                       | 573              | - | D. alata | Saski et al. (2015) |
| EST-SSR     | 108                     | 90               | Genetic diversity studies | D. cayenensis, D. alata, D. rotundata | Tamiru et al. (2015) |
|             | 2                       | 380              | - | D. alata | Saski et al. (2015) |
|             | 94                      | 380              | Genetic map and QTL identification | D. alata | Bhattacharjee et al. (2018) |
| SNP         | 95                      | 2,215            | Genetic diversity and ploidy analysis | D. rotundata, D. cayenensis, D. mangenotiana, D. praehensilis, D. togoensis, D. burkillana and D. abyssinica | Girma et al. (2014) |
|             | 2                       | 288,505          | - | D. alata | Saski et al. (2015) |
|             | 100                     | -                | QTL analysis | D. rotundata | Tamiru et al. (2017) |
|             | 44                      | 6,371            | Genetic diversity and ploidy analysis | D. dumetorum | Siadjeu et al. (2018) |
|             | 167                     | 3,570,940        | Domestication and genetic diversity | D. rotundata, D. abyssinica, and D. praehensils | Scarcelli et al. (2019) |
|             | 320                     | 1,548            | Linkage map and QTL identification | D. alata | Cormier et al. (2019) |
generated from two *D. alata* genotypes (susceptible and resistant) out of which 388 were validated as polymorphic showing a polymorphism rate of 34% when tested on two diverse parents targeted for anthracnose disease. Microsatellite markers have been utilized to investigate the genetic diversity, ploidy level, inheritance patterns and parentage analysis of various *Dioscorea* species (Table 3).

### 4.3 | Next-generation-based genotyping procedures

The field of genomics has been markedly transformed in recent years due to the advances in high-throughput sequencing technologies, making it feasible to generate large volumes of sequence data quickly and at a considerably lower cost (Elshire et al., 2011). The high-marker density methodologies presented by next-generation-based genotyping procedures such as genotyping by sequencing (GBS) can help to unravel the magnitude of genetic similarity and diversity within and between cultivated species and their wild relatives (Spindel et al., 2013). The GBS procedure is based on minimizing genome complexity with restriction enzymes, coupled with multiplex next-generation sequencing for high-density single nucleotide polymorphism (SNP) discovery (Elshire et al., 2011).

Girma et al. (2014) used the GBS approach to expound the origin and domestication of *D. rotundata* as well as the contribution of wild relatives to the cultivated guinea yam. The 2,215 SNP markers generated from the GBS data enabled the elucidation of the nature of genetic diversity within and between *D. rotundata* and *D. cayenensis* and five wild relatives (*D. mangenotiana*, *D. praehensilis*, *D. togoensis*, *D. burkilliana* and *D. abyssinica*) (Girma et al., 2014).

Genotyping by sequencing of single nucleotide polymorphism (GBS-SNP) was successfully applied to determine the genetic diversity, population structure and ploidy level of 44 accessions of *D. dumetorum* from Cameroon (Siadjeu, Mayland-Quellhorst, & Albach, 2018). Saski et al. (2015) utilized NGS techniques such as expressed sequence tags (EST) sequencing, de novo sequencing and GBS profiles on two *D. alata* genotypes viz. TDa95/00328 (resistant to anthracnose) and TDa95/310 (susceptible to anthracnose) to produce genomic resources for use in yam improvement programmes. They developed a comprehensive set of EST-SSRs, genomic SSRs, whole-genome SNPs and reduced representation SNPs for resistance to yam anthracnose disease and other characters in *D. alata*. The limitations of this study as well as all infection studies are that many of the SNPs identified are likely to be associated with broad stress or infection response.

### 4.4 | Transcriptome sequencing

Analysis of genome-wide differential RNA expression gives researchers a better understanding of biological pathways and molecular mechanisms that control important but complex traits in plants. Narina et al. (2011) investigated gene expression by large-scale generation of ESTs from a susceptible (TDA95/0310) and two resistant yam genotypes (TDA87/01091 and TDA95/0328) infected with the fungus *C. gloeosporioides*. They annotated and analysed nearly 56% of total ESTs for functional categorization and differential expression of genes for tolerance to anthracnose disease. The assembly process generated 15,196 ESTs in TDA95/0328; 15,984 ESTs in TDA95/0310; and 13,577 ESTs in TDA87/01091 with average sequence lengths of 426, 411 and 524 bases, respectively. TDA95/0328 and TDA87/01091 had 115 and 180 unique ESTs, respectively, which could be responsible for or explain their tolerance to *C. gloeosporioides*. The unique ESTs of the resistant accessions were found to be related to carbohydrate metabolism, cell wall biogenesis, lipid and amino acid metabolism, secondary and hormone metabolism, transcription factors, protein synthesis, and signalling proteins as well as multiple pathogenesis-related and host defence-related genes (Narina et al., 2011). A total of 104 candidate SNPs were also discovered between TDA95/0310 and TDA95/0328 libraries that were homologous within each genotype and useful for genotyping and developing genetic maps in yam (Narina et al., 2011). A setback of this study is that some of the SNP markers identified are likely to be associated with broad stress or infection response and not necessarily anthracnose infection alone.

Wu et al. (2015) studied the gene expression of flavonoid (purple flesh colour) of *D. alata* tubers using Illumina sequencing to characterize the transcriptomes of tubers from a purple-flesh and a white-flesh variety. They found 125,123 unigenes from the purple-flesh and white-flesh cDNA libraries, out of which 49.5% were elucidated in publicly accessible protein databases. Biochemical pathway analysis and functional annotation showed that 511 genes were more than two-fold differentially expressed between the purple and white fleshed yam varieties of which 223 genes were down-regulated and 288 genes up-regulated in the purple-flesh tubers. Sixty-one unigenes encoding various well-known enzymes in the flavonoid biosynthesis pathway were detected by transcriptome analysis, and their expression was further confirmed by quantitative real-time PCR (qRT-PCR) (Wu et al., 2015). With these unigenes, 11,793 SSRs were detected and 6,082 SSR markers were developed.

### 4.5 | Metabolomics

The efficacy of trait characterization is enormously enhanced when genomics is combined with other “-omics” approaches such as transcriptomics, proteomics, metabolomics and phenomics (Fukushima, Kusano, Redestig, Arita, & Saito, 2009). This is very true of metabolomics where, in many instances, desirable characters can be directly linked with metabolite composition (Bino et al., 2004). Metabolic techniques produce extensive biochemical phenotypes that can be indicative of quality traits.

Detecting biochemical signals of phenotypic characters would permit metabolite-marker-based breeding (Fernie & Schauer, 2009). Association of specific plant traits to metabolite compositions provides quantifiable markers similar to genetic quantitative trait loci, for example metabolite quantitative trait loci (mQTL) which can be recorded through breeding programmes both independent of underlying genetic mechanisms and coupled with typical genomic analysis.
to improve association of genotype with phenotype, such as metabolite-based genome-wide association analysis (mGWAS) for functional genomics (Adamski & Suhre, 2013; Luo, 2015).

Price et al. (2016) performed a detailed examination of polar extracts from leaf and petiole tissues of 28 Dioscorea accessions from 19 species through gas chromatography-mass spectrometry. A total of 151 metabolites were detected and measured from the polar extracts of the leaves which allowed the demarcation of the different species. The metabolite profiles observed in their study gave enormous insight into biochemically related species and revealed the Dioscorea species as potential sources of essential compounds such as shikimic acid (precursor utilized in the manufacture of the anti-viral oseltamivir). Their study further revealed a large number of unknown metabolites many of which are abundant and emphasizes the understudied nature of genus Dioscorea. Even though this study of Price et al. (2016) encompassed the major clades of the genus, it lacked intra-species diversity for non-cultivated crop wild relatives. Access to materials is a limitation for all studies as germplasm resources are not diverse especially for the wild relatives.

Price et al. (2017) in their study of metabolite profiling of 49 yam accessions belonging to five species via gas chromatography-mass spectrometry produced a comprehensive visual pathway illustration of measured yam tuber metabolome as a resource for biochemical assessment of yam genotypes. The over 200 compounds detected and routinely measured in tubers offer a major development for the chemo-typing of yam. Leaf and tuber analysis identified a subgroup of metabolites useful for accurate species classification and emphasized the possibility of predicting tuber composition from leaf profiles. They also found that metabolic differences were accession specific and usually confined to compound classes and will therefore support trait-targeting for metabolite markers. Though much progress has been made for chemo-typing yam, there is the need for integration with other data (e.g. traits) to fully interpret biochemical compositions and identify biomarkers.

High-performance thin-layer chromatography (HP-TLC) is a novel technology for rapid nutritional analysis of multiple samples at a lower cost compared to column chromatography. Lebot, Malapa, and Molisalé (2019) have recently developed and optimized an HP-TLC protocol for the rapid quantification of individual sugars, al-lantoin, phenolic acids, catechins and saponins in yam tuber flours. This technique was successfully used for the rapid quantification of compounds related to tuber flour quality of 522 accessions of eight Dioscorea species.

Price et al. (2018) investigated the cross-species carotenoid profiling of 46 yam accessions belonging to five species (D. alata, D. bulbifera, D. cayenensis, D. dumetorum and D. rotundata) regularly utilized in yam improvement programmes and provided clarity about the carotenoid composition of various Dioscorea species including the non-significant differences between the D. rotundata and D. alata accessions on β-carotene content and provitamin A activity. Their study further elucidated lack of a clear link between yellow tuber flesh colour and provitamin A content in yam as opposed to other crops like cassava. The methodology employed also allowed concurrent fingerprint profiling of other isoprenoids, such as tocopherols and quinones. Their study revealed varied species profiles and analysis of elite genotypes identified those with high provitamin A content, putative blocks in the carotenoid biosynthetic pathway and tentative identification of the C25-epoxy-apocarotenoid persicaxanthin, which may influence tuber dormancy. The possibility to associate biochemical signatures with several agronomic and sensory characters and study inheritance independent of the causal genetic mechanisms offers potential to expedite breeding by increasing the speed of selection.

4.6 Identification of molecular markers linked to traits

Molecular markers are used to locate genes and QTLs responsible for the inheritance of traits. An important step in the process of trait mapping is the development of mapping populations. Several mapping populations have been developed to determine chromosomal regions having genes or QTLs for traits of interest in yam (Cormier et al., 2019; Mignouna et al., 2002a, 2002b; Petro et al., 2011; Sartie & Asiedu, 2011). Earlier efforts in trait mapping in yam predominantly focused on disease resistance. Mignouna, Abang, Onasanya, Agiodotan, and Asiedu (2002) applied a bulked segregant analysis on an F2 progeny emanating from a cross between TDr89/01444 (resistant male parent) and TDr87/00571 (susceptible female parent) with the aim of detecting RAPD markers linked to yam mosaic virus disease resistance. They identified a single locus conditioning yam mosaic virus resistance in TDr89/01444 and named it Ymv-1. They again found two RAPD markers tightly linked in coupling phase with Ymv-1 on the same linkage group. The two markers were successfully utilized to identify Ymv-1 resistant genotypes among D. rotundata varieties and in resistant F2 genotypes from crosses, demonstrating their potential usefulness in marker-assisted selection.

Mignouna et al. (2002b) applied 469 co-dominantly scored AFLP markers segregating in an intraspecific F1 cross to generate a genetic linkage map of D. alata. Quantitative trait loci mapping discovered one AFLP marker E-14/M52-307 positioned on linkage group 2 that was associated with anthracnose disease resistance, explaining 10% of the total phenotypic variance. A genetic linkage map of the D. rotundata was developed based on 341 co-dominantly scored AFLP markers segregating in an intraspecific F1 cross (Mignouna et al., 2002a). One QTL for yam mosaic virus resistance was associated with the marker P16/M16-126 on linkage group 1, which explained 24% of the total phenotypic variance and two QTLs linked with P14/M22-418 and P17/M22-238 on linkage group 8 which explained 22 and 35% of the phenotypic variance on the maternal linkage group, respectively. Two QTLs for yam mosaic virus were also identified on the paternal linkage group 4 and were associated with the markers P12/M19-241 and P16/M15-81 that explained 13 and 16% of the phenotypic variation, respectively.

An intraspecific genetic linkage map of D. alata was constructed using 523 polymorphic AFLP markers and nine putative QTL(s)
identified for anthracnose disease resistance on five different linkage groups (Petro et al., 2011). The phenotypic variance explained by each QTL ranged from 7.0% to 32.9% while all significant QTLs accounted for 26.4 to 73.7% of total phenotypic variance depending on the isolate and the variable considered (Petro et al., 2011). A genetic linkage map of D. alata was developed from 380 EST-SSRs on 20 linkage groups for the identification of QTLs controlling anthracnose disease resistance (Bhattacharjee et al., 2018). Linkage analysis conducted independently on data collected for three years and average scored data consistently found one QTL on linkage group 14. This QTL observed at a position interval of 71.1–84.8 cm explained 68.5% of the total phenotypic variation in the average score data.

The genetics of sex determination was also elucidated by performing whole-genome resequencing of bulked segregants in an F1 progeny segregating for male and female plants. This analysis revealed a genomic region on pseudo-chromosome 11 tightly associated with feminality within a female heterogametic sex-determination system and SNP markers developed for sex identification in D. rotundata plants at the seedling stage (Tamiru et al., 2017). These sex determination SNPs may not be transferable to the other species. Another limitation is that the ZW genotype shows unstable gender which is problematic; hence, the SNPs detected can only predict the likelihood of feminality. Cormier et al. (2019) constructed the first high-density reference genetic map of D. alata from 1,579 SNPs on 20 linkage groups using SNP data of two F1 outcrossed populations. One QTL was identified per population on linkage group 5 homologs and only in the male maps, which allowed the prediction of plant sex in 77% to 85% of the cases.

In a gene expression study of D. rotundata using SuperSAGE transcriptome profiling to identify flowering and sex-related genes, Girma et al. (2019) found 88 tags significantly differentially expressed in male, female and monoecious plants. Eighteen of these 88 differentially expressed SuperSAGE tags corresponded to previously implicated genes for flower development and sex determination in many plant species.

Genetic mapping (GWAS and linkage mapping) studies are currently ongoing at IITA, Nigeria to identify QTLs for various traits in D. rotundata and D. alata under the ongoing AfricaYam and NSF-BREAD projects. These studies will generate additional genomic information and resources to facilitate marker-assisted breeding in yam. Identification of the key genes underlying relevant traits will expedite their speedy incorporation into elite cultivars or farmer-preferred varieties via marker-assisted selection.

5 | HIGH-THROUGHPUT PHENOTYPING IN YAM

Visual selection has been the main breeding approach used in yam and other crops to identify individuals with striking plant type differences. Making steady breeding progress in yield and quality traits with visual selection is challenging. The development and application of new methods allowing for high-throughput screening or phenotyping of numerous accessions for nutritional and culinary quality, disease resistance, tuber characteristics and yield might optimize the evaluation accuracy and contribute to more precise selection processes.

Substantial progress has been made with the development of high-throughput phenotyping tools for yam. Near-infrared spectroscopy (NIRS) calibration for profiling quality traits, methods for mechanical yam virus inoculation and yam anthracnose assay, and tools and applications for rapid virus detection, and yam anthracnose severity estimation are among the tools that are available for accurate phenotyping of the yam crop. Near-infrared spectroscopy calibration models have been developed for rapid and reliable assessment of food quality attributes in various Dioscorea spp. (Alamu, Adesokan, & Maziya-Dixon, 2019; Ehounou et al., 2019; Lebot & Malapa, 2013; Zhuang, Ni, & Kokot, 2015). Equations of NIRS calibration with high $r^2$ values (> .84) for prediction of starch, sugars and proteins (equivalent N) in various Dioscorea spp. have been developed (Lebot & Malapa, 2013). Alamu et al. (2019) developed NIRS calibration model for prediction of moisture, ash, protein, crude fibre and tannin content in dry tuber samples (flour) of diverse D. rotundata breeding lines with high coefficient of determination values ($r^2 > .80$) for the calibration curve and medium to high $r^2$ values in cross-validation ($r^2 = .50$ for tannin to .80 for moisture content). Ehounou et al. (2019) also demonstrated the feasibility of NIRS to predict physicochemical (dry matter content, starches, sugars and proteins) and textural characteristics (hardness, springiness, adhesiveness) on a panel of contrasting D. alata accessions. Development of reliable NIRS prediction models that adequately describe quality attributes in fresh tubers of yam would facilitate rapid selection of superior clones in breeding trials.

Furthermore, a method for successful transmission (with 95% success rate) of YMV from source yam plants to and from Nicotiana benthamiana was developed at IITA. Silva et al. (2018) reported the development of a reliable, rapid and cost-effective detection method for the two most important potyviruses infecting yam based on reverse transcription-recombinase polymerase amplification (RT-RPA). The method named “Direct RT-RPA” is an isothermal assay that offers robust, accurate, sensitive and quick results (under 15 minutes). It is a low-cost assay with minimal sample preparation requirements and applicable in laboratories with limited settings and also in the fields. The method for mechanical inoculation and new assay for virus detection opens a new opportunity for accurate phenotyping of D. rotundata breeding population for virus resistance. Detached leaf assay (DLA), the “Leaf Doctor” and “ESTIMATE” applications have been standardized and optimized for high-throughput phenotyping of D. alata for anthracnose disease resistance screening under the ongoing AfricaYam project (https://africayam.org/the-africayam-new-app-for-yam-anthracnose-disease/; Kolade, Oguntade, Ajamu, Bhattacharjee, & Kumar, 2018). The “ESTIMATE” application uses yam anthracnose disease standard area diagrams for image-based phenotyping in the field and DLA. The “Leaf Doctor” and “ESTIMATE” applications are quantitative tools for precise evaluation of percentage symptomatic tissue area
of a diseased leaf based on image analysis (Pethybridge & Nelson, 2015). The applications help to differentiate healthy from diseased leaf tissues based on artificial intelligence and machine learning. A phenotyping system based on DLA, “Leaf Doctor” and “ESTIMATE” software enhances the throughput and precision and expedites the selection of promising lines for further evaluation (Kolade et al., 2018). An essential feature of the tools is the elimination of bias that arises during conventional visual scoring. The optimization of the detached leaf assay and the software applications for yam anthracnose disease evaluation has resulted in the harmonization of the phenotyping process across different countries in addition to the comparison of results and performance of genotypes. The use of these high-throughput phenotyping methods optimized for yam and others such as NIRS and ground-penetrating radar (for non-destructive estimation of root bulking rate) is expected to provide more data that could contribute to efficient product profiling and value addition.

6 | INNOVATIVE METHODS OF GENETIC IMPROVEMENT IN YAM

6.1 | Genetic engineering and gene editing for yam improvement

Genetic engineering has emerged as an important alternative and complementary methodology to improve crops including yam. The application of transgenic methods to yam improvement is particularly compelling due to the difficulties associated with conventional yam breeding. However, an efficient plant regeneration system is the main prerequisite for the achievement of successful transformation (Nyaboga, Tripathi, Manoharan, & Tripathi, 2014). Due to its ease of accessibility, ability to transfer low copies of DNA fragments carrying the desirable genes at higher efficiencies with minimal cost as well as the transfer of very large DNA fragments with low rearrangement, Agrobacterium-mediated gene delivery system is the most preferred (Gelvin, 2003; Shibata & Liu, 2000). Quain, Egnin, Bey, Thompson, and Bonsi (2011) developed a transient transformation of D. rotundata using Agrobacterium but generated no transgenic plants. Nyaboga et al. (2014) developed the first fast, efficient and reproducible protocol for Agrobacterium-mediated transformation of D. rotundata. This protocol resulted in the generation of stable transformations and the regeneration of complete transgenic plants. This advancement in Agrobacterium-mediated transformation has laid the foundation for the full implementation of genetic engineering and gene editing in yam.

Targeted genome alteration approach has become a promising tool for crop breeding. The recently established gene-editing technique, the clustered regularly interspaced short palindromic repeats (CRISPR/Cas9) system, resulting from the adaptive immune system of Streptococcus pyogenes, has been demonstrated to be a potent tool for targeted genome editing in many species (Feng et al., 2018). To facilitate the use of gene editing and genetic engineering technologies in improving the productivity and nutritional quality of yam, the Genome-Enabled Platforms for Yam Project was launched in 2016 in collaboration between scientists at IITA and Iowa State University (https://www.nsf.gov/awardsearch/showAward?AWD_ID=1543888). Additionally, a genome-editing tool for yam using pytoene desaturase (a key enzyme in the β-carotene biosynthesis pathway, which converts the colourless pytoene to coloured carotenoids) as a marker is being developed (Tripathi, 2018). Targeted traits for yam gene editing and genetic engineering include resistance to yam mosaic virus and anthracnose diseases, herbicide tolerance and nematode resistance.

Feng et al. (2018) successfully applied the CRISPR/Cas9-mediated targeted mutagenesis in D. zingiberensis using an A. tumefaciens-mediated transformation method aimed at the farnesyl pyrophosphate synthase gene (Dzfps) (an essential gene involved in the synthesis of secondary metabolites). They detected five types of mutations among the transformed plants at the predicted double-stranded break site. Feng et al. (2018) further discovered that the transcript levels of Dzfps and the content of squalene in isolated mutants were drastically decreased compared with those in wild-type plants and concluded that CRISPR/Cas9 provided a rapid and efficient approach for targeted genome modification in D. zingiberensis.

The successful application of the CRISPR/Cas9 technology to inactivate the endogenous banana streak virus by editing the virus sequences to develop resistant plantain (Tripathi et al., 2019) clearly indicates that such an approach can be implemented to develop yam varieties resistant to yam mosaic virus, in that, as in the case of banana streak virus, viruses affecting yam have also been found to be integrated into the genome of yam (Seal et al., 2014; Umber et al., 2014). Genome editing should therefore be incorporated into the yam improvement programme and traits to be targeted should be decided in consultation with breeders. The ethics and regulation of genetically modified and gene-edited crops should be taken into serious consideration in the application of these technologies. The major challenge of the CRISPR/Cas9 technology is that it may recognize sequences with up to five mismatched bases suggesting high rates of off-target effects (Roy et al., 2018). Some approaches such as DNA-RNA chimeric guides, Cpf1, a single RNA endonuclease that employs a T-rich PAM on the 5’ side of the guide, and specific point mutations have been developed to mitigate this limitation (Kleinstiver et al., 2016; Zetsche et al., 2016).

6.2 | Marker-assisted selection (MAS)

To our knowledge, there is no released yam variety whose development utilized MAS technique till date, even though the potential usefulness of MAS in yam improvement has been demonstrated for important traits such as yam mosaic virus (Mignouna, Abang, Onasanya, et al., 2002) and yam anthracnose (Bhattacharjee et al., 2018; Mignouna et al., 2002b) diseases and plant sex (Tamiru et
al., 2017). The massive advancements in yam genomics such as the development of the reference genome sequence for the two most economically important species, generation of a wide array of molecular markers and progress in yam metabolomics and transcriptomics open a new avenue for the successful deployment of DNA-informed breeding techniques such as marker-assisted breeding and genomic selection. QTLs controlling important traits in yam such as plant sex (Cormier et al., 2019; Tamiru et al., 2017), resistance to yam anthracnose disease (Bhattacharjee et al., 2018; Mignouna et al., 2002b; Petro et al., 2011) and yam mosaic virus disease (Mignouna, Abang, Onasanya, et al., 2002; Mignouna et al., 2002a) have been identified. Marker discovery for other essential traits such as tuber flesh oxidation, starch property and dry matter content is ongoing at IITA and other research institutions in collaboration with several international partners and national agricultural research programmes across SSA and beyond (https://africayam.org). The next step is the conversion of these QTLs to diagnostic SNP markers. These markers will then go through verification and subsequent deployment in breeding programmes. The QTLs identified for plant sex determination in D. rotundata by Tamiru et al. (2017) have successfully gone through this process, and SNP markers are available for use. These SNP markers have been successfully deployed in ongoing work at IITA to predict or determine the sex of early generation genotypes in the yam breeding programme. The application of these novel methods will enhance yam breeding efforts and ensure the quick delivery of high yielding, nutrient-dense and climate-resilient varieties to farmers.

6.3 Parentage reconstruction

For many root and tuber crops such as yam, planned crosses are quite challenging due to inherent biological bottlenecks such as cross-incompatibility, non-synchronous and erratic flowering and polyploidy. A viable alternative for genetic improvement in outcrossing species that are constrained in executing planned and controlled crosses is half-sib breeding which entails the random pollination among desirable parents (Norman et al., 2018). The progeny emanating from half-sib breeding must therefore be authenticated in order to ascertain the selection gain in the breeding programme. Parentage analysis anchored by DNA markers is a reliable method for breeders to improve genetic gain in a breeding programme. This entails DNA profiling of progeny and possible parents and comparing their alleles for determination and validation of existing relationships (Jones, Small, Paczolt, & Ratterman, 2010). It can help to elucidate the identity of half-sib progenies and reconstruct the pedigree in the outcrossing crops (Tefel et al., 2015). Potential application and usefulness of parentage analysis in crop improvement programmes include reliable estimation of paternal breeding values in the half-sib family, reduces pollination and labelling errors, assessment of the level of inbreeding and incompatibility, and estimation of genetic effects including general and specific combining abilities in the breeding programme.

Zoundijehkpon, Hamon, Tio-Touré, and Hamon (1994) performed the first parentage analysis in cultivated yam applying six isozyme markers. They validated the progenies of crosses involving well-known genitors (one male and three females). Parentage analysis facilitated by isozyme markers enabled the identification of half-sib progenies and reconstruction of the pedigree of progenies emanating from both controlled and open pollination. Sartie and Asiedu, (2011) employed nine SSR markers to determine the success of hybridization of seven D. rotundata and D. alata mapping populations. The genotypes of each of the mapping populations showed combinations of their parental alleles indicating the success of hybridization. Information on segregation discrepancies in the pedigree information of yam germplasm and breeding lines is lacking. However, an ongoing study at IITA on paternity assignment using half-sib progenies derived from an open pollinated polycross nursery utilizing SNP markers from DaT genotyping platform effectively assigned respective male parents of the progenies. Paternity assignment was carried out on eight half-sib families derived from an open pollinated polycross mating design involving eight female and three male parents and using 6,602 informative SNP markers. Paternity identity of 352 half-sib progenies was reconstructed from the sample of 394 polycross-derived progenies. Among the three paternal genotypes, clone TDr9501932 made the largest contribution of 231 hybrid progenies (65.63%), compared to paternal genotypes TDr89027898 and TDr9902607, which contributed 35 (9.94%) and 86 (24.43%) to total hybrid progenies developed. This finding opens up the whole potential of half-sib breeding for yam improvement in replacing the expensive and time-consuming controlled hand pollination.

6.4 Polyploidy breeding

Yam is represented by multiple species with varying intraspecific and interspecific ploidy levels ranging from diploid to octoploid. The different ploidy levels in yam constitute a challenge but also an opportunity when it comes to its genetic improvement through breeding. It is a challenge as it hinders the effective transfer of relevant genes among individuals with different ploidy levels due to cross-incompatibility and erratic flowering. Ploidy manipulation through induced polyploid or conventional hybridization, however, in many crops has been reported as a potent breeding tool for improving yield potential and also resistance to biotic and tolerance for abiotic stresses. Association of ploidy variation with yield potential and other plant traits has also been reported in yams. Higher vigour and tuber yield advantage were reported with tetraploid (2n = 80) and triploid (2n = 60) water yam compared to its diploid (2n = 40) counterpart (Arnau et al., 2007; Lebot, 2009). The positive effect of artificially induced polyploid on chlorophyll content, leaf shape, and stomata density, plant width, and fruit set has been reported in water yam (Abraham, Nemorin, & Lebot, 2013; Ajayi, Adesoye, Asiedu, & Sartie, 2010; Babal et al., 2010). Kenji, Ohara, and Iwasa (2005) reported a shorter and thicker vine...
in *D. japonica* with artificially induced tetraploid. Likewise, Huang, Gao, Chen, and Jiao (2008) reported an increase in the diosgenin content in *D. zingiberensis* with induced polyploidy. However, a preliminary observation on artificially induced auto-tetraploid in *D. rotundata* accessions at IITA has not shown a clear advantage over their diploid counterparts for tuber yield traits.

The discovery of tetraploid (2n = 80) with a high degree of sexual fertility in *D. alata* has opened a new perspective in polyploidy breeding using the conventional hybridization (Arnau et al., 2010). The tetraploid clones were found to be crossable among themselves, and the inter-ploidy crosses between diploid females and tetraploid males were reported successful. By this new avenue of breeding in *D. alata*, superior polyploid hybrid selections combining several desirable traits, including anthracnose resistance, were identified in Guadeloupe, French West Indies (Arnau et al., 2007). In Vanuatu (South Pacific), anthracnose-resistant *D. alata* hybrids were produced for the first time utilizing the tetraploid fertility in addition to combining other desirable traits (Lebot, Abraham, et al., 2019).

Ploidy breeding might hold potential for increasing yield, improving product quality and increasing resistance to biotic and tolerance for abiotic stresses in yam but its application requires accurate knowledge of the level of ploidy of the genotype (Gamiette, Bakry, & Ano, 1999). Heritability and segregation studies have been instrumental in ploidy determination of yam. The analysis of the segregation of two isozyme loci and six microsatellite markers revealed that only the diploid and tetraploid genetic models elucidated the segregation patterns shown by the eight markers (Scarcelli, Dainou, Agbangla, Tostain, & Pham, 2005). However, due to the nature of the markers studied, Scarcelli et al. (2005) concluded based on the most parsimonious hypothesis that *D. rotundata* is diploid. Similarly, Bousalem et al. (2006) provided genetic evidence to buttress the tetrasomic behaviour of the *D. trifida* genome based on chromosomal segregation pattern analysis of eight SSR markers in three different crosses. All the aforementioned reports show the potential of polyploidy breeding in genetic enhancement of yam. More specifically, the success with conventional hybridization in *D. alata* could be applied in other *Dioscorea* species as well as to develop agronomically successful cultivars.

### 6.5 Breeding data management

The rapid advancement and application of high-throughput genotyping and phenotyping technologies, coupled with the expansion of breeding activities, has resulted in the generation of large volumes of data. To make these data easily available and accessible in real time to the yam breeding research community scattered across Africa and beyond, a database system called "yambase" has been developed to store and retrieve phenotypic and genotypic data (https://yambase.org/) under the AfricaYam project. Several relevant statistical methods and bioinformatics tools for data quality control, pedigreed information visualization, experimental design, breeding value estimation and training population design have been developed and integrated into yambase (https://yambase.org/). Yambase as of April 2019 holds about 414,000 phenotype scores of over 55,434 accessions from over 325 trials conducted by seven breeding programmes as well as a detailed ontology of 182 traits.

### 7 CONCLUSION AND PROSPECTS

Though several inherent biological constraints make yam breeding a very arduous and lengthy endeavour, significant milestones have been achieved in empirical breeding leading to the development of many improved varieties. The advancement of yam improvement programmes to contemporary levels for developing new high yielding varieties with resistance to and tolerance for biotic and abiotic stresses and other end-user-preferred attributes requires systematic knowledge and smart way of understanding of the genetics and genomics of the crop along with mechanisms of trait expression. A wide array of genomic resources, including markers for genetic studies, techniques for ploidy determination, and QTLs for crucial traits such as yam anthracnose and yam mosaic virus diseases and plant sex are now available. Prospect for discovering additional molecular markers linked to genes and QTLs of agronomic relevance, and applying marker-assisted selection in yam breeding is high primarily due to the drastic reduction in sequencing cost and availability of the reference genome in two widely cultivated species, *D. rotundata* and *D. alata*. The current progress with high-throughput "omics" tools will substantially increase the identification of functionally characterized regions of the genome causally affecting phenotypic trait variation for the development of informative markers in yam breeding. Moreover, some of the molecular markers have been optimized and now available, for instance, markers for plant sex assay in *D. rotundata*.

The practical translation of existing and emerging breeding technologies into improved cultivars in yam is expected to enhance the precision and efficiency of breeding. Use of functional markers would facilitate screening for alleles of interest in germplasm collection and breeding populations, accurate description of the genetic potential of parents, crosses and new varieties, and fast track plants with desired alleles of the target traits to the advanced performance trials. Markers application would also facilitate the assessment of plant sex for efficient crossing plan, hybridity in progenies from artificial hand pollination, paternity in natural open pollination polycross blocks, variety description for registration, and tracking genetic purity of varieties in seed multiplication and breeding trials. The advances in genomics also pave the way for the implementation of genomic selection and prediction in yam breeding programmes. The use of genomic tools will save time, resources and cycles required in the breeding pipelines and contribute to overcome the low success rates in crosses. The value of genomic tools in yam breeding would further increase...
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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR’S CONTRIBUTION

AA and KD planned the content, wrote the draft and revision. BO and RA contributed in write up and revision. AA, KD and RA did formatting.

ORCID

Kwabena Darkwa https://orcid.org/0000-0002-6877-8527
Bunmi Olasanni https://orcid.org/0000-0002-8427-7992
Robert Asiedu https://orcid.org/0000-0001-8943-2376
Asrat Asfaw https://orcid.org/0000-0002-4859-0631

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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