SIERRA LEONE AGRICULTURAL RESEARCH INSTITUTE

ADVANCES IN WHITE YAM (*Dioscorea rotundata*) IMPROVEMENT FOR YIELD, FOOD AND QUALITY TRAITS

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ADVANCES IN WHITE YAM (*Dioscorea rotundata*) IMPROVEMENT FOR YIELD, FOOD AND QUALITY TRAITS

By

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PREFACE

The Sierra Leone Agricultural Research Institute (SLARI) was established by an Act of parliament in 2007 as a semi-autonomous government agency, as part of the continuing efforts to revive agricultural research. The SLARI is governed by the SLARI Council. Funding for SLARI comes from the government of Sierra Leone, and from private, national and international donor agencies as well as commercialization of elite technologies.

SLARI conducts research, training, and germplasm and information exchange activities in partnership with regional and national programmes in sub Saharan Africa. The research focuses on smallholder cropping systems in the country and on the following food crops: rice, maize, sorghum, millet, cassava, sweetpotato, yam, cocoyam, groundnut, cowpea, pigeonpea, soybean, forestry, tree and horticultural crops, livestock, fisheries as well as cross cutting issues affecting, climate change, land, soil and water. It addresses crop improvement, plant health, and resource and crop management issues within a farming systems framework. The overall goal is to generate, adapt, validate and broker demand-led, climate-smart agricultural knowledge and technologies; commercialize responsibly under clear public-interest guardrails; provide timely evidence for agricultural policy; and build national research capacity in line with Sierra Leone's development priorities.

This monograph aims to synthesize the significant advancements in the understanding of yams, particularly focusing on integration of innovative agricultural technologies and analytical tools into the breeding process targeted at enhancing yam breeding efforts that contribute to the rapid deployment of improved genotypes possessing superior desired agronomic and quality traits. their ecological dynamics, human interaction, and taxonomic classification. The research presented herein draws upon a decade of dedicated study, integrating field observations, molecular analyses, and historical ecological perspectives to provide a comprehensive overview of this vital plant group.

Chief Dr. Alfred G.O. Dixon

Chair of SLARI Council

EXECUTIVE SUMMARY

Yam (*Dioscorea rotundata*) is an important tuber crop with enormous food, feed and industrial applications with growing efforts to increase its productivity and production. However, the genetic improvement of the crop for yield, food and quality traits, is fraught with various genetic, non-genetic, biotic and abiotic constraints. This paper reviews the progress made in the genetic improvement of white yam for yield, food and quality traits in West Africa. Over years, the yam has led to the identification and deployment of several genotypes with a wide range of adaptation and improved productivity across varying environmental conditions including climate, as well as market oriented improved food value traits. Specifically, this paper highlights advances in the phenotypic and genotypic profiling of yams to identify genotypes with suitable and complementary traits for balanced breeding progress; paternity assignment hybridization pipeline; and discovery of quantitative trait nucleotides and candidate genes linked to tuber yield and yam mosaic virus tolerance in white yam. These advances involved the integration of innovative agricultural technologies and analytical tools into the breeding process targeted at enhancing yam breeding efforts that contribute to the rapid deployment of improved genotypes possessing superior desired agronomic and quality traits.

Keywords: trait profiling, agronomic and breeding constraints, quantitative trait nucleotides, paternity determination, white yam

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CHAPTER ONE

INTRODUCTION

Yam (Dioscorea spp.) is among the extensively cultivated root and tuber crops in the tropical and subtropical regions of Africa, Asia, America, the Pacific, and the Caribbean (Coursey, 1976). The global yam production is estimated at 88.3 million tons, with West Africa contributing 96% of the world yam production (FAOSTAT, 2022). In West Africa, yam is a highly preferred staple and cash crop, contributing more than 15 percent of the daily per capita calorie intake and 32 percent farm income for over 300 million people (Price et al., 2017). It is a food of choice in the yam-belt of West and Central Africa, where it exhibits a deep-rooted connection with the people's social and cultural facets (Obidiegwu and Akpabio, 2017).

Among the cultivated yam species, white Guinea yam (*D. rotundata* Poir) indigenous to West Africa is the most important and widely planted crop (Tamiru et al., 2017). It has an immense but underutilized yield potential. The yield gap on farmer fields is enormous, with an achieved yield estimated as 20 percent of the attainable yield potential of 40 to 50 tons per ha (Bassey and Akpan, 2015). Achieving high and stable tuber yield with acceptable end use quality is the primary target of the yam growers. Crop cultivar is among the factors that account for yield differences among farmer's fields. Genetic improvement through breeding can unleash the yam yield potential and increase sustainable production by ensuring stable yields and marketable quality. A better understanding of the genetic values of breeding lines used in crop improvement programs is essential to address the yield gaps and resilience to biotic and abiotic stresses.

Genes controlling key traits such as resistance to pests and diseases, tuber yield, and tuber quality traits exhibit quantitative inheritance. They may not be linked in a preferred direction, making improvement of these traits cumbersome using conventional breeding techniques only (Darkwa et al., 2020a; 2020b). In quantitative trait loci (QTL) mapping studies, the variation in virus resistance is attributed to a single major locus with a modest contribution (Mignouna et al., 2002). Two random amplifications of polymorphic DNA (RAPD) markers tightly linked in the coupling phase with Ymv-1 locus on the same linkage group were reported in resistant genotypes of *D. rotundata*. The genome wide association studies (GWAS) strategy using naturally occurring variants is a more robust and efficient method for identifying significant loci and the genes involved in the genetic control of complex traits. The GWAS strategy has increasingly been utilized in many crops, including root and tuber crops, to dissect the underlying genetic control mechanism in complex traits.

Supporting yam breeding efforts based on quantitative genetics principles and genomics tools is indispensable to increase the program's effectiveness for increasing productivity. Yam cultivar development using conventional strategies spans at least ten years from crossing to variety release recommendation (Darkwa et al., 2020a). The complementation of the traditional breeding techniques with advanced molecular tools has reduced the breeding cycle in crops (Norman et al., 2018). In theory, genotypic information from molecular markers, when associated with phenotypic traits of interest, may be extensively used to select individuals with higher genetic value through marker-assisted selection (MAS) (Jiang et al., 2013).

Profiling of breeding lines involves genetic analysis of the existing divergence among genotypes and determining functional relationships in the traits that constitute the genotypes. Trait profiles of genotypes are utilized in many studies such as multiple QTL mapping (Bink et al., 2002), association mapping (Baldwin et al., 2011), the heritability of disease resistance (Song et al., 2005), and determination of genetic estimates, breeding values and relationships (Gjedrem, 2010). Trait profiling also helps in the selection process to match the selection decisions to the end-users needs. Over the years, the yam breeding goals have been refocused and restructured to target increased adoption of future releases of elite yam genotypes with correct product profiles and high market penetration potential (Darkwa et al., 2020a). The breeding targets have transformed from undifferentiated products to a differentiated product concept where the client/customer needs are profiled and translated to product specifications. The product concept involves breeding for the desired traits demanded by the target clients (producers, processors, marketers, and consumers) (Darkwa et al., 2020a). Thus, a good understanding of the genetic profile of traits in yams could help yam breeders employ a suitable breeding strategy to develop superior cultivars that drive breeding program success (Arnau et al., 2017; Norman et al., 2018).

Various molecular and phenotypic methods have been used to dissect trait profile of breeding lines in yam improvement programs (Asiedu and Sartie, 2010; Nemorin et al., 2013; Girma et al., 2014; Souza, 2015; Arnau et al., 2017; Tamiru et al., 2017; Agre et al., 2019; Darkwa et al., 2020b). Identifying suitable parents and heterotic groups in the breeding population helps breeders select the population improvement strategy and make short-term variety release. Moreover, understanding the genetic variability in yam breeder's collection is necessary to utilize trait variants within the available gene pool to obtain desired genetic gains. This study aimed to assess the progress made in the genetic improvement of white yam for yield, food and quality traits in West Africa.

CHAPTER TWO

PHENOTYPIC AND MOLECULAR TRAIT PROFILING IN WHITE YAM

Phenotypic and genotypic profiling helps identify genotypes with suitable and complementary traits for making genetic progress. The evaluation of an array of plant traits that define the genetic merits of breeding lines for yam improvement was done using different analytical tools. These tools aided the identification and prioritization of relevant traits defining the genetic merits of breeding lines in the yam improvement program. The assessment of 32 traits in 36 genotypes of white Guinea yam established in a 6 × 6 triple lattice design demonstrated that, of the 32 traits measured, the linear combination of 14 traits that minimize within-group variance and maximize between-group variance for discriminating the genetic values of yam breeding lines were identified. When best linear unbiased prediction with genomic relationship matrix (GBLUP) was used, the accuracies of genomic breeding values were higher ($r=0.87$ to 0.97) for the seven traits (dry matter content, intensity of flesh oxidization of shredded tuber, pasting temperature, pasting time, tuber flesh color, yam mosaic virus and fresh tuber yield) with high broad-sense heritability values ($H^2 > 0.6$). While, for the remaining seven traits with low heritability ($H^2 < 0.3$). These values are indicative of presence of high genetic variability and the potential usefulness of the studied genotypes for genetic improvement of white yam (Norman et al., 2023). Similarly, Shete et al. (2000) and Norman et al. (2020) noted the influence of heterozygosity and polymorphic information content on the genetic variability and response to selection. Pruvost et al. (2013)

reported the influence of allelic diversity and genetic differences on the genome transmission mode and number of successful hybridizations.

High tuber yield and quality attributes in some genotypes indicate their suitability for selection for yam population improvement targeted at food and industrial applications (Jansson et al., 2009). Fresh and dry tuber yields of yam vary with genotypes, species, and environment (Frossard et al., 2017). Fresh tuber yield potential of 40 t ha^{-1} and 50 t ha^{-1} were reported for *D. rotundata* and *D. alata*, respectively (Diby et al., 2011; Bassey and Akpan, 2015). The dry matter content of yam tubers ranges from 7–40% (Eka, 1985). The protein content, ash content, starch and related food quality traits significantly varied among breeding lines from diverse genetic background (Norman et al., 2023). The pasting behavior of the breeding lines is similar to the intermediate pasting temperature of 83°C noted in starches from *D. alata* and *D. cayenensis-rotundata* complex, but lower than those observed in *D. dumetorum* (87°C) and higher than *D. esculenta* starch (78.7°C) (Amani et al., 2005). Genotypes with high pasting temperature indicate that the starch exhibits restriction to swelling (Kaur and Singh, 2005), while those with reduced peak time and pasting temperatures imply reduced energy requirements. Genotypes with lower pasting temperature indicates they exhibit a higher gelatinisation temperature, a longer cooking time, lower energy requirement, and lower energy cost. These findings are supported by the view that genotypes with lower pasting temperatures exhibit a lower gelatinisation temperature and a shorter cooking time (Otegbayo et al., 2006). Accordingly, *D. rotundata* genotypes with low pasting temperature, high peak viscosities, holding strength, breakdown, final viscosities and setback exhibited pounded yam with good textural qualities, moderate softness, springiness, cohesiveness and smoothness (Otegbayo et al., 2006). The starch pasting temperatures are higher than the pasting temperature of 65.2° C reported for potato (Pérez et al., 2011). Pasting and swelling attributes of starch granules have been reportedly inhibited by the amounts of amylose and lipids, whereas both properties are enhanced by the quantum of amylopectin (Falade and Okafor, 2013). Other factors noted to inhibit pasting properties include plant source, starch content, interaction among attributes and testing conditions (Liu et al., 2006). Thus, in the present study, the variations in the pasting characteristics indicate further studies required on amylose and amylopectin contents, lipids, interaction among attributes and genotypes. These aspects would form part of future studies.

CHAPTER THREE

2.1 Prediction accuracy for genetic values for the key traits

The prediction accuracies of GEBV under the GBLUP model ranged from 0.43–0.96 at low narrow-sense heritability of < 0.30; from 0.83–0.94 at moderate narrow sense heritability ranging from 0.31–0.59; and from 0.84-0.97 at high heritability of > 0.60 (Norman et al., 2023). The medium to high prediction accuracies indicates medium to high reliability and a medium to low risk of genotypic performance based on GEBV. Wimmer et al. (2013) demonstrated that, for a given number of markers, higher heritability estimates, and a larger training population increase the prediction accuracy of marker effects. The determination of marker effects with improved accuracy produced higher prediction accuracy for the progeny mean (Yao et al., 2018). The marker-based relationship matrix enhances the capacity to estimate the narrow-sense heritability based on additive genetic effects (Lee et al., 2010). The breeding value approach that captures a large proportion of the variance due to additive and non-additive effects often inflates the genetic gain estimates (Hill et al., 2008).

The genotype-by-trait (GT) analysis revealed the associations among the 14 key traits and the genotypes indicating the relevance of assessing multiple traits in yam breeding trials to ensure that the selected genotype(s) have acceptable performance and possess desirable traits that meet the demands of the producers, processors and consumers (Norman et al., 2023). These findings concur with the suggestion that white yam genotypes should be selected based on desired high fresh tuber yield, higher tuber dry matter content, and field tolerance to YMV (Darkwa et al., 2020a). according to Yan and Frégeau-Reid (2008) and Norman et al. (2021), the GT biplot provides vital information that could be useful for parental selection aimed at improving key traits. Thus, the genotypes that exhibited good attributes would be useful as parents in a hybridization program aimed at population improvement for high fresh tuber yields, tuber dry matter content, resistance to YMV and other key complementary traits.

3.2 Quantitative trait nucleotides for tuber yield and yam mosaic virus in white yam

Improvement of tuber yield and tolerance to viruses are priority objectives in white Guinea yam breeding programs. However, phenotypic selection for these traits is quite challenging due to phenotypic plasticity and cumbersome screening of phenotypic-induced variations. Agre et al. (2021) assessed quantitative trait nucleotides (QTNs) and the underlying candidate genes related to tuber yield per plant (TYP) and yam mosaic virus (YMV) tolerance in a panel of 406 white Guinea yam (*Dioscorea rotundata*) breeding lines using a genome-wide association study (GWAS). Population structure analysis using 5,581 SNPs differentiated the 406 genotypes into seven distinct sub-groups based delta K (Figure 1). Marker-trait association (MTA) analysis using the multi-locus linear model (mrMLM) identified 17 QTN regions significant for TYP and five for YMV with various effects (Figures 2 and 3). The 17 QTNs were detected on nine chromosomes, while the five QTNs were identified on five chromosomes. Variants responsible for predicting higher yield and low virus severity scores in the breeding panel were identified through the marker-effect prediction. Gene annotation for the significant SNP loci identified several essential putative genes associated with the growth and development of tuber yield and those that code for tolerance to mosaic virus.

Of the 17 SNP markers associated with tuber yield, four were mapped on chromosome 4, two on chromosome 5, two each on chromosomes 8, 10, 14, and 17 and a single SNP each on chromosomes 13, 15, and 19 (Table 1). The SNP marker chr05_24682916 explained the highest total phenotypic variance 8.47% (Table 1).

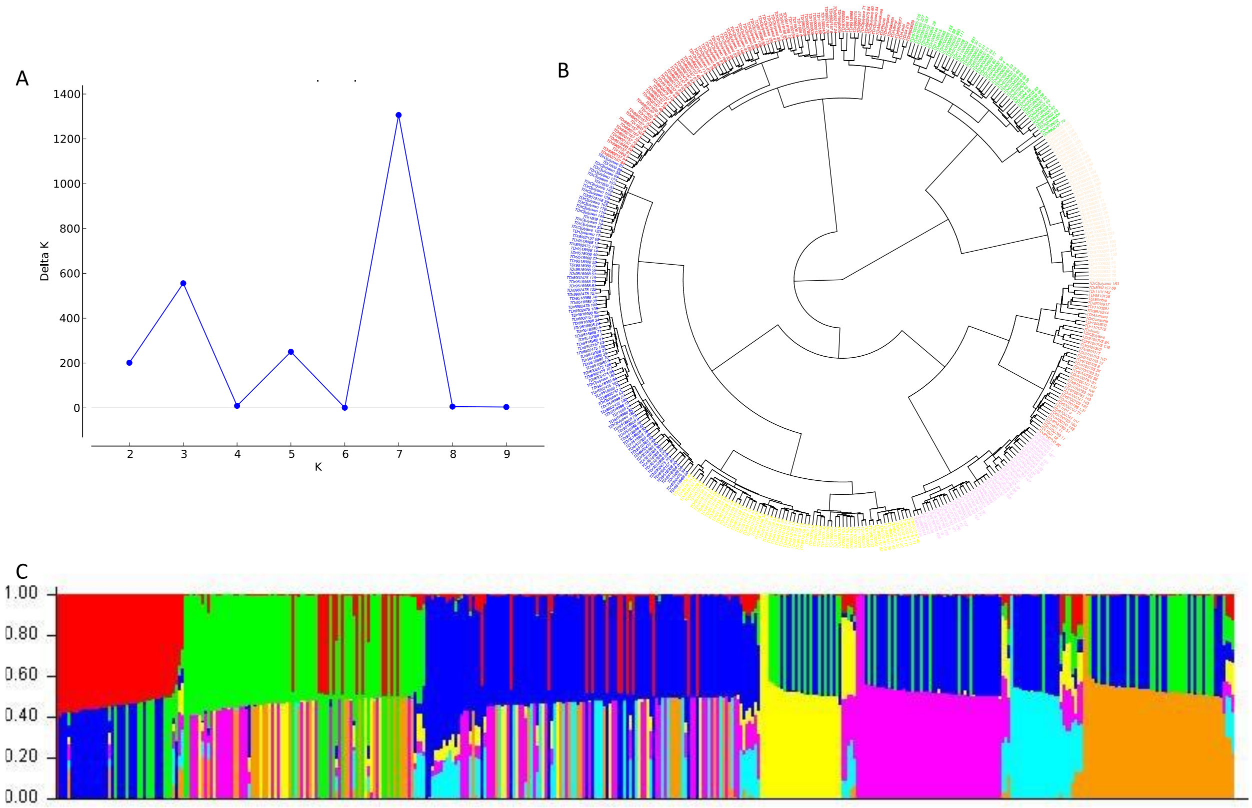

Figure 1. Graphical representation of the population structure of the 406 yam diversity panel. (A) Plot of mean likelihood of delta K against the number of K groups. The highest peak observed at K=7 signifies the grouping of accessions into seven groups. (B) Phylogeny tree showing the 7 Sub-populations. The colors represent each sub-population. (C) Population structure originated from the STRUCTURE based K=7. Each vertical barplot represents a single yam clone

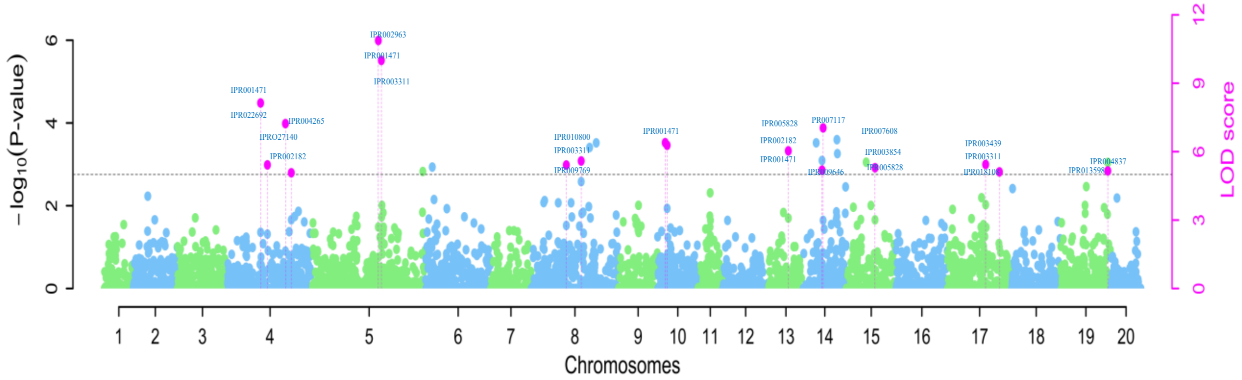

Figure 2. Genome-wide association analysis of tuber yield per plant. Manhattan plot indicating three SNP markers located on chromosomes 4, 5, 8, 10, 13, 14, 15, 17 and 19 associated with the

tuber yield per plant. The blue light letters are the interpro ID for the different putative genes near the SNP markers associated with the tuber fresh weight. Source: Agre et al. (2021)

Of the significant SNPs associated with YMV, three markers named chr03_6338751, chr05_30671001 and chr16_1482029 displayed negative quantitative trait nucleotide effects (Figure 2). Using different genetic model for the SNP association SNP marker chr15_3906069 located on chromosome 15 was identified by two methods pLARmEB and pKWmEB. The total phenotypic variance explained by the markers associated with the yam mosaic virus vary from 0.33% to 5.96%. The minor allele frequency (MAF) of the associated SNP marker ranged from 0.16 to 0.49.

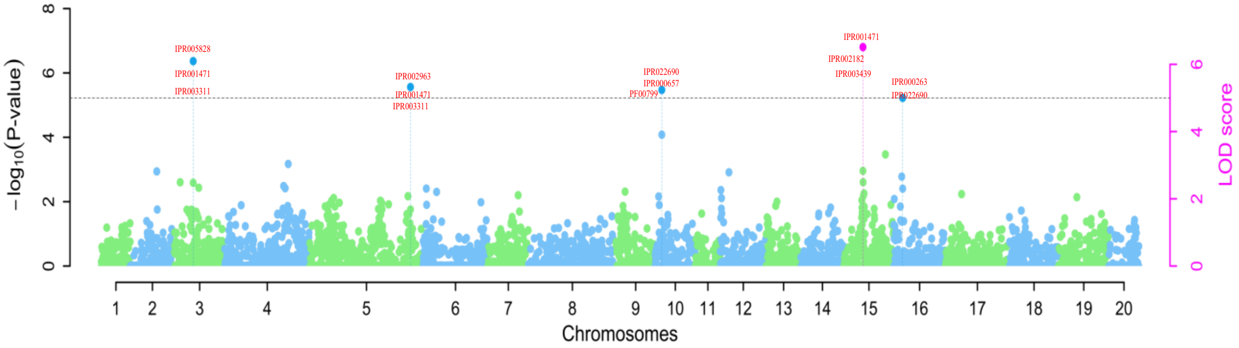

Figure 3. Genome-wide association analysis of yam mosaic virus. Manhattan plot indicating SNPs associated with the YMV. The *y-axis* represents the *p-value* of the marker-trait association on a $-\log_{10}$ scale. The red letters are the interpro ID for the different putative genes near the SNP markers associated with the tuber fresh weight. Source: Agre et al. (2021)

Table 1. SNP markers associated with the tuber yield per plant (TYP) and yam mosaic virus severity score

Trait	Method	SNP marker	Chr	pos (bp)	QTN effect	LOD score	'-log10(P)'	r^2 (%)	MAF	Genotype for code 1
YMV	pLARmEB	chr03_6338751	3	6338751	-143.86	6.10	6.93	4.68	0.46	T
	pKWmEB	chr05_30671001	5	30671001	-109.57	5.32	6.13	5.96	0.49	A
	pLARmEB	chr10_1116193	10	1116193	206.37	5.24	6.05	3.87	0.26	A
	pLARmEB	chr15_3906069	15	3906069	211.65	6.88	7.74	0.31	0.16	A
	pKWmEB	chr15_3906069	15	3906069	174.41	6.15	6.99	0.33	0.16	A
	pKWmEB	chr16_1482029	16	1482029	-100.04	5.00	5.80	3.29	0.49	T
TYP	MrMLM	chr04_23401186	4	23401186	-0.02	5.07	5.87	3.76	0.45	A
	pLARmEB	chr04_8196378	4	8196378	-0.03	5.42	6.23	0.43	0.17	T
	pLARmEB	chr04_18269860	4	18269860	-0.02	7.23	8.10	1.41	0.48	C
	pKWmEB	chr04_6236404	4	6236404	-0.03	8.14	9.03	5.25	0.25	T
	pLARmEB	chr05_24237388	5	24237388	-0.02	10.88	11.83	1.86	0.45	T
	pKWmEB	chr05_24682916	5	24682916	0.03	10.00	10.94	8.47	0.39	A
	pKWmEB	chr08_7046574	8	7046574	-0.01	5.41	6.23	7.38	0.21	A
	pKWmEB	chr08_10135940	8	10135940	-0.02	5.59	6.41	1.64	0.26	C
	pKWmEB	chr10_1571815	10	1571815	-0.03	6.28	7.12	0.86	0.15	C
	pKWmEB	chr10_1317508	10	1317508	-0.01	6.39	7.24	2.41	0.41	T
	FASTmrMLM	chr13_13467988	13	13467988	-0.02	6.04	6.87	2.93	0.41	T

FASTmrMLM	chr14_11301309	14	11301309	-0.08	7.04	7.91	1.08	0.11	A
pLARmEB	chr14_11128124	14	11128124	-0.04	5.19	5.99	1.78	0.15	G
pLARmEB	chr15_5858214	15	5858214	0.02	5.30	6.10	0.39	0.32	T
MrMLM	chr17_15363223	17	15363223	-0.06	5.44	6.25	0.01	0.10	T
pLARmEB	chr17_19041958	17	19041958	-0.02	5.11	5.91	0.16	0.14	C
pLARmEB	chr19_9446619	19	9446619	-0.03	5.16	5.96	0.70	0.09	G

TYP: tuber yield (kg plant^{-1}), YMV: Yam mosaic virus severity score (AUDPC value); LOD: Logarithm of odds; Chr: chromosomes; Pos: position; bp: base-pair; MAF: Minor allele frequency; r^2: r-square; and QTN: quantitative trait nucleotide. Source: Agre et al. (2021)

3.3 Paternity determination in white yam

Open pollination produces half-sib progenies with unstructured pedigree. DNA profiling of progeny and possible parents and comparing their alleles for determination and validation of existing relationships (Jones et al., 2010) is a viable tool to elucidate the identity of half-sib progenies and reconstruct the pedigree in the outcrossing crops (Telfer et al., 2015). The technique works on the principle that progeny constitutes allelic contributions from maternal and paternal parents (Herbinger et al., 1995). Such an analysis can provide a reliable estimation of paternal breeding values in the half-sib family and reduces crossing and labeling errors associated with conventional hand pollination. Zoundjihékpon et al. (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). Sartie and Asiedu (2011) employed nine SSR markers to determine the success of the hybridization of seven *D. rotundata* and *D. alata* mapping populations. The progenies of each of the mapping populations showed combinations of their parental alleles, indicating the success of hybridization.

Paternity testing improves selection gains by increasing parental control in the selection gain equation (Mammadov et al., 2012). Accurate determination of parentage and pedigree relationships helps in determining trait inheritability and ascertaining the genetic progress (Nybom et al., 2014). Parentage analysis using DNA markers has not been utilized to exploit the potential of open pollination in polycross blocks for yam breeding. Norman et al. (2020) studied paternity assignment in white Guinea yam (*Dioscorea rotundata*) half-sib progenies from polycross mating design using SNP markers. The genetic parameters and proportions of progenies with fully recovered paternal identities are presented in Tables 2 and 3. Expected heterozygosity ranged from 0.272-0.328. The average minor allele frequency ranged from the highest of 0.238 in family TDr1689 to the lowest, 0.185 in family TDr1690. Of the 394 half-sib progenies sampled, 352 (96.2%) of progenies were with fully recovered pollen parent identity, whereas 3.8% lacked paternal identity. The pollen parent contribution to offspring varied among male parents included in the crosses. The paternal contribution to the progenies was highest for male parent TDr9501932 (65.63%), followed by TDr9902607 (24.43%) and lowest for TDr8902789 (9.94%). Families TDr1685 and TDr1688 had 100% of progenies with fully recovered pedigree, whereas

TDr1689 had the lowest proportion of offspring (56%) with successfully assigned paternity. Of the 50 offspring in family TDr1685; 52, 46 and 2% were contributions from male parents TDr9501932, TDr9902607 and TDr9902789, respectively (Table 3, Figures 4 and 5). Generally, there were less than 8% missing gametes in all families studied. The proportions of non-missing gametes and missing gametes ranged from 0.926–0.949 and 0.051–0.074, respectively. Families TDr1690 (0.949) and TDr1686 (0.074) had the highest non-missing gametes and missing gametes, respectively; whilst families TDr1686 (0.926) and TDr1690 (0.051) had the lowest. Of the 50 progenies of polycross family TDr1686 genotyped and analyzed, 37 (74%) of progenies were hybrids, whilst 13 (26.0%) were outliers. Outliers occurred where the contributions of two male parents were more than the female parent. Of the 37 true hybrids, 12 (24.0%) progenies were cross combinations of TDr8902157 × TDr9501932, 25 (50.0%) progenies were cross combination of TDr8902157 × TDr9902607 and none was cross combination of TDr8902157 × TDr9902789 (Figure 6). Family TDr1687 had 46 (92.0%) hybrid formation. All the 46 hybrids were cross combinations of TDr8902475 × TDr9501932 (Figure 7).

Table 2. Summary statistics: MAF (minor allele frequency), HE (expected heterozygousity based on Herdy Wieinberg Equilibrium for each family at 0.5) and QC= quality check of genetic (6,602 SNPs, 394 individuals) of segregating progenies of white yam

Family	Sample	Sample after QC	Hybrid	He	MAF
TDr1685	50	50	50	0.276	0.205
TDr1686	50	50	37	0.276	0.211
TDr1687	50	46	46	0.291	0.209
TDr1688	50	50	50	0.327	0.233
TDr1689	50	28	28	**0.328**	**0.238**
TDr1690	45	44	44	**0.272**	**0.185**
TDr1691	49	48	48	0.281	0.204
TDr1692	50	50	49	0.293	0.208

Source: Norman et al. (2020)

Table 3. Proportions of true hybrid progeny of white yam generated in polycross design with known maternity

		Male			**Total hybrid progeny**	**Percent hybrid progeny**
Female	**Family**	**TDr9501932**	**TDr9902789**	**TDr9902607**		
TDr9700793	TDr1685	26 (52.0%)	1 (2.0%)	23 (46.0%)	50	100.0
TDr8902157	TDr1686	12 (24.0%)	0 (0%)	25 (50.0%)	37	74.0
TDr8902475	TDr1687	46 (92.0%)	0 (0%)	0 (0%)	46	92.0
TDr9700632	TDr1688	23 (46.0%)	1 (2%)	26 (52.0%)	50	100.0
TDr9700205	TDr1689	18 (36.0%)	6 (12.0%)	4 (8.0%)	28	56.0
TDr9519158	TDr1690	39 (86.7%)	0 (0%)	5 (11.1%)	44	97.8
TDr9518988	TDr1691	45 (91.8%)	0 (0%)	3 (6.1%)	48	97.9
Ojuiyawo	TDr1692	22 (44.0%)	27 (54.0%)	0 (0%)	49	98.0
Total contribution		**231**	**35**	**86**	**352**	
Percent contribution		**65.63**	**9.94**	**24.43**	**100**	**96.2**

Source: Norman et al. (2020)

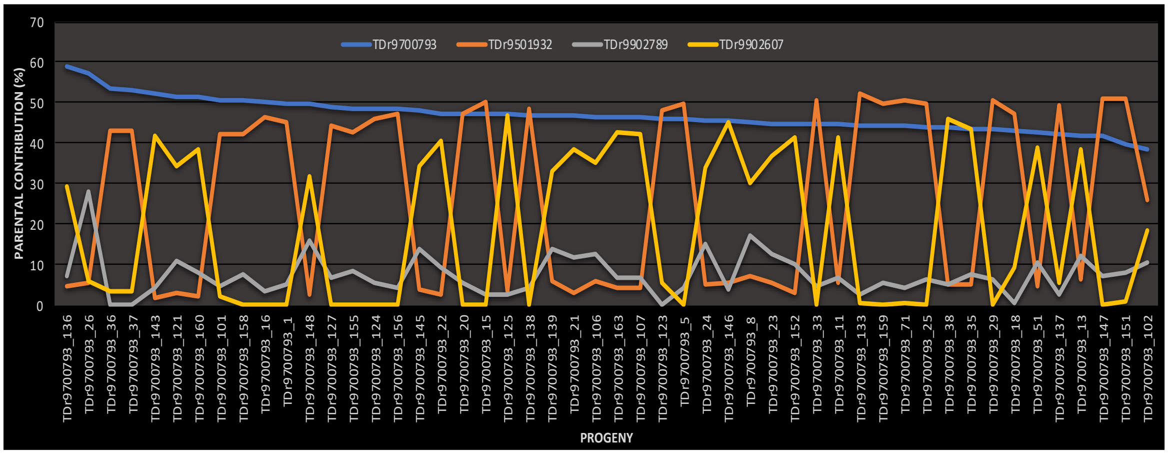

Figure 4. Pedigree reconstruction of polycross family TDr1685 based on genetic contribution of shared parental alleles in progeny**.** TDr9501932, TDr9902789 and TDr9902607 = male parents; TDr9700793 = female parent. Source: Norman et al. (2020)

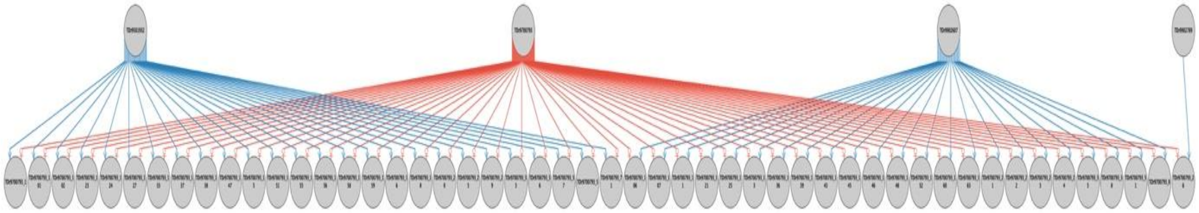

Figure 5. Pedigree reconstruction of polycross family TDr1685 based on Helium pedigree visualization**.** TDr9501932, TDr9902789 and TDr9902607 = male parents (blue); TDr9700793 = female parent (red). Source: Norman et al. (2020)

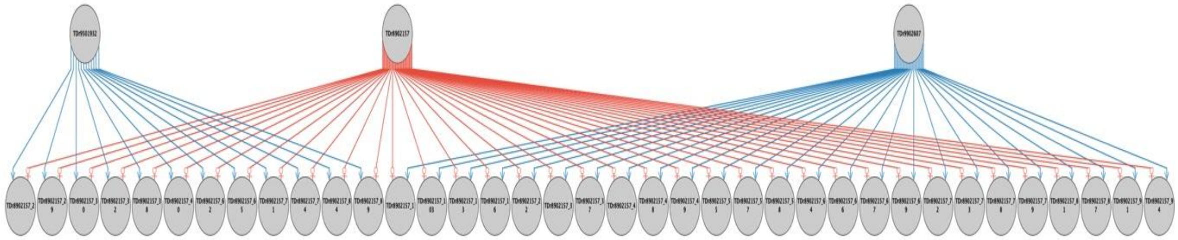

Figure 6. Pedigree reconstruction of polycross family TDr1686 based on Helium pedigree visualization**.** TDr9501932 and TDr9902607 = male parents (blue); TDr8902157 = female parent (red). Source: Norman et al. (2020)

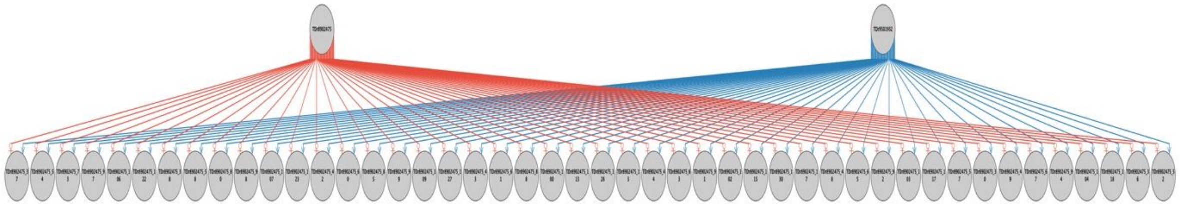

Figure 7. Pedigree reconstruction of polycross family TDr1687 based on Helium pedigree visualization. TDr9501932 = male parent (blue); TDr8902475 = female parent (red). Source: Norman et al. (2020)

Family TDr1688 had 50 (100%) hybrid formation. Of the 50 hybrids, 23 (46.0%) progenies were cross combinations of TDr9700632 × TDr9501932, 27 (54.0%) progenies were cross combination of TDr9700632 × TDr9902607 and none was cross combination of TDr9700632 × TDr9902789 (Figure 8). Family TDr1689 had 28 (56.0%) hybrid formation. Of the 28 hybrids, 18 (36.0%) progenies were cross combinations of TDr9700205 × TDr9501932, 4 (8.0%) progenies were cross combination of TDr9700205 × TDr9902607 and 6 (12.0%) was cross combination of TDr9700205 × TDr9902789 (Figure 9). Family TDr1690 had 44 (97.8%) hybrid formation. Of the 44 hybrids, 39 (86.7%) progenies were cross combinations of TDr9519158 × TDr9501932, and 5 (11.1%) progenies were cross combination of TDr9519158 × TDr9902607 (Figure 10). Family TDr1691 had 48 (98.0%) hybrid formation. Of the 48 true hybrids, 45 (91.8%) progeny were cross combinations of TDr9518988 × TDr9501932 and the remaining 3 (6.1%) progenies were cross combination of TDr9518988 × TDr9902607 (Figure 11). Family TDr1692 had 49 (98.0%) hybrid formation. Of the 49 hybrids, 22 (44.0%) progenies were cross combinations of Ojuiyawo × TDr9501932 and 27 (54.0%) progenies were cross combination of Ojuiyawo × TDr9902789 (Table 3).

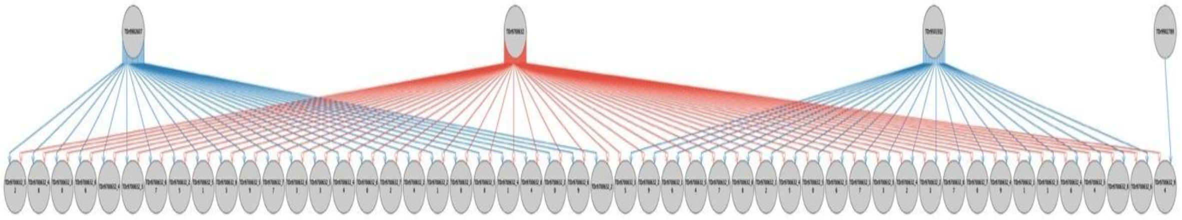

Figure 8. Pedigree reconstruction of polycross family TDr1688 based on Helium pedigree visualization**.** TDr9902607, TDr9501932 and TDr9902789 = male parents (blue); TDr9700632 = female parent (red). Source: Norman et al. (2020)

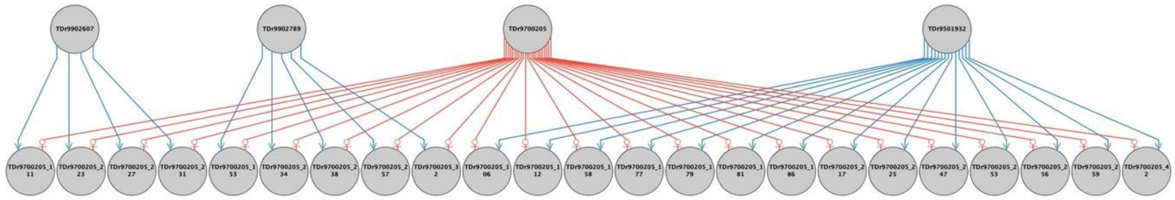

Figure 9. Pedigree reconstruction of polycross family TDr1689 based on Helium pedigree visualization**.** TDr9501932, TDr9902789 and TDr9902607 = male parents (blue); TDr9700205 = female parent (red). Source: Norman et al. (2020)

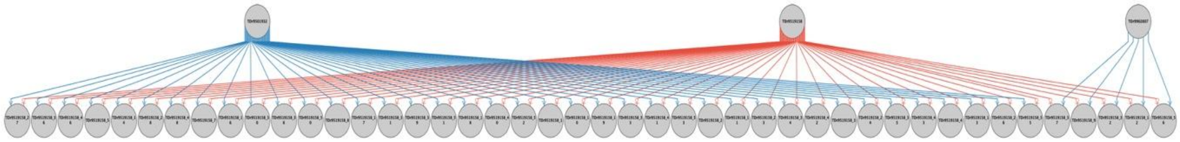

Figure 10. Pedigree reconstruction of polycross family TDr1690 based on Helium pedigree visualization**.** TDr9501932 and TDr9902607 = male parents (blue); TDr9519158 = female parent (red). Source: Norman et al. (2020)

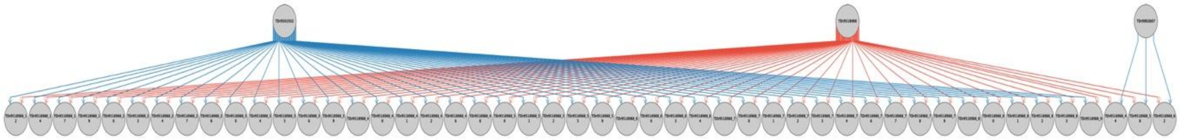

Figure 11. Pedigree reconstruction of polycross family TDr1691 based on Helium pedigree visualization**.** TDr9501932 and TDr9902607 = male parents (blue); TDr9518988 = female parent (red). Source: Norman et al. (2020)

The eight polycross families exhibited higher percent non-missing gametes ranging from 92.6-94.9% (Table 4). Family TDr1686 had the highest proportion of non-missing gametes (94.9%) compared to family TDr1690 (92.6%), which had the lowest. The missing gametes were less than 7.5% for all families.

Table 4. Gamete frequency of eight polycross-derived families of yam

Family	Number of non-missing gametes	Proportion of non-missing gametes	Number of missing gametes	Proportion of missing gametes
TDr1685	669930	0.940	42870	0.060
TDr1686	660336	**0.926**	**52680**	**0.074**
TDr1687	672606	0.943	40410	0.057
TDr1688	676128	0.948	36888	0.052
TDr1689	**681738**	0.939	44482	0.061
TDr1690	**601600**	**0.949**	**32192**	**0.051**
TDr1691	643928	0.938	42680	0.062
TDr1692	674222	0.946	38794	0.054

Source: Norman et al. (2020)

The higher expected heterozygosity relative to observed heterozygosity implying the richness and evenness of the breeding population investigated. The richness and evenness of the studied polycross families indicate the evolutionary or long-term potential of the breeding population, their adaptability to future environmental changes, persistence, selection and response to selection. Petit *et al*. (1998) and Zeng and Cockerham (1990) also found that the allelic richness and the initial allelic composition, determine selection and response to selection, respectively. The high allelic richness also indicates higher accessibility of larger fraction of the genotypic space by fewer mutational events (Wagner, 2008). The heterozygosity and allelic richness of a breeding population may be recovered by gene flow induced by migrants carrying lost alleles (Greenbaum *et al*., 2014). Thus, open pollination may facilitate introduction of new alleles that resolve the founder events in yam populations.

3.4 Genetic gain in yam breeding programme

Monitoring genetic gain is crucial in ensuring effectiveness of breeding programs and identifying potential constraints and mitigating strategies for improvement. Historical data (2010–2022) from multiple generations of breeding cycles evaluated at 31 sites in the white Guinea yam (*Dioscorea rotundata* Poir) breeding pipeline and 28 sites in the water yam (*Dioscorea alata* L.) breeding pipeline of IITA and its national partners in West Africa shows positive genetic trends in fresh tuber yield with a gain of 1.38% (99.17 kg ha^{-1} per year) in the white Guinea yam and 2.18% (252.41 kg ha^{-1} per year) in the water yam breeding pipelines (Asfaw et al., 2024). Genetic trends for virus and anthracnose resistance were in the desired direction but negligible in white Guinea yam, while significant for virus and nonsignificant for anthracnose resistance in water yam. Even though the yam breeding program has succeeded in enhancing tuber yield, post-harvest tuber dry matter content and disease resistance (yam mosaic virus and anthracnose) is yet to follow a similar trend in the genetic materials developed. This suggests that the yam breeding program should strike a balance between various traits, to ensure that increased yield does not compromise food quality or disease resistance. Genetic gain depends on availability of genetic diversity, the breeding methods employed, and the challenges posed by specific stresses in different regions.

3.5 Unraveling breeding potential of white yam for low soil nutrients and added nutrient supply

Tolerance of white Guinea yam (*Dioscorea rotundata*) genotypes to available low soil nutrients and responsive to added nutrient supply are viable components of an integrated soil fertility management strategy for sustainable and productive yam farming systems in West Africa (Matsumoto et al., 2021). The existence of useful variation is critical for exploitation through breeding and genetic studies to develop improved genotypes for low and high input production systems in West Africa. In a study involving 20 advanced breeding lines and a local variety (Amula) under contrasting soil fertility, genotypes expressed differential yield response to low soil fertility (LF) stress and added fertilizer input. Soil fertility susceptibility index (SFSI) ranged from 0.64 to 1.34 for tuber yield and 0.60 to 1.30 for shoot dry weight. Genotypes R034, R041, R050, R052, R060, R100, and R125 combined lower SFSI with a low rate of reduction in tuber yield were identified as tolerant to LF stress related to the soil mineral deficiency. Similarly, genotypes R109, R119, and R131 showed high susceptibility to soil fertility level and/or fertilizer response. Genotypes R025 and R034 had the tuber yielding potential twice of that the local variety under low soil nutrient conditions. Shoot dry weight and tuber yield showed a positive correlation both under low and high soil fertility conditions (r = 0.69 and 0.75, respectively), indicating the vigor biomass may be a morphological marker for selecting genotypes of white Guinea yam for higher tuber yield.

CONCLUDING REMARKS AND FUTURE OUTLOOK

The study established that yam breeding lines possess functional variability and complementary traits values for yam population improvement and selection for short release program. Breeders could exploit the useful variability in molecular and phenotypic trait values in selecting a suitable breeding strategy and elite parents for the genetic improvement of the crop. Complementation of estimated breeding values with genomic estimated breeding values revealed higher prediction accuracy and genetic values of breeding lines profiled white yam traits.

Application of different multi-locus models of GWAS identified 22 QTNs. The genetic architecture of tuber yield per plant and yam mosaic virus (YMV) are regulated by varied QTNs unevenly distributed on the 20 chromosomes of white yam. Among the 4 MLM models, pKWmEB and pLARmEB are most robust in identifying more QTNs. The associated SNP markers could be potentially employed for targeted and accelerated tuber yield per plant and YMV resistance in white yam. The information from on SNP variants and genes could help design new breeding strategies to hoard superior alleles for tuber yield per plant and yam mosaic virus in future marker-based breeding. The chromosomal regions controlling these studied traits could be exploited for selection and effective pyramiding of favorable alleles in white yam population improvement. Findings are relevant for population improvement of desirable TYP and YMV traits using marker assisted breeding (MAB) and haplotype-based scheme.

The identification of parentage relationships in the half-sib progenies of white Guinea yam using SNP markers aids the accurate traceability of genotypes with unknown identity, and determination of genetic diversity across families and generations that could be exploited for breeding.

Advances in breeding technologies and methodologies, as well as the availability of high-quality historical trial data, continue to drive improvements in white yam genotypes for tuber yield, food and quality (disease resistance) traits. Moreover, sustained investments and collaborations are imperative to ascertain continued desired trend of genetic gain, thereby ensuring the development of high-yielding and disease resistant yam genotypes to meet present and future demands and ensure food and nutrition security.

Information from this review could be useful in designing future marker-based breeding as well as genetic conservation of the crop. The long-term effects of plant domestication, pleiotropy and selective breeding for desired agronomic traits of yam forms part of future work on the crop.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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