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Genetic parameter estimates and improvement of yam for tuber yield, quality and related attributes: A review

Prince E Norman[1*], Pangirayi B Tongoona[2]
[1] Agricultural Research Institute (SLARI), Sierra Leone
[2] West Africa Centre for Crop Improvement, College of Basic and Applied Sciences, University of Ghana, Ghana

Abstract
Determination of genetic variability, parameter estimates and improvement using traditional breeding technique alone is challenging. High degree of genetic heterozygosity, poor-flowering low seed set, variation in flowering intensity over seasons and across locations, low multiplication ratio of planting materials, genealogy overlap, polyploidy, biotic and abiotic stresses limit the efficiency of breeding progress in yams. The extent of genetic variability and selection gain in the crop is limited by lack of well-articulated information on genetic parameter estimates of quantitative traits. Knowledge of genetic parameter estimates and improvement of yam for tuber yield, quality and related attributes would facilitate the formulation of effective strategies for genetic conservation, management and utilization. Complementation of traditional method of computing genetic parameter estimates with molecular marker information is among the available handy tools for crop breeders to maximize genetic gain in a breeding program. This paper reviews the genetic variability and heritability in yam breeding, genetic improvement of yam for tuber yield and quality traits and related attributes. It assesses the limitations of genetic parameter estimates and the ways of improving genetic gain in yam breeding programs. Utilization of complementary techniques for determination of genetic parameter estimates in yam improvement programs can increase the selection gain and reliable exploitation of the heritable variation in the desired direction.

Keywords: heritability, genetic variance, genetic gain, genetic models, dioscorea spp

Introduction
Yams (Dioscorea spp.) are important crops with increasing food, feed and industrial applications in Sub-Saharan Africa and many other regions of the world (Norman, 2019) [35]. Yams possess great potential to contribute to food, nutrition and income security of many livelihoods worldwide, but this potential is yet to be fully exploited. Variety development through breeding is among key strategies targeted at unlocking the potential of yam for food, feed and industrial applications (Norman *et al*., 2018) [36]. Yam breeding aims at the genetic improvement of genotypes for their resilience and productivity amidst the dynamics of current and future production challenges thereby meeting the demands of various stakeholders in the yam value chain including producers and consumers (Darkwa *et al*., 2020) [11]. Selection of adequate parents for creation of new genetic variants, and the identification and selection of superior recombinants possessing the desired traits are among the key activities in the plant breeding process. In selecting parents for hybridization and elite progenies with desired superior trait values for targeted end-users, several economic traits are simultaneously considered (Mondal *et al*., 2007). Moreover, effective selection of breeding plans is contingent upon a good knowledge of the heritable variations and genetic correlations among traits of economic importance, and the expected occurrences of the desired progenies within the breeding population (Norman, 2019) [35]. Evaluation and prediction of genetic parameters have extensively been utilized in crop improvement programs for optimization of various breeding schemes and selection of an efficient breeding technique used for genetic improvement (Falconer and Mackay, 1996) [19]. In yam, genetic parameter studies have primarily focused on the dissection of the genetic variance within germplasm at the pre-breeding stage (Darkwa *et al*., 2020) [11].
Reliable estimates of genetic parameters are imperative for the design of efficient improvement programmes and accurate prediction of breeding values. Genetic parameter estimation involves the partitioning of phenotypic covariances between relatives into two or more components such as additive genetic effects, dominance, epistasis, and permanent and temporary environmental effects (Falconer and Mackay, 1996) [14]. Heritability estimates and common environmental variance effects are functions of variance components that may be specific for a particular population and time period. Genetic parameter estimates of quantitative traits such as heritability, are important because they indicate the ability of a species to respond to selection and thus, the potential of that species to evolve (Falconer and Mackay, 1996) [14]. Genetic parameter estimates are also useful in conservation studies for the estimation of the total genetic variability of a population (Norman, 2019) [35].

Traditional methods utilized for estimation of variance components require knowledge of the relationships among the individuals recorded (Lynch and Walsh, 1998) [29]. In natural populations, there is lack of detailed information on the pedigree in all except the most carefully studied populations, which may be subject to errors. The incorporation of molecular marker data using robust molecular analytical tools provides a means to infer relationship lacking full pedigree (Norman *et al*., 2020) [34].

Molecular-based tools used for determination of genetic relationships are grouped into two main categories including method-of-moments estimators and likelihood techniques (Norman, 2019) [35]. The method-of-moments estimators are used to estimate relatedness, as a continuous measure, on the basis of shared alleles at marker loci whereas the likelihood methods are useful for determination of the likelihood of a pair falling into particular relationship classes such as full sibs or non-sibs, given the observed marker information.

Lynch and Walsh (1998) [29] and Mousseau *et al*. (1998) [32] have proposed two techniques that permit the estimation of quantitative genetic parameters associated with a trait without reference to the exact pedigree. These techniques utilize molecular data to infer pairwise relationships between individuals. Several approaches have been proposed for determination of parameter estimation. The first technique, known as the regression approach, is utilized where measures of pairwise phenotypic similarity are regressed against pairwise relatedness (Lynch and Walsh, 1998) [29]. If prior information exists on population structure, likelihood-based procedures may be adopted. This technique involves placing of pairs into a predetermined population structure according to the probability of observing their genotype and phenotype (Thomas *et al*., 2000) [45, 46]. Variance components have been determined using a simple two-step procedure: first, families of sibs are reconstructed using a Markov chain Monte Carlo (MCMC) procedure, and second, the reconstructed sibships are used to estimate variance components (Thomas and Hill, 2000) [45, 46]. Thus, a good understanding of genetic parameter estimates and improvement of yam for tuber yield, quality and related attributes is imperative for the formulation of effective strategies for genetic conservation, management and utilization of genotypes in breeding and genetics programs. In this paper, we review the genetic parameter estimates, advances in improvement of yam for tuber yield, quality and related traits as well as their potential in facilitating breeding activities in yams.

Genetic variability and estimates of genetic parameter in yam breeding

Knowledge of the magnitude and pattern of existing genetic variation of traits is a fundamental requirement for its genetic improvement (Norman, 2019) [35]. Breeders often use efficient selection criteria in the large numbers of early generations especially for quantitatively inherited traits. Most of the key economic traits such as specific disease resistance, quality, yield and related traits, are under quantitative genetic control (Koutsika-Sotiriou *et al*., 2013) [25]. Effective utilization of genetic variability of crosses depends on the crossing parents and the selection procedures of early generations (Koutsika-Sotiriou *et al*., 2013) [25].

Increase in yam productivity depends on improvement in genetic traits and their heritability from one generation to the next (Akoroda, 1983) [4]. Increased productivity is often achieved through the use of genetically superior genotypes and improved agronomic practices (Norman, 2019) [35]. The introduction of genetically superior genotypes, also known as genetic gain, is frequently expressed in yield increase per year, and often illustrated using the maize model crop (Norman, 2019) [35]. The pattern of genetic gain in most crops does not follow similar trend of genetic gain found in maize. For instance, in tomato, a 0.9% genetic gain in fruit yield was established (Higashide and Heuvelink, 2009) [18]. In potatoes, Rijk *et al*. (2013) [43] noted limited genetic progress in the fresh marketable root yield, shape and size. In yams, limited information exists regarding genetic gain on economic traits partly due to genetic, environmental and market factors.

Heritability is one of the key genetic estimates often studied. Heritability is the measure of the phenotypic variance due to genetic causes that has a predictive function in plant breeding. In yams, contrasting results have been reported on genetic parameter estimates for various traits in yams (Alam *et al*., 2014) [5]. The heritability estimates reported for fresh storage tuber yield in *D. florinbunda* were 12.4 and 58.6%, respectively (Martin and Cabanillas, 1967) [30]. In *D. rotundata* (white yam), the broad sense heritability estimates for yam mosaic virus, fresh tuber yield and tuber dry matter contents were 58, 38, 36%, respectively (Norman *et al*., 2021) [33]. Earlier report of heritability estimate for fresh storage tuber yield was lower in plants grown from seeds of mixed cultivars (27.0%) compared to plants from open-pollinated seeds (54.0%) (IITA, 1974). Moreover, genetic estimates were noted to differ between plants from clonal propagation and those from seed propagation (Akoroda, 1983) [4]. In *D. alata* (water yam), high broad sense heritability estimates were found for days to emergence (97.4%), first leaf emergence (98.6%), internode length (98.5%), petiole length (93.9%), starch content (99.4%), total phenols (96.6%), and total sugar (93.6%) (Norman, 2019) [35]. High heritability and high genetic advance were also reported for days to emergence, starch content, first leaf emergence, internode length, petiole length, total phenols and total sugar in water yam suggesting a preponderance of additive gene control on the expression of these traits (Alam *et al*., 2014) [5]. The broad sense heritability estimates for fresh tuber yield per unit area (t ha^{-1}), tuber weight per plant (kg $plant^{-1}$), tuber number per plant, average tuber weight (g) and tuber dry matter content were >50% (Darkwa *et al*., 2020) [11]. In both *D. alata* and *D. rotundata*, the phenotypic coefficient of variation (PCV) was noted to be higher than the genotypic coefficient of variation (GCV) for tuber yield, tuber weight per plant, number of tubers per plant, tuber width and tuber dry matter content indicating the influence of environment on the heritability of these traits (Alam *et al*., 2014) [5]. Similarly, Norman *et al*. (2021) [33] found higher PCV relative to the GCV for yam mosaic virus, tuber yield and tuber dry matter content in genotypes of *D. rotundata*. In *D. cayenensis*, Akoroda (1984) [3] found intermediate heritability values for plant

leafiness and number of tubers per hill, and Alam *et al*. (2014) [5] noted high phenotypic and genotypic coefficient of variation values for the same traits. However, phenotypic and genotypic variances only provide apparent genetic variability in traits rather than precise insight on variability in materials (Alam *et al*., 2014) [5]. Findings suggest that the rate of genetic advance and selection should be determined using the phenotypic variance and heritability in yield components and environmental effect in *Dioscorea rotundata*.

Genetic advance is defined as the degree of gain obtained in a character under a particular selection pressure. Both high genetic advance and high heritability estimates offer the most suitable condition for selection (Norman *et al*., 2021) [33]. In *D. rotuntata*, high genetic gain and intermediate genetic gain were found for fresh tuber yield and yam mosaic virus, respectively (Norman *et al*., 2021) [33]. Asfaw *et al*. (2021) [7] assessed the genetic parameters and breeding values accounting for additive and dominance effects in prediction for six key traits in white Guinea yam (*Dioscorea rotundata* Poir.) breeding population using pedigree-based best linear unbiased prediction (P-BLUP) technique. The models used to determine the variance component estimates for the six yam traits are shown in Table 1. The inclusion of either the additive or dominance variance–covariance structures into the baseline model significantly improved the description of the variances for all the traits studied (Table 1). However, the optimal fit was obtained by modeling the additive effect alone for average tuber weight, tuber number per plant, and tuber dry matter. Modeling involving dominance exhibited a significant effect for YMV severity and tuber yield (per unit area or per plant).

Table 1: Log-likelihood ratio test (LRT) comparing the goodness of fit for genetic models (A and A+D) using variance–covariance structure from a pedigree relationship and heritability estimates on six yam traits relative to a baseline model (B) with an independent clone effect

Model	TTY	TTWPL	ATW	TTNPL	DM	YMV
B vs. A	7.02**	5.63	28.51***	34.317***	24.02***	15.82***
B vs. A+D	19.84***	13.95***	31.496***	39.47***	25.54***	25.55***
A vs. A+D	12.82***	8.316***	2.98*	5.15	1.52	9.72***
H^2 (A)	0.50	0.62	0.65	0.57	0.52	0.78
H^2 (B)	0.45	0.51	0.66	0.52	0.50	0.77
H^2 (A+D)	0.48	0.60	0.53	0.58	0.57	0.80
h^2 (A)	0.10	0.10	0.24	0.15	0.19	0.10
h^2 (B)	0.10	0.10	0.24	0.15	0.19	0.10
h^2 (A+D)	0.00	0.00	0.20	0.12	0.17	0.03

A=model fitted with additive variance–covariance structure; A+D=model fitted with additive plus dominance variance–covariance structure. TTY=fresh tuber yield; TTWPL=fresh tuber yield per plant; ATW=average tuber weight; TTNL=tubers per plant; DM=tuber dry matter content; YMV=Yam mosaic virus severity. *=Significant at the 0.10 probability level; **=Significant at the 0.01 probability level; ***=Significant at the 0.001 probability level. (Source: Asfaw *et al*., 2021) [7].

Generally, variances due to genotypic effect were higher than the random error effect for all the six traits, with the coefficient of relative variation ranging between 1.1 for fresh tuber yield (t ha^{-1}) and 4.45 for YMV severity (Table 2). The coefficient of determination of the plot effect (C_p^2) was low for all the traits ranging between 0.03 for tubers per plant and 0.11 for tuber dry matter. The error coefficient variation (CVe) was relatively low, ranging from 7.72% for YMV severity to 28.14% for average tuber weight per tuber. Yam mosaic virus severity score and tuber dry matter content had medium (10-20%) values of the genotypic and phenotypic coefficient of the estimated variances, whereas fresh tuber yield, tuber yield per plant, average tuber weight per tuber and number of tubers per plant had higher (28-54%) values of the genotypic and phenotypic coefficient of the estimated variances.

The narrow-sense and broad-sense heritability estimates differed among the six traits and the different models used (Table 2). The narrow-sense heritability estimates decreased with the inclusion of the dominance effect in the model, whereas the broad-sense heritability estimates increased with the fitting of the genetic variance–covariance structure into the baseline model for the measured traits except for YMV severity (Table 2).

Table 2: Estimates of genetic parameters and expected genetic gain based on 5% selection differential for six traits assessed in early-generation evaluation trials of white Guinea yam

Estimates of parameters	Fresh tuber yield (t ha^{-1})	Tuber yield per plant (kg)	Average tuber weight (kg $tuber^{-1}$)	Tubers per plant	Tuber dry matter (%)	YMV severity score (AUDPC value)
Mean	16.25 ± 4.01	1.78 ± 0.46	1.28 ± 0.45	1.51 ± 0.21	32.88 ± 3.67	228.89 ± 29.14
σ_g^2	21.13 ± 5.03	0.33 ± 0.06	0.30 ± 0.06	0.21 ± 0.03	15.59 ± 2.04	1,389.46 ± 111.05
σ_b^2	3.31 ± 1.45	0.03 ± 0.02	0.03 ± 0.02	0.01 ± 0.03	3.11 ± 0.75	47.93 ± 21.05
σ_e^2	19.19 ± 3.94	0.19 ± 0.05	0.14 ± 0.05	0.16 ± 0.03	8.78 ± 1.45	312.18 ± 76.77
σ_p^2	43.63 ± 2.56	0.56 ± 0.03	0.47 ± 0.03	0.37 ± 0.02	27.48 ± 1.58	1,749.58 ± 80.92

C_p^2	0.08	0.05	0.06	0.03	0.11	0.03
CV_g (%)	28.29	32.32	43.2	30.35	12.01	16.29
CV_p (%)	40.65	42.04	53.56	40.28	15.94	18.27
CV_e (%)	26.96	24.81	28.14	26.49	9.01	7.72
CV_r	1.10	1.74	2.14	1.31	1.78	4.45
ΔG	0.05	0.02	0.31	0.19	1.77	3.32
ΔG_t	0.01	0.01	0.08	0.05	0.44	0.83

σ_g^2=genetic variance; σ_b^2=environmental variance between plots within experiments; σ_e^2=within-plot error variance; σ_p^2=individual phenotypic variance, which is sum the variance components for the trait; C_p^2=coefficient of determination of plot effect; CV_g=coefficient of genotypic variation; CV_p=coefficient of phenotypic variation; CV_e=residual coefficient of variation; CV_r=coefficient of relative variation (σ_g^2 / σ_e^2); Δ*G*=genetic gain per cycle; ΔG_t=genetic gain per year. (Source: Asfaw *et al*., 2021) [7]

Asfaw *et al*. (2021) [7] further demonstrated that selection of the top 5% progenies based on the multi-trait index technique indicates positive genetic gains for fresh tuber yield (t ha^{-1}), tuber yield (kg plant^{-1}), and average tuber weight per tuber (kg), whereas tuber dry matter content and yam mosaic virus resistance had negative genetic gain compared with standard genotypes. The findings of their study also demonstrated the usefulness of P-BLUP for the selection of desired superior parental genotypes and progenies with higher breeding values for interbreeding and higher genotypic value for yam population improvement.

Based on the articulated information on genetic estimates, it can be deduced that the variances obtained are possibly due to the different species, plant materials or genotypes, different test locations with different prevailing environmental conditions. Moreover, since genes controlling desired traits (tuber yield, tuber quality, resistance to pests and diseases) are quantitatively inherited and less likely linked, this makes their improvement through empirical breeding very difficult. Thus, the efficiency and effectiveness of genetic improvement of these traits in yam necessitate the use of genomic and genetic assisted breeding techniques. This illustrates that a good knowledge of genetic parameters existing in various traits and the relative proportion of genetic information in quantitative traits is imperative for effective yam population improvement.

Genetic improvement of yam

1. Genetic improvement of yam for tuber yield and related attributes

Fresh tuber yield of yam is influenced by several genetic, biotic and abiotic factors. Some of the key factors affecting tuber yield include maturity, shoot emergence time, tuber initiation time, tuber dormancy period and tuber dry matter content (Sartie *et al*., 2012) [44]. Tuber maturity is defined as an increase in the accumulation of citric and malic acids in the tuber, reduction in metabolic activity that supports plant growth, reduction in starch content, dry matter accumulation, and total sugar content. An immature tuber has a poor taste, short shelf-life and more susceptible to diseases.

Previously, physiological maturity in yams was noted to occur when the foliage completely senesces or dries (Okoli *et al*., 1984). The senescence phase of the aerial organ of yam coincides with the end of suberization of the tuber surface, which begins in proximal region of the tuber at the first stages of growth. However, early or induced senescing or drying of foliage might be due to biotic and abiotic factors such as disease incidence, drought, or other stresses. Recent studies in this aspect utilized alternative indicators with little or no influence by the environment. Traditional farmers also utilized the dramatic change in leaf pigmentation from green to dark green as an indicator of early maturing yams. However, studies have shown non-significant and low correlations between tuber maturity and the colour indices of leaves and tubers (Sartie *et al*., 2012) [44]. The proximal end or head portion of a yam tuber is also believed to matures earlier than the distal end or tail portion. Thus, uniformity in tuber parenchyma colour may serve as an indicator for tuber maturity, if it occurs during the maturity phase of the crop. Early and late maturing genotypes of yam could be distinguished by time of attainment of uniform parenchyma colour within a tuber, length of tuber dormancy period and time of shoot senescence. Early planting of yams has been noted to increase tuber yield, whereas late planting reduces tuber yield due to shorter growth cycle and reduced effective tuber growth duration (Sartie *et al*., 2012) [44]. Early field emergence, early tuber initiation, short tuber dormancy duration and low tuber dry matter content have also been implicated to influence tuber yield in yams (Sartie *et al*., 2012) [44].

The fresh and dry tuber yields of yams differ with genotypes, species and environment (Frossard *et al*., 2017) [17]. The average fresh tuber yield increased from 7.8 – 8.8 t ha^{-1} during 1961 – 2014 (FAOSTAT, 2016). The estimated fresh tuber yields of 40 t ha^{-1} and 50 t ha^{-1} were reported for *D. rotundata* and *D. alata*, respectively (Bassey and Akpan, 2015) [9]. Tuber dry matter content is another key trait often considered in the yam genetic improvement program. Dry matter content measures the quantity of photosynthates that influence the yam tuber quality traits used in various industrial applications (Chukwu *et al*., 2007) [10]. The moisture content and dry matter content of yam tubers reported range from 60 – 80% and 7 – 40%, respectively (Eka, 1985). In *D.*

rotundata, different dry tuber yield estimates ranging from 3.4 t ha^{-1} (Kikuno *et al*., 2015) to 18.0 t ha^{-1} (Irizarry and Rivera, 1985) have been reported. The dry matter content values noted by Norman *et al*. (2021) [33] ranged between 27.61 and 35.96%. In *D. alata*, different dry tuber yield estimates of 6.2 t ha^{-1}, 1.9 t ha^{-1}, 4.6 t ha^{-1}, 8.7 t ha^{-1} and 10.0 t ha^{-1} were reported by Frossard *et al*. (2017) [17].

Screening and selection of elite genotypes with high dry matter content can be direct or indirect depending on the correlation between dry matter content and other traits (Norman, 2019) [35]. The direct method of dry matter content determination involves screening of genotypes based on the weight of dry tubers (Norman, 2019) [35]. The indirect technique involves the selection of clones with a high dry matter content through quantification of the starch content of the tuber based on a highly positive correlation between dry matter and starch contents.

The shape of fresh product yam tubers may influence its acceptability and marketability. The shape of fresh yam tubers exhibits intra- and inter-genotypic variability due to the influence of genetic and environmental factors (Nwachukwu, 2017) [37]. The variability in tuber shapes influences mechanical and manual harvesting, contributing to increased tuber damage and economic yield loss (Nwachukwu, 2017) [37].

2. Genetic improvement of food quality traits in yams

2.1 Starch content and pasting attributes of fresh yam tubers

The starch content of yam tubers primarily depends on the genotypes and species (Pérez *et al*., 2011) [40]. Starch is a glucan biopolymer formed in higher plants, mosses, ferns, and some microorganism (Keeling and Myers, 2010). Starch granules are microscopic structures with different shape categories of lenticular, spherical, elliptical, oval, kidney-shaped or polyhedral and diameter measuring between 0.5 and 150 μm (Keeling and Myers, 2010). According to Pérez *et al*. (2011) [40], waxy yam starches of genotypes of *Dioscorea trifida* possess large, triangular, or shell-shaped starch granules with monomodal particle sizes ranging between 24.5 and 35.5 μm. The starch content of the waxy yam starches of these genotypes ranged from 24 – 40% with the highest observed in the genotype with the highest amylose content (Pérez *et al*., 2011) [40]. The determination of amylose using different techniques such as iodo-colorimetric, amperometric, and differential scanning calorimetry (DSC) exhibited 1.4 – 8.7%, 2.2 – 5.9%, and 1.4 – 3.5% for Amazonian genotypes, compared with 12.0, 9.5, and 8.7% amylose, respectively, obtained in commercial Mapuey starches of *Dioscorea trifida* (Pérez *et al*., 2011) [40].

Pasting attributes of various yam products are key quality traits considered for various industrial applications. Pasting involves swelling of starch grains, exudation of their molecules and disruption of starch grains that accompany gelatinization (Atwell *et al*., 1988). The pasting properties of yam tuber starches differ with genotypes and species (Pérez *et al*., 2011) [40]. In *Dioscorea trifida*, waxy yam starches exhibited a peak viscosity of 2250 cP similar to the normal and waxy potatoes with peak viscosity values of 2441 – 2550 cP (Pérez *et al*., 2011) [40]. However, the peak viscosity values of yam starch are usually higher than those observed in normal cassava (954 cP) and waxy cassava (1119 cP) starches, normal maize (176 cP) and waxy maize (973 cP), and normal rice (343 cP) and waxy rice (498 cP) (Pérez *et al*., 2011) [40]. The high peak viscosity values of starch granules of genotypes is attributed to weaker cohesive forces within starch granules of putative genotypes, leading to easier disintegration relative to those with lower peak viscosity values.

Amani *et al*. (2004) investigated the variability in starch physicochemical and functional properties of yam (*Dioscorea* spp.) cultivated in Ivory Coast. Accordingly, *D. dumetorum* starch showed the highest pasting temperature of 87.0°C, followed by an intermediate pasting temperature of 83.0°C exhibited by *D. alata* and *D. cayenensis-rotundata* starches, whereas *D. esculenta* starch had the lowest pasting temperature of 78.7°C. Pérez *et al*. (2011) [40] found higher pasting temperatures of 75.5 – 80.0°C in yam tubers than the 65.2°C obtained in potato (Pérez *et al*., 2011) [40].

The pasting attributes of yam starch are also influenced by average starch grain size, starch grain distribution, amylose/amylopectin ratio and mineral content (Akinwande *et al*., 2007). The amounts of amylose and lipids in starches has been found to limit the pasting and swelling attributes of starch granules (Pérez *et al*., 2011) [40]. Other inhibitory factors of pasting properties reported by Liu *et al*. (2006) [26] include plant source, starch content, interaction among attributes and testing conditions. High paste stability is among industrial criteria evaluated for identification of elite genotypes with good starch (Pérez *et al*., 2011) [40]. The cold paste viscosity criterion is more important in foods with cold thickening capacity such as instant soup, cream or sauce (Pérez *et al*., 2011; Norman, 2019) [40, 35]. Knowledge of pasting properties is relevant especially in canning and other food processing activities.

2.2 Storage tuber protein, vitamin and ash contents

The amount of crude protein present in yam depends on genotypes, species, storage duration and products (Omohimi *et al*., 2018). The mean crude protein content of fresh storage tubers of *D. alata* was 7.4%. The crude protein content of dry samples of tubers of *D. rotundata* ranges from 2.7 – 4.3% (Omohimi *et al*., 2018). Crude protein values of 7.3 and 7.7% were reported for yam chips stored for one and six months, respectively (Jonathan *et al*., 2011). In *D. cayenensis* subsp. *rotundata*, different crude protein values have been reported including 2.4 – 2.6% (Adejumo *et al*., 2013), 2.6 – 2.9% (Omohimi *et al*., 2018), 3.5 – 5.7% (Djeri *et al*., 2015), and 2.8 – 5.6% (Norman, 2019) [35]. Vitamin content in fresh and processed products of yam is another important quality attributes. Wanasundera and Ravindran (1994) reported vitamin C content of 13.0 – 24.7 mg/100 g fresh weight for yam tubers of *D. alata*. Ash content in yam products is an important food quality attribute. It denotes the mineral proportion in foods (Norman, 2019) [35]. The ash content in chips, flakes and flours of *D. rotundata*

genotypes ranges from 1.3 – 1.7%, 1.3 – 2.0% and 1.7 – 3.0%, respectively (Omohimi *et al*., 2018). The ash content in dried chips of 36 genotypes of white yam ranges from 2.1 – 4.1% (Norman, 2019) [35]. The variations in the range of values for protein, vitamin and ash contents could be attributable to the different species, genotypes, storage conditions and sampling locations.

The challenges and achievements of genetic improvement of food quality traits in yams are enormous. The phenotypic plasticity and dioecious nature of yam, cross-incompatibility of inter- and intra-species hybridization, limit the stacking of several interdependent food quality traits and their evaluation (Price *et al*., 2017; Darkwa *et al*., 2020; Norman, 2019) [42, 11, 35]. Dearth of well-articulated knowledge on the genetics of food quality traits of yam contributes to the limitations of breeding enabling technologies. Moreover, breeding strategies for the genetic improvement of yams through biofortification are currently limited by the lack of genetic resources and unreliable historical data regarding nutritional contents (Price *et al*., 2018) [41]. The lack of better understanding of the effect of biochemical composition on organoleptic properties of yam significantly limit the ability to detect the genetic/biochemical trait markers that effectively translate genetic diversity into end-user desired genetic gain (Price *et al*., 2017) [42].

Despite these problems, several achievements have been made in yam population improvement for quality traits. The breeding goals or specifications for new yam genotypes have been refocused and restructured to target increased adoption of future releases of elite yam genotypes with correct product profile and high market penetration potential (Darkwa *et al*., 2020; Norman, 2019) [11, 35]. The breeding targets have metamorphosed from undifferentiated product to a differentiated product concept where the client/customer needs are profiled and translated to product specifications. The product concept involves breeding for desired traits for the target clients such as producers, processors, marketers and consumers. The yam variety development plan in Africa is currently client/customer needs-oriented. The client/customer needs-oriented yam breeding strategy aims at identifying and prioritizing a clear roadmap to achieve the target product(s) within a specified timeframe (Darkwa *et al*., 2020) [11]. Price *et al*. (2018) [41] reported the rich diversity in carotenoid profiles of various yam species that could be exploited for the genetic improvement of the crop.

Genetic parameter estimation techniques

In the early stages of crop improvement programs, a large number of test genotypes and a limited available planting material constrain the use of complete experimental designs with replications. A class of unreplicated experimental designs such as augmented designs serve as a potential solution to resolve this problem (Federer and Raghavarao, 1975) [16]. In the augmented design, control clones are arranged in a standard design such as a Latin square with several replications in soil-homogeneous blocks. The blocks are augmented to accommodate unreplicated test genotypes. Since check varieties are in a standard design, the block effects can be calculated to adjust the observations of the test genotypes, and the error effects within check varieties can be used to test the significance of performance variations among clones. Lin and Poushinsky (1983) [28] proposed a modified augmented design (MAD) comprising two types. The type 1 MAD (MAD1) is used for square plots (Lin and Poushinsky, 1983) [28] and the type 2 MAD (MAD2) for rectangular plots (Lin and Poushinsky, 1985) [27]. The MAD2 is an efficient unreplicated experimental design utilized for the evaluation of large numbers of genotypes in plant breeding and the assessment of genetic variation in a population. This technique is superior to the general augmented design in systematic placement of check varieties and test genotypes within a block to enhance adjustment for soil heterogeneity (Lin and Poushinsky, 1983) [28].

The MAD2 technique is largely utilized for early evaluation of breeding lines, field evaluation of various traits of agronomic and economic importance and for purposes of QTL identification, association mapping, and genomic selection (You *et al*., 2016) [49]. In genetic experiments, genotypes may have adequate amounts of planting materials for replicated trials, however, it may be impractical to accommodate hundreds of entries in one homogeneous block of a field, due to soil heterogeneity. You *et al*. (2013) [50] demonstrated adequate adjustment of soil heterogeneity for measured traits using the MAD2 technique, implying that genetic variance of traits can be determined using a MAD2 method. A breeding pipeline module using SAS and Perl has been developed to facilitate data analysis (http://probes.pw.usda.gov/bioinformatics_ tools/ MADPipeline/index.html). The Delta technique was also utilized to derive formulas for calculation of the sampling variances of the genetic parameters (You *et al*., 2016) [49]. Based on computer simulations, the MAD2 technique is feasible for determination of genetic parameters and sampling variances, with high positive association between the reliability of the estimates and the level of heritability of the trait (You *et al*., 2016) [49].

Incorporation of relationship matrices in modeling for genetic parameter estimation is a powerful technique utilized to dissect the genetic architecture of complex traits and facilitate successful implementation of breeding strategies and design (Norman, 2019) [35]. Relationship matrices are useful for calculation of expected fraction of genes identical by state (genomic relationship matrix G), actual fraction of DNA shared by descent (additive genetic relationship matrix A), or fraction of alleles shared for loci affecting trait(s) of interest (relationship matrix T) (VanRaden, 2007; Norman *et al*., 2021) [47, 33]. These matrices are applicable for the management of genetic diversity, genomics selection and pa rentage determination (Norman, 2019) [35]. Models that utilize genomic data for determination of genetic relationships are more accurate in predicting genetic effects than those that use expected relationships from pedigrees (VanRaden, 2007) [47]. In yams, genomic relationship matrices have been successfully utilized to dissect genetic effects that contribute to the selection of superior clones for further testing and subsequent recommendation for release as new variety (Norman *et al*., 2021) [33]. The

technique facilitated the adequate estimation of genetic parameters for fresh tuber yield, dry matter content and yam mosaic virus severity in white yam breeding trials using molecular marker information (Norman *et al*., 2021) [33]. The P-BLUP/REML analytical technique has also been utilized for determination of genetic parameter estimates, prediction, and selection in a white Guinea yam early-generation breeding population using pedigree information (Asfaw *et al*., 2021) [7]. Accordingly, progeny data facilitated the identification of superior parental genotypes based on their progeny performance (backward selection) and the choice of best-performing progenies with outstanding potential for utilization as putative parents (forward selection) using a multi-trait selection index. Since the narrow-sense heritability values were low for many of the studied traits, the progeny test permitted the selection of superior progenitors for the generation of a new base breeding population that contribute to drive the genetic gain in traits with low heritability values (Hill and Mackay, 2004) [19].

Conclusion and future perspectives

Population improvement is an important breeding strategy to harness genetic gain in yam. Maintenance of high genetic variability from generation to generation facilitates long-term sustainability of yam breeding programs. The knowledge of genetic parameter estimates and improvement of yam for tuber yield, quality and related attributes reviewed in this study would facilitate the formulation of effective strategies for genetic conservation, management and utilization.

The future prospects of yam breeding should target the reduction of the long breeding cycle of the crop, use of robust complementary techniques to complement traditional methods for determination of genetic parameter estimates in yam improvement programs, genetic improvement of desired consumer and market traits and improved collaboration with relevant stakeholders in the crops' product value chains. Accurate estimation of genetic effects can increase the selection gain and reliable exploitation of the heritable variation in the desired direction. Despite these prospects, more efforts are needed in yams regarding the contribution of advanced analytical tools to improve estimates of genetic parameters.

From the foregoing, more research is needed to elucidate the breeding, molecular genetics and biochemical bases of quality traits metabolic pathways in yam. These might require the use of complementary approaches such as: (i) a genetic approach involving utilization of (exotic) germplasm collections, development of breeding populations and extensive genotyping and phenotyping to identify QTLs underlying tuber and product quality attributes and (ii) a functional genomics/metabolomics approach to elucidate the biochemical pathways and key genes underlying specific quality-related volatiles and metabolites.

References

1. Adejumo BA, Okundare RO, Afolayan OI, Balogun SA. Quality attributes of yam flour (Elubo) as affected by blanching, water temperature and soaking time. International Journal of Engineering and Science,2013:2(1):216-221.
2. Akinwande BA, Adeyemi IA, Maziya-Dixon B, Asiedu R. Effect of tuber harvest time and storage period on the pasting properties of yam (*Dioscorea rotundata*) starch. World Journal of Agricultural Science,2007:3(6):781-787.
3. Akoroda MO. Variability, repeatability, character correlation and path analysis in yellow yam. Theoretical and Applied Genetics,1984:69(2):227-232.
4. Akoroda MO. Variation, heritability and genetic advance of eight characters in yam. Theoretical and Applied Genetics,1983:66(1):51-54.
5. Alam S, Shylla E, Bora P, Saud BK. Genetic variation in different cultivars of Greater yam (*Dioscorea alata*). Journal of Root Crops,2014:40(1):1-5.
6. Amani NG, Dufour D, Mestres C, Bule´on A, Kamenan A, Colonna P. Variability in starch physicochemical and functional properties of yam (*Dioscorea* sp.) cultivated in Ivory Coast. Journal of Science, Food and Agriculture,2004:84(15):2085-2096.
7. Asfaw A, Aderonmu DS, Darkwa K, De Koeyer D, Agre P, Abe A *et al*. Genetic parameters, prediction, and selection in a white Guinea yam early-generation breeding population using pedigree information. Crop Science,2021:61:1038-1051. DOI: 10.1002/csc2.20382
8. Atwell WA, Hood WF, Lineback DR. The terminology and methodology associated with the basic starch phenomena. Cereal Foods World,1988:33(3):306-311.
9. Bassey EE, Akpan US. Evaluation of guinea white yam (*Dioscorea rotundata* Poir) for yield and yield components in Nigeria. American Journal of Experimental Agriculture,2015:8(4):216-223.
10. Chukwu GO, Ezenwa MIS, Osunde A, Asiedu R, Ogbogu NJ. Qualities of yam tubers grown on typic paleudults: hybrid yam and fertilizer effects. Scientific Research and Essay,2007:2(12):508-511.
11. Darkwa K, Olasanmi B, Asiedu R, Asfaw A. Review of empirical and emerging breeding methods and tools for yam (Dioscorea spp.) improvement: Status and prospects. Plant Breed,2020:139:474-497. https://doi.org/10.1111/pbr.12783
12. Djeri B, Tchobo PF, Adjrah Y, Karou DS, Ameyapoh Y, Soumanou MM. Nutritional potential of yam chips (*Dioscorea cayenensis* and *Dioscorea rotundata* Poir) obtained using two methods of production in Togo. Afr J Food Sci,2015:9:278-284. doi:10.5897/AJFS2014.1207
13. Eka OU. The chemical composition of yam In: Advances in Yam Research, Osuji G (ed.), 1985, 51-72.

14. Falconer DS, Mackay TFC. *Introduction to Quantitative Genetics*, Ed. 4. Longman, Harlow, Essex, United Kingdom, 1996.
15. FAOSTAT Food and Agriculture Organization Statistical Databases. Food and Agriculture Organization of the United Nations 2016. https://www.fao.org/faostat/en/#home Accessed on 19/03/2017.
16. Federer WT, Raghavarao D. On augmented designs, Biometrics,1975:31:29-35.
17. Frossard E, Aighewi BA, Aké S, Barjolle D, Baumann P, Bernet T, Dao D *et al*. The challenge of improving soil fertility in yam cropping systems of West Africa. Frontiers in Plant Science,1953-2017:8:1-8. https://doi.org/10.3389/fpls.2017. 01953
18. Higashide T, Heuvelink E. Physiological and morphological changes over the past 50 years in yield components in tomato. Journal of the American Society for Horticultural Science,2009:134(4):460-465.
19. Hill WG, Mackay TFC. D. S. Falconer and introduction to quantitative genetics. Genetics,2004:167(4):1529-1536.
20. IITA International Institute of Tropical Agriculture. 1974 Annual Report IITA, Ibadan, Nigeria, 1974, 48.
21. Irizarry H, Rivera E. Nutrient uptake and dry matter production by intensively managed yam grown in an Ultisol. Journal of Agriculture, University of Puerto Rico,1985:LXIX(1):1-9.
22. Jonathan G, Ajayi I, Omitade Y. Nutritional compositions, fungi and aflatoxin detection in stored 'gbodo' (fermented *Dioscorea rotundata*) and 'elubo egede' (fermented Musa parasidiaca) from South western Nigeria. African Journal of Food Science,2011:5(2):105-110.
23. Keeling PL, Myers M. Biochemistry and genetics of starch synthesis. Annual Review of Food Science Technology,2010:1(1):271-303.
24. Kikuno H, Shiwachi H, Hasegawa Y, Asiedu R. Effects of nitrogen application on off-season yam cropping after lowland rice in a derived savanna zone in Nigeria. Tropical Agriculture and Development,2015:59(3):146-153.
25. Koutsika-Sotiriou M, Tsivelikas AL, Gogas Ch, Mylonas IG, Avdikos I, Traka-Mavrona E. Breeding methodology meets sustainable agriculture. International Journal of Plant Breeding and Genetics,2013:7(1):1-20.
26. Liu Q, Donner E, Yin Y, Huang RL, Fan MZ. The physicochemical properties and in vitro digestibility of selected cereals, tubers and legumes grown in China. Food Chemistry,2006:99(3):470-477.
27. Lin CS, Poushinsky G. A modified augmented design (type 2) for rectangular plots, Canadian Journal Plant Science,1985:65:743-749.
28. Lin CS, Poushinsky G. A modified augmented design for an early stage of plant selection involving a large number of test lines without replication, Biometrics,1983:39:553-561.
29. Lynch M, Walsh B. *Genetics and Analysis of Quantitative Traits.* Sinauer Associates, Sunderland, MA, 1998, 980.
30. Martin FW, Cabanillas E. Heritability of yields in *Dioscorea floribunda*. Tropical Agriculture (Trinidad),1967:44(1):45-51.
31. Mondal M, Hossain M, Rasul M, Uddin MS. Genetic diversity in potato. Bangladesh Journal of Botany,2007:36:121-125. https: //doi.org/10.3329/bjb.v36i2.1499
32. Mousseau TA, Ritland K, Heath DD. A novel method for estimating heritability using molecular markers. Heredity,1998:80:218-224.
33. Norman PE, Tongoona PB, Danquah A, Danquah EY, Asiedu R, Agbona A *et al*. Genetic parameter estimation and selection in advanced breeding population of white Guinea yam. Journal of Crop Improvement,2021:35(6):790-815. https:// doi.org/10.1080/15427528.2021.1881012
34. Norman PE, Paterne AA, Danquah A, Tongoona PB, Danquah EY, De Koeyer D *et al*. Paternity Assignment in White Guinea Yam (*Dioscorea rotundata*) Half-Sib Progenies from Polycross Mating Design Using SNP Markers. Plants,2020:9:527. https://doi:10.3390/plants9040527.
35. Norman PE. Genetic analysis of tuber yield and quality traits in white yam (*Dioscorea rotundata* Poir). PhD Thesis, University of Ghana, Ghana, 2019, 213.
36. Norman PE, Asfaw A, Tongoona PB, Danquah A, Danquah EY, Koeyer DD. Can parentage analysis facilitate breeding activities in root and tuber crops? Agriculture Journal,2018:8(95):1-24. https://dx.doi.org/10.3390/agriculture8070095
37. Nwachukwu EC. Stability of tuber shape in *Dioscorea rotundata* variants. International Journal of Life-Sciences Scientific Research,2017:3(1):779-782.
38. Okoli OO, Nwokoye JU, Udugwu CC. Economic indices for clonal selection and breeding of yams. In: Terry ER, Doku EV, Arene OB and Mahungu NM (eds.). Tropical Root Crops-Production and uses in Africa, IDRC-221e, 1984, 125-128.
39. Omohimi CI, Piccirillo C, Roritz M, Ferraro V, Vasconcelos MW, Sanni LO *et al*. Study of the proximate and mineral composition of different Nigerian yam chips, flakes and flours. Journal of Food Science and Technology,2018:55(1):42-51.
40. Pérez E, Gibert O, Rolland-Sabaté A, Jiménez Y, Sánchez T, Giraldo A *et al*. Physicochemical, functional, and macromolecular properties of waxy yam starches discovered from "Mapuey" (*Dioscorea trifida*) genotypes in the Venezuelan Amazon. Journal of Agriculture and Food Chemistry,2011:59(1):263-273.
41. Price EJ, Bhattacharjee R, Lopez-Montes A, Fraser PD. Carotenoid profiling of yams: Clarity, comparisons and diversity. Food Chemistry,2018:259:130-138.

42. Price EJ, Bhattacharjee R, Lopez-Montes A, Fraser PD. Metabolite profiling of yam (Dioscorea spp.) accessions for use in crop improvement programmes. Metabolomics,2017:13(11):144. https://doi.org/10.1007/s11306-017-1279-7.
43. Rijk B, van Ittersum M, Withagen J. Genetic progress in Dutch crop yields. Field Crops Research,2013:149:262-268.
44. Sartie A, Franco J, Asiedu R. Phenotypic analysis of tuber yield- and maturity-related traits in white yam (*Dioscorea rotundata*). African Journal of Biotechnology,2012:11(17):3964-3975.
45. Thomas SC, Pemberton JM, Hill WG. Estimating variance components in natural populations using inferred relationships. Heredity,2000:84:427-436.
46. Thomas SC, Hill WG. Estimating Quantitative Genetic Parameters Using Sibships Reconstructed From Marker Data. Genetics,2000:155(4):1961-1972.
47. VanRaden PM. Genomic measures of relationship and inbreeding. Animal Improvement. Interbull Bulletin,2007:37(1):33-36. https://journal.interbull.org/index.php/ib /issue56
48. Wanasundera JP, Ravindran G. Nutritional assessment of yam (*Dioscorea alata*) tubers. Plant Foods for Human Nutrition,1994:46(1):33–39.
49. You FM, Song O, Jia G, Cheng Y, Duguid S, Booker H *et al*. Estimation of genetic parameters and their sampling variances for quantitative traits in the type 2 modified augmented design. The Crop Journal,2016:4:107-118. http://dx.doi.org/10.1016/j.cj.2016.01.003
50. You FM, Duguid SD, Thambugala D, Cloutier S. Statistical analysis and field evaluation of the type 2 modified augmented design (MAD) in phenotyping of flax (*Linum usitatissimum*) germplasms in multiple environments, Australian Journal of Crop Science,2013:7:1789-1800.