

ORIGINAL ARTICLE

Crop Breeding & Genetics

Trends in genetic gain for yam in the IITA breeding program

Asrat Asfaw¹  | Paterne A. Agre¹ | Ibnou Dieng¹  | Patrick Adebola¹ |
 Jude E. Obidiegwu² | Emmanuel Chamba³ | Kwabena Darkwa³ | Emmanuel Otoo⁴ |
 Alexandre Dansi⁵ | Konan Evrard Brice Dibi⁶  | Amani Michel Kouakou⁶ |
 Robert Asiedu¹

¹Yam Breeding Program, International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria

²Yam Research Program, National Root Crops Research Institute (NRCRI), Umudike, Abia State, Nigeria

³Yam Improvement Program, CSIR-Savannah Agricultural Research Institute, Tamale, Ghana

⁴Root and Tuber Division, CSIR-Crops Research Institute, Kumasi, Ghana

⁵Technologies, Engineering and Mathematics (UNSTIM), National High School of Biosciences and Applied Biotechnologies (ENSBBA), National University of Sciences, Dassa, Benin

⁶CNRA, Station de Recherche sur les Cultures Vivrières (SRCV), Bouaké, Côte d'Ivoire

Correspondence

Asrat Asfaw, International Institute of Tropical Agriculture, IITA, Ibadan, Nigeria.
 Email: a.amele@cgiar.org

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Abstract

Monitoring genetic gain is crucial to ensure breeding programs' effectiveness and identify potential challenges and areas for their improvement. Our study provides a first overview of the trends in genetic gain for tuber yield and disease resistance traits in the IITA's (International Institute of Tropical Agriculture) yam breeding program. We used historical data (2010–2022) from multiple generations of past 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. Our result shows positive genetic trends in fresh tuber yield while recording a gain of 1.38% or 99.17 kg ha⁻¹ per year in the white Guinea yam and 2.18% or 252.41 kg ha⁻¹ per year in the water yam breeding pipelines. 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. Our findings indicate that while the breeding program has succeeded in enhancing tuber yield, post-harvest tuber dry matter content and disease resistance (yam mosaic virus and anthracnose) did not follow a similar trend in the material being developed. This implies that the yam breeding program needs to strike a balance between various traits, ensuring that increased yield does not come at a cost to food quality or disease resistance. Our results highlight the importance of continually monitoring and assessing the performance of a breeding program and making informed decisions about which traits to focus on for future improvement.

Abbreviations: BLUEs, best linear unbiased estimates; IITA, International Institute of Tropical Agriculture; NARS, National Agricultural Research System; rAUDPC, relative area under disease progression curve; SSA, sub-Saharan Africa; YAD, yam anthracnose disease; YMV, yam mosaic virus.

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1 | INTRODUCTION

Cultivated yam (*Dioscorea* spp.) is among the primary root and tuber crops that provide the staple food for billions of people in the tropics and subtropics. There are 11 cultivated yam species, of which *Dioscorea rotundata* Poir

(white Guinea yam), native to Africa, and *Dioscorea alata* L. (water yam), originated in Asia, are the primary food yams most planted, produced, and consumed globally (Darkwa et al., 2020; Degras, 1993). Based on its cultivated area, yam ranks fourth worldwide among root and tuber crops after cassava (*Manihot esculenta* L.), potato (*Solanum tuberosum*), and sweet potato [*Ipomoea batatas* (L.) Lam], and second in West Africa after cassava (Alabi et al., 2019). However, yam generates a gross value of >15 billion dollars per year, which is higher than the combined value of cassava and other cereals such as maize, rice, and sorghum in sub-Saharan Africa (SSA) (FAOSTAT, 2022). Each year, >70 million metric tons of yam are produced in SSA on an area of 8.3 million ha, with over 95% of its production in West Africa (FAOSTAT, 2022). Several attributes of the yam plant, such as the potential for high yield and long-term storage, make this crop vital for food security in Africa (Alabi et al., 2019; Lebot, 2009). Despite yam's importance as a staple food, in traditional medicines for its richness in bioactive compounds, and as a source of steroidal precursors (Adoménienė & Venskutonis, 2022; Kanu et al., 2018; Kim et al., 2021; Lebot et al., 2023; Obidiegwu et al., 2020), it remains understudied (Darkwa et al., 2020).

Yam production has significantly increased in the last two decades, with an annual rate of around 3.8% (Matsumoto et al., 2021). However, the yield increase is not as remarkable as that of area expansion, which doubled from 4 million in 2000 to 8.6 million ha in 2021 (FAOSTAT, 2022). The average yam yield at the smallholder farmer field level remained around 8–12 t ha⁻¹, far below its potential of up to 50 t ha⁻¹ (Frossard et al., 2017). Closing the yield gap and attaining incremental gains in crop productivity is a multi-disciplinary effort requiring genetic and agronomy innovations. Genetic innovation has played a crucial role in providing improved seeds to farmers, effectively raising the productivity of many crops (Cobb et al., 2019; Li et al., 2018). The genetic improvement work on yam dates back to the 1970s. The International Institute of Tropical Agriculture (IITA) and its partner National Agricultural Research System (NARS) programs in Africa are among the public institutions working on the genetic improvement of yam to unlock its potential for sustainable food supply and wealth creation. Their work comprises the development and deployment of highly impactful varieties that are resilient, productive, and respond well to the dynamics of current and future production challenges while meeting market demand, which is a priority for ongoing research (Asiedu & Sartie, 2010; Darkwa et al., 2020).

Breeding strategies for yam crops require meticulous consideration of the plant's dual reproductive modes, encompassing both sexual and asexual methods (Darkwa et al., 2020). This intricate landscape necessitates a nuanced approach, integrating market insights and precise product specifications to align breeding objectives with the specific demands

Core Ideas

- Periodic monitoring of genetic gain is crucial to making informed decisions about which traits to focus on.
- Yam breeding program needs to strike a balance between various traits for ensuring sustained genetic gain.
- High-quality historical trial data crucial for assessing genetic gain trends in breeding programs.

of the diverse market, strategic selection and recycling of parents to exploit complementary genetics to achieve sustainable improvement, and rigorous testing, spanning both on-station and on-farm trials for identifying and advancing superior genotypes, ultimately leading to the delivery of impactful varieties to end-users. This comprehensive process involves multifaceted approaches such as trait discovery and deployment, parent selection, and mate pairing, as well as rigorous field trials and assessments geared toward enhanced tuber yield, resistance to diseases (virus, anthracnose, and nematodes), and overall food quality for consumption. The meticulously defined stages, each aligned with specific tasks, characterize breeding programs, ensuring the systematic advancement of genotypes targeting traits for improvement.

Unlike cereal crops, the breakthrough in breeding has not been noted in yam programs. Due to its inherent biological constraints, yam is among the most challenging crops to breed for. Many factors, such as multiple species, lengthy crop cycle, vegetative propagation, low multiplication ratio, climbing growth habit, mostly dioecious flowering with obligate outcrossing nature, and high heterozygosity with varying intraspecific and interspecific ploidy levels ranging from diploid to octoploid ($2n = 40, 60, 80$) (Caddick et al., 2002) negatively influence achieving genetic gains such as those recorded with the main cereal staples (Darkwa et al., 2020). Moreover, the application of innovative breeding technologies and partnerships that have the potential to achieve the genetic gain targets required in yam is still constrained due to less research investment. Despite all these challenges, the yam breeding at IITA and its African NARS partners have evolved through time in breeding strategies and recorded significant milestones leading to the development of several improved varieties. Breeding goals and specification for targets have been refocused and restructured to expedite market penetration of varieties released from the program, and a wide array of genomic resources, including markers for genetic studies, quantitative trait loci of agronomic relevance, and techniques for phenotyping disease and food quality attributes, are now available, among the many modernization efforts currently being implemented (Darkwa et al., 2020).

Progress from crop breeding is monitored by the rate of genetic gain achieved and delivered to farmers. Periodic assessment of the rate of genetic gain within the breeding pipeline, an intricately structured procedure encompassing successive stages of supervised or unsupervised plant crosses, comprehensive progeny assessments, and iterative advancement of superior individuals through successive generations to develop new and improved varieties tailored for the specific market segment and corresponding product specifications, stands as a customary procedure within proprietary crop breeding initiatives. However, comparable estimates are notably scarce in the public breeding domain (Cobb et al., 2019). To date, such assessments of the rate of genetic gain delivered by yam breeding programs to farmers are not well documented, except for a few studies reporting expected genetic gain within breeding trials (Asfaw et al., 2021). Different methods of analysis are used to estimate the trend of genetic progress in breeding programs (de la Vega et al., 2007; Eberhart, 1964; Falconer & Mackay, 2005; Mackay et al., 2011; Piepho et al., 2014). These methods are generally categorized as expected and realized genetic gain. The technique for expected genetic gain utilizes trial information at a single selection stage to predict the anticipated improvement in desired traits through theoretical calculations and planned breeding strategies.

On the other hand, the realized genetic gain method employs phenotypic information from representative samples of germplasm at a specific testing stage, evaluated through era or historical trials, to deduce the actual progress observed in the field due to successive breeding efforts. An era trial involves pooling varieties or breeding lines developed in different years within a breeding program and evaluating them in a standardized trial setup to minimize variations arising from agronomic practices, soil, and climatic differences that can confound the genetic trend estimate. Such a trial is good enough to provide a precise estimate of genetic gain, but it has logistical challenges, including extra trial costs to the program. Moreover, era trials also do not permit real-time monitoring and timely diagnosis of the efficiency and effectiveness of a breeding strategy for possible adjustment (Menkir et al., 2022; Prasanna et al., 2022).

Breeding programs regularly conduct multi-environment trials over the years and across sites. Data from such historical trials conducted with standard checks included over the years and across sites provide reliable estimates of a trend of genetic gain in breeding programs (Mackay et al., 2011; Piepho & Mehring, 2006; Piepho et al., 2014) that permit periodic monitoring and fine-tuning of the program for better accomplishment. Such analysis has been effectively implemented in many crop breeding programs (Asea et al., 2023; Duvick, 2005; de la Vega et al., 2007; Khanna et al., 2022; Menkir et al., 2022; Prasanna et al., 2022; Seck et al., 2023).

Our study seeks to estimate the genetic trends of target economic traits in yam breeding pipelines of IITA in West Africa using the data from historical advanced-stage trials from 2010 to 2022. The study provides a template for our strategic reassessment toward optimizing future investments in yam breeding.

2 | MATERIALS AND METHODS

2.1 | Description of historical data

This study used historical trial data from the two IITA yam breeding pipelines: white Guinea yam (*D. rotundata*) and water yam (*D. alata*). The sources of the historical data included breeding testing stages 3 and 4 trials that were conducted on-station (31 sites for white Guinea yam [Figure 1] and 28 sites for water yam [Figure 2]) by IITA and its national partners in West Africa yam belt from 2010 to 2022 (12 years). Stage 3 represents the first multisite trial, often executed for 1 year. In contrast, the stage 4 trial is an advancement of genetic materials from stage 3 testing that is usually conducted for at least 2 years and at a more extensive set of sites. The genetic materials used in this study were elite clones all developed by the IITA yam breeding program, except for the benchmark check cultivars accessed from popular landrace cultivars and those from national breeding programs. The trials were executed in varied experimental designs, including alpha lattice, augmented block, and randomized complete block. They were conducted following the standard operating protocol for yam breeding testing (Asfaw, 2016). The plot size varied with trials, but primarily, two-row plots of 10 or 5 m long with a spacing of 1 m between ridges and 1 m between plants within the ridge were used. The dataset treats a combination of experiment, year, and site as a trial. This study's historical data comprise 194 trials with 10,799 data points and 867 unique genotypes in the white Guinea yam breeding pipeline and 193 trials with 11,161 data points and 646 unique genotypes in the water yam breeding pipeline. The data from each trial were checked for quality, including extreme observations and missing values. Trials with missing values of >20% were dropped from further analysis. Data for five major traits—fresh tuber yield (t ha^{-1}), average tuber weight (kg), tuber dry matter content (%), yam mosaic virus (YMV), and yam anthracnose disease (YAD) severity scores (relative area under disease progression curve [rAUDPC] value)—were analyzed. The procedure described in yam trait ontology (http://www.cropontology.org/ontology/CO_343/Yam) was used for collecting data on these traits, and for more detail on data recording on these traits, see Asfaw et al. (2021). [Correction added on 24 June 2024, after first online publication: in subsection 2.1 description of historical data the <20% (less than) symbol is replaced by a >20% (greater than) symbol.]

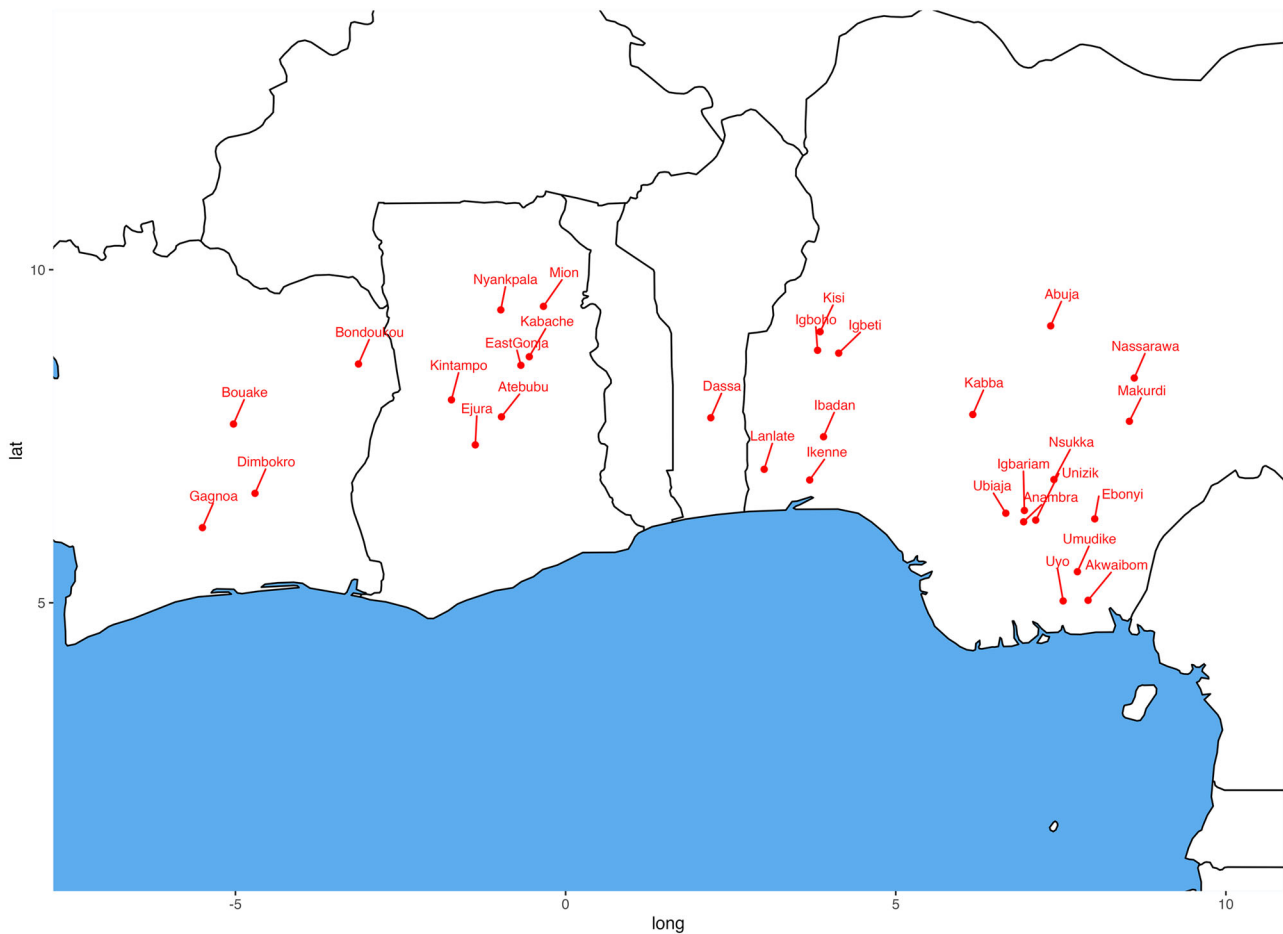


FIGURE 1 Map showing the distribution of white yam (*Dioscorea rotundata*) testing sites in the West Africa yam belt.

2.2 | Statistical analysis

We used a three-stage analysis to estimate the realized genetic gain for each trait under consideration.

In the initial stage, the data from individual trials were analyzed using a linear mixed model, accounting for different experimental designs in each breeding pipeline.

The model tailored for the alpha lattice trials is:

$$y_{ijk} = \mu + G_i + R_k + B_{jk} + e_{ijk}$$

where y_{ijk} is the vector of phenotype data of the i th genotype (clone) of the j th block nested into the k th replication, μ is the overall mean; G_i is the effect of the i th genotype; R_k is the effect of the k th replication; B_{jk} is the effect of the j th block nested into the k th replication; and e_{ijk} is the residual, with the assumptions $e_{ijk} \sim N(0, \sigma_e^2)$. Replication was considered a fixed effect, and the block was considered random.

The model above was modified by omitting the B_{jk} parameter, and replications R_k were considered as complete blocks (fixed effect) when fitting the randomized complete block

design trials as:

$$y_{ik} = \mu + G_i + R_k + e_{ik}$$

For the augmented designs trials, the R_k term was omitted and the B_j parameter is the random effect of the j th block on the following model:

$$y_{ij} = \mu + G_i + B_j + e_{ij}$$

Furthermore, in instances where row and column information was available, we modeled a first-order autoregressive variance structure in both row and column directions for the residual error (Gilmour et al., 1997).

For each of the model, we first fitted genotype as a random effect in the model to calculate trait heritability using the formula described in Cullis et al. (2006).

$$H_{\text{Cullis}}^2 = 1 - \frac{V_{\Delta}^{\text{BLUP}}}{2\sigma_g^2}$$

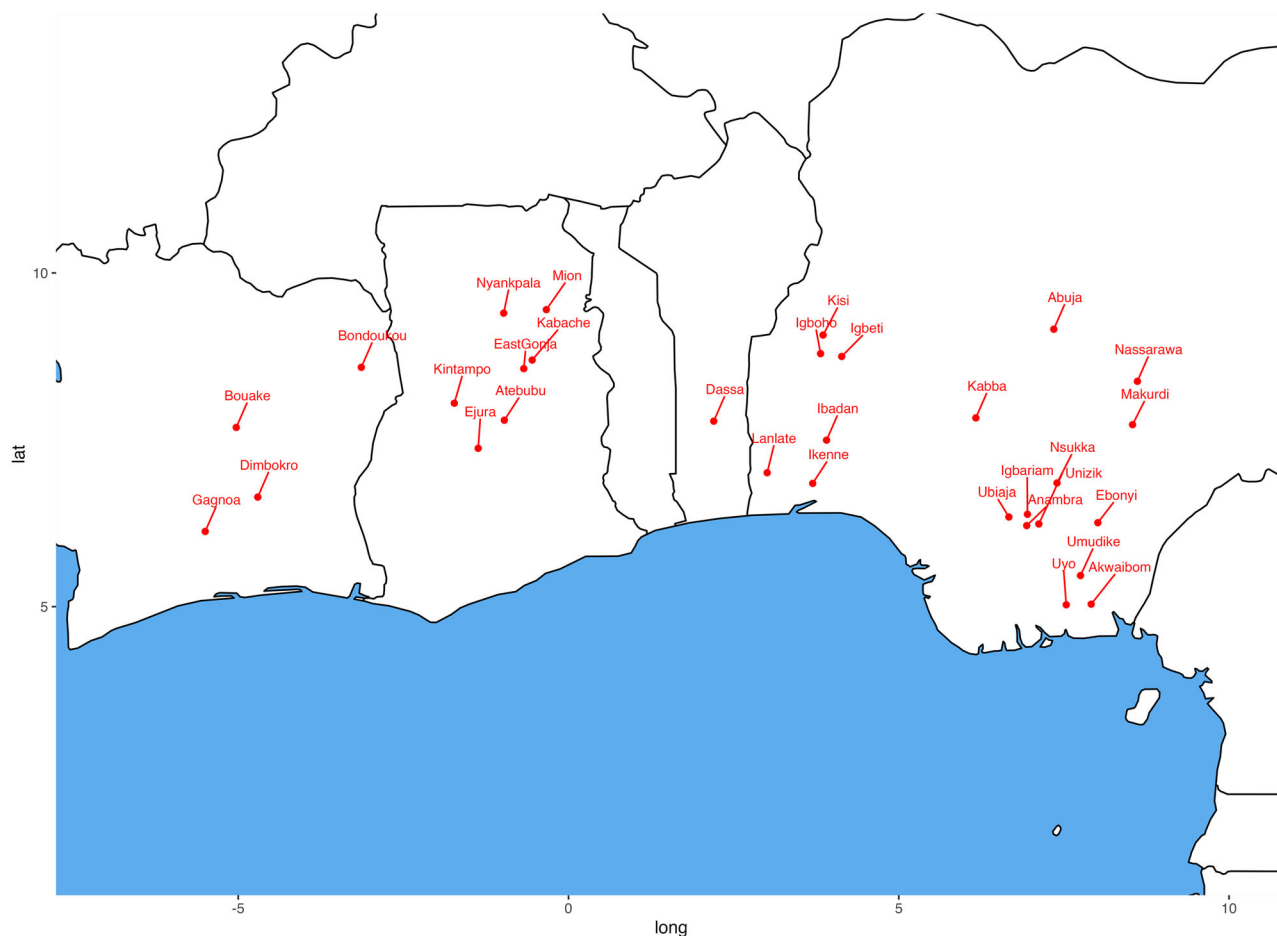


FIGURE 2 Map showing the distribution of water yam (*Dioscorea alata*) testing sites in the West Africa yam belt.

where V_{Δ}^{BLUP} is the average standard error of the clonal genotypic best linear unbiased predictions (BLUPs) and σ_g^2 is the clonal genotypic variance. Trials with a heritability of <0.2 were dropped from downstream analysis.

Adjusted means as best linear unbiased estimates (BLUEs) and their standard errors for each genotype were then estimated using a model that accounted for genotype as a fixed effect and the design-based field blocking structure effect appropriate to the specific trials. In each model, sett weight (weight of seed tubers used for planting) and the number of plants at harvest were fitted as covariates for tuber yield to reduce the error caused by variation in sett weight at planting and plant population at harvest for the genotypes. The covariates were centered and rescaled with a mean of 0 and a variance of 1.

In the second stage, we fitted a linear mixed model:

$$\bar{y}_{ijk} = \mu + G_i + Y_j + (GY)_{ij} + S_{jk} + (GS)_{ijk} + \xi$$

where $\bar{y}_{ijk}$ is the adjusted means of the i th genotype in year j at site k derived from the linear mixed models at stage 1, μ is the overall mean, G_i is the main effect of the i th genotype,

Y_j is the main effect of the j th year, $(GY)_{ij}$ is the interaction of genotype i in year j , S_{jk} is the effect of site j within year k , $(GS)_{ijk}$ is the interaction effect between the genotype and site within year, and ξ is the error associated with the estimation of the adjusted means with variance matrix assumed known from stage 1. We considered genotype as a fixed effect and fitted a weighted-combined mixed model using BLUEs and weights (the inverse of the squared standard errors of the BLUEs of the genotypes) extracted from the first stage analysis to obtain the adjusted means of each genotype within each environment, a site $\times$ year combination (Smith et al., 2001). Year was also treated as a fixed factor in the combined analysis to remove the improvement due to non-genetic reasons (Mackay et al., 2011). Genetic progress is studied to identify a non-genetic trend component due to agronomic practices and/or climate change and a genetic trend component due to genetics. Because of these two trends, a simple mixed model with independent random genotype and year main effects would potentially yield biased results due to anticipated large, potentially non-linear trends over time for both genotype and year effects (Mackay et al., 2011). Hence, we adopted a multi-stage analytical approach of Mackay et al. (2011), assuming

all effects except μ , G_i , and Y_j to be random and independent, each with constant variance as our data are from historical trials and its inherent imbalance.

In the final stage, a linear regression model was then fitted for genotype-adjusted means against the year of origin of genotypes to calculate the rate of genetic gain for the traits assessed. The year of origin is the year a cross was made to generate the genotype used in this study. The rate of genetic gain in percent was estimated as a ratio of the regression slope to the y-intercept of the regression plus the slope multiplied by the year of first testing. The genetic trend was estimated only for IITA-bred genotypes, excluding benchmark checks accessed from local landraces and national breeding programs.

We explored the potential of alternative regression models to offer a more accurate depiction of the realized genetic gain accomplished by the IITA yam breeding programs. Segmented linear regression technique, a form of regression that allows multiple linear regression to fit the data for different ranges of years was used (Grassini et al., 2013). The year 2011 was considered as a breakpoint, corresponding to two periods before and after implementing a new yam breeding strategy. We also used quantile regression (Koenker, 2017) due to its robustness to outliers. Unlike linear regression, which estimates the conditional mean of the response variable based on predictor variables, quantile regression estimates the conditional median (or other quantiles) of the response variable. We employed diverse models across a range of quantiles, spanning from the 5th to the 95th percentile, with an increment of 0.05. The model exhibiting the lowest Akaike information criterion was selected.

All analyses for data from each breeding pipeline and trait were performed separately using ASReml-R 4.2 package (Butler et al., 2023) in the R environment (R Core Team, 2023).

3 | RESULTS

3.1 | Historical data connectivity and repeatability

Tables 1 and 2 present the historical data connectivity of 194 trials in the white Guinea yam and 193 trials in the water yam breeding pipelines. The current datasets showed a good level of connectivity with a substantial number of common genotypes being tested across different trials. Considering the white Guinea yam pipeline, the highest trial connectivity was observed between trials established during 2013 and 2014, with 166 as common genotypes. Trials established in 2010 showed no trial connectivity with several trials established in 2019, 2021, and 2022 (Table 1). In the water yam pipeline (Table 2), the trial set in 2015 displayed high trial connec-

tivity with the rest of the trials, while the trials established in 2010 had no connectivity with trials established in 2019, 2021, and 2022.

Figures 3 and 4 display the variation of broad sense heritability values for all the evaluated traits across breeding stages and over the years. The heritability for fresh tuber yield estimates varied between 0.21 and 0.92 with a mean of 0.60 in the white Guinea yam pipeline and 0.20 and 0.92 with a mean of 0.60 in the water yam breeding pipeline. Across the breeding stages, all the evaluated traits of the white Guinea yam pipeline recorded the highest broad sense heritability at stage 4 with the highest average value being reported with YMV severity score (rAUDPC value) (Figure 3a). For the water yam pipeline, the highest average broad sense heritability value was recorded at stage 4 for fresh tuber yield and average tuber weight, while for the rest of the traits, it was highest at stage 3 (Figure 4a). For all traits, the heritability values recorded for trials fluctuated over the years in both pipelines (Figures 3b and 4b).

3.2 | Trends of genetic gain for yield and disease resistance traits in white Guinea yam

The genetic trends estimated for different traits of the genotypes from IITA's decades of white Guinea yam breeding program are presented in Table 3 and Figure 5. The genetic trend estimates for fresh tuber yield, average tuber weight, and tuber dry matter content were significant at p -values < 0.001, while the genetic gain was nonsignificant for YMV and anthracnose disease severity scores. Fresh tuber yield showed an annual increase of 97.17 kg ha⁻¹ at a relative genetic gain of 1.38% per year for the period of 21 years breeding window. Such a trend showed the highest increase for tuber weight with an annual genetic gain of 2.33% but decreased linearly at 0.41% per year for tuber dry matter content. Further results from applying the segmented linear regression method have provided additional insights into the temporal dynamics of the genetic gain pertaining to fresh tuber yield (Figures S1 and S2). In contrast, the method for quantile regression did not show much difference from the outcome derived from the linear regression method (Figure S3). The temporal rates of genetic gain for fresh tuber yield amounted to 0.52% per annum preceding the year 2011, with marked increase to 2.19% per annum after the aforementioned year (Table S1).

3.3 | Trends of genetic gain for water yam yield and disease resistance traits

Trends of genetic gain in water yam genotypes assessed for fresh tuber yield traits and mosaic virus resistance were significant ($p < 0.05$) but not for YAD (Table 4; Figure 6). The rate of genetic gain was 2.18% or 252 kg ha⁻¹ per year

TABLE 1 Connectivity of historical trial data in white Guinea yam genotypes across years from 2010 to 2022.

	2010	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
2010	123											
2012	73	147										
2013	26	78	404									
2014	29	66	166	290								
2015	24	49	70	148	162							
2016	6	12	31	38	37	45						
2017	2	5	28	55	32	21	90					
2018	1	1	3	13	14	2	18	18				
2019	0	2	3	7	4	2	16	3	44			
2020	4	18	28	35	31	21	31	3	30	119		
2021	0	5	6	12	9	4	19	5	43	36	150	
2022	0	4	4	6	7	4	7	4	18	18	62	100

TABLE 2 Connectivity of historical trial data in water yam genotypes across years from 2010 to 2022.

	2010	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
2010	132											
2012	122	135										
2013	108	115	416									
2014	86	88	328	371								
2015	32	33	227	259	305							
2016	2	2	10	10	11	12						
2017	4	7	23	27	27	12	32					
2018	2	5	14	18	17	1	19	21				
2019	0	1	6	6	6	1	2	2	24			
2020	0	1	6	6	6	1	3	2	10	11		
2021	1	2	9	8	9	3	5	2	24	11	119	
2022	0	1	2	2	2	1	3	1	15	2	44	47

TABLE 3 Trends in genetic gain for white Guinea yam yield and disease resistance traits.

Trait	NY	Year of origin		Genetic gain (%)	Slope	SE	Intercept	p value
		First	Last					
Average tuber weight (kg)	21	1989	2017	2.33	0.0111	0.0013	−21.678	0.0000
Tuber dry matter (%)	14	1989	2017	−0.41	−0.1406	0.0363	313.941	0.0001
rAUDPCYAD	18	1989	2017	−0.108	−0.00002	0.0000	0.057	0.2515
rAUDPCYMV	18	1989	2017	−0.066	−0.00001	0.0000	0.054	0.5513
Fresh tuber yield (t ha ^{−1})	21	1989	2017	1.38	0.09917	0.0156	−190.074	0.0000

Abbreviations: NY, number of years; rAUDPCYAD, relative area under disease progression curve for yam anthracnose disease severity score; rAUDPCYMV, relative area under disease progression curve for yam mosaic virus severity score; SE, slope standard error.

for fresh tuber yield and 0.67% or 4.8 g per year for average tuber weight. However, the genetic gain for the tuber dry matter showed a decreasing trend at a rate of 1.47% per year. The genetic trend was in the desired direction, with an annual rate of 1.22% and 0.28% per year for YMV and anthracnose dis-

ease resistance, respectively. However, such genetic gain for yam anthracnose resistance was statistically significant at a *p*-value 0.12.

In the context of our additional analysis, employing the segmented linear regression method has unveiled temporal

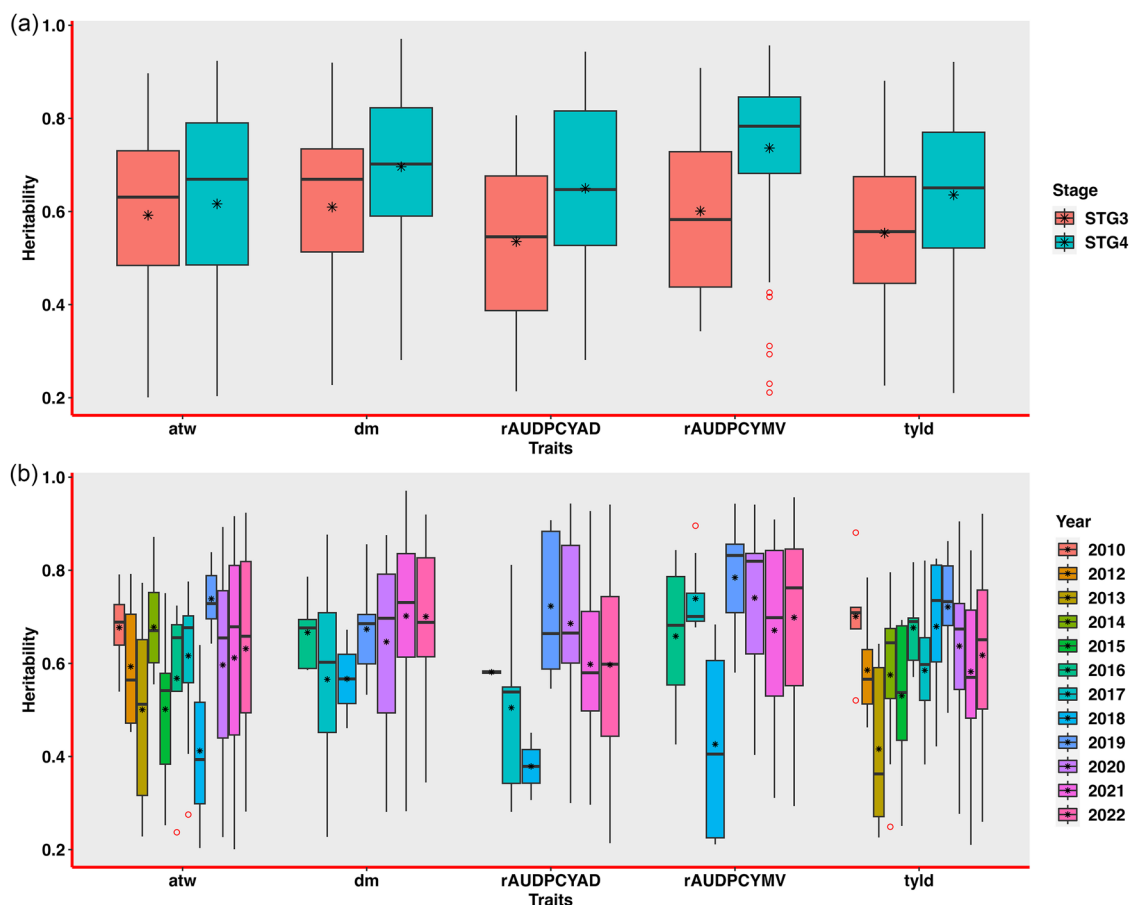


FIGURE 3 Box plots showing the variation of broad-sense heritability on entry-mean basis of traits at different breeding stages and trial testing years in white Guinea yam breeding pipeline: A = breeding stage; B = testing years. The black line and circle inside each boxplot represent the median and mean values, respectively. atw, average tuber weight (kg); dm, tuber dry matter content (%); rAUDPCYAD, relative area under disease progression curve for yam anthracnose disease severity score; rAUDPCYMV, relative area under disease progression curve for yam mosaic virus severity score; tyld, fresh tuber yield (t ha^{-1}).

TABLE 4 Trends of genetic gain for yield and disease resistance traits in water yam breeding pipeline.

Traits	NY	Year of origin		Genetic gain (%)	Slope	SE	Intercept	<i>p</i> value
		First	Last					
Average tuber weight (kg)	14	2000	2017	0.67	0.0048	0.002	−8.874	0.03
Dry matter (%)	10	2001	2017	−1.47	−0.4923	0.087	1019.267	0.0000
rAUDPCYAD	10	2001	2017	−0.28	−0.0007	0.000	0.155	0.12
rAUDPCYMV	10	2001	2017	−1.22	−0.0003	0.000	0.566	0.0000
Fresh tuber yield (t ha^{-1})	14	2000	2017	2.18	0.252	0.033	−493.257	0.0000

Abbreviations: NY, number of years; rAUDPCYAD, relative area under disease progression curve for yam anthracnose disease severity score; rAUDPCYMV, relative area under disease progression curve for yam mosaic virus severity score; SE, slope standard error.

trends in genetic gain for fresh tuber yield (Figures S4 and S5). However, with the quantile regression method, the outcomes exhibited minimal deviation from those derived through the conventional linear regression method, as elucidated in the Figure S6. Specifically, the temporal trajectory of genetic gain in fresh tuber yield revealed rates of 0.70% and 15.82% per annum, respectively, pre- and post-2011 (Table S2).

4 | DISCUSSION

In today's rapidly evolving agricultural landscape, including the effect of climate change, public breeding programs play a crucial role in developing improved cultivars that meet the diverse needs of farmers and consumers, particularly in the global South. Development of improved crop varieties is a

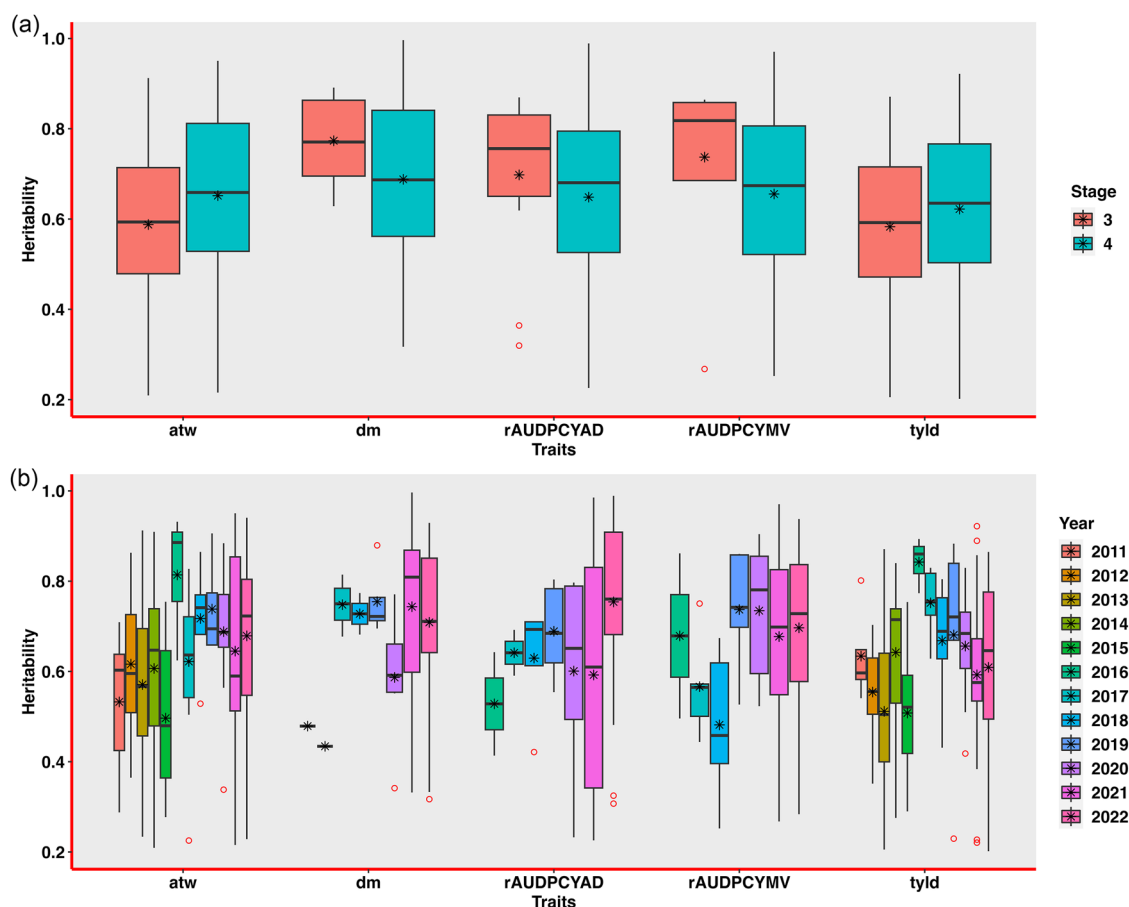


FIGURE 4 Box plots showing the variation of traits' broad-sense heritability on entry-mean basis at different breeding stages and trial testing years in the water yam breeding pipeline: A = breeding stage; B = testing years. The black line and circle inside each boxplot represent the median and mean values, respectively. atw, average tuber weight (kg); dm, tuber dry matter content (%); rAUDPCYAD, relative area under disease progression curve for yam anthracnose disease severity score; rAUDPCYMV, relative area under disease progression curve for yam mosaic virus severity score; tyld, fresh tuber yield (t ha^{-1}).

process that requires predefined target product profiles, identification and introgression of desired alleles associated with the traits being improved, and its deployment in the target set of environments. In such a process, periodic monitoring of the rate of genetic gain achieved and delivered to farmers by public programs is a topic of concern. Genetic gain, which quantifies the average annual improvement in a particular trait, has been used to assess progress achieved and proposes strategies to ensure their continued success. Several studies, such as those conducted by Mackay et al. (2011), Menkir et al. (2022), Khanna et al. (2022), and Prasanna et al. (2022), underscore the significance of periodically monitoring genetic gain to evaluate the effectiveness of breeding strategies and to guide future efforts. The IITA and its research partners in the African NARS have engaged in yam breeding in Africa since the 1970s. Over time, the IITA's breeding strategies have evolved, resulting in the release of several improved yam varieties in West Africa (Asiedu et al., 2012; Darkwa et al., 2020), which could be considered as an indicator of the program's success (Atlin et al., 2017). However,

the efficiency and impact of the breeding program should be measured by more than just the number of varieties released (Prasanna et al., 2022). In this paper, we explored historical trial data to analyze the trends in genetic gain for traits related to tuber yield and disease resistance within the IITA's yam breeding program.

Historical trial data, which include information on various yam genotypes and their performance under different conditions, are crucial for assessing genetic gain trends. Analyzing data from multiple trials over the years allows breeders to identify which traits have improved over time and how quickly these improvements have occurred. Our analysis using historical trial data shows that the genetic gain in fresh tuber yield has achieved a positive trend over time. The genetic gain for fresh tuber yield was found to be highest (2.18% per year) in the water yam breeding pipeline compared to the white Guinea yam pipeline (1.38% per year). Positive genetic gain for fresh tuber yield in the yam breeding program indicated that the current yam breeding strategies being implemented at IITA are on the right track for its improvement. Though it

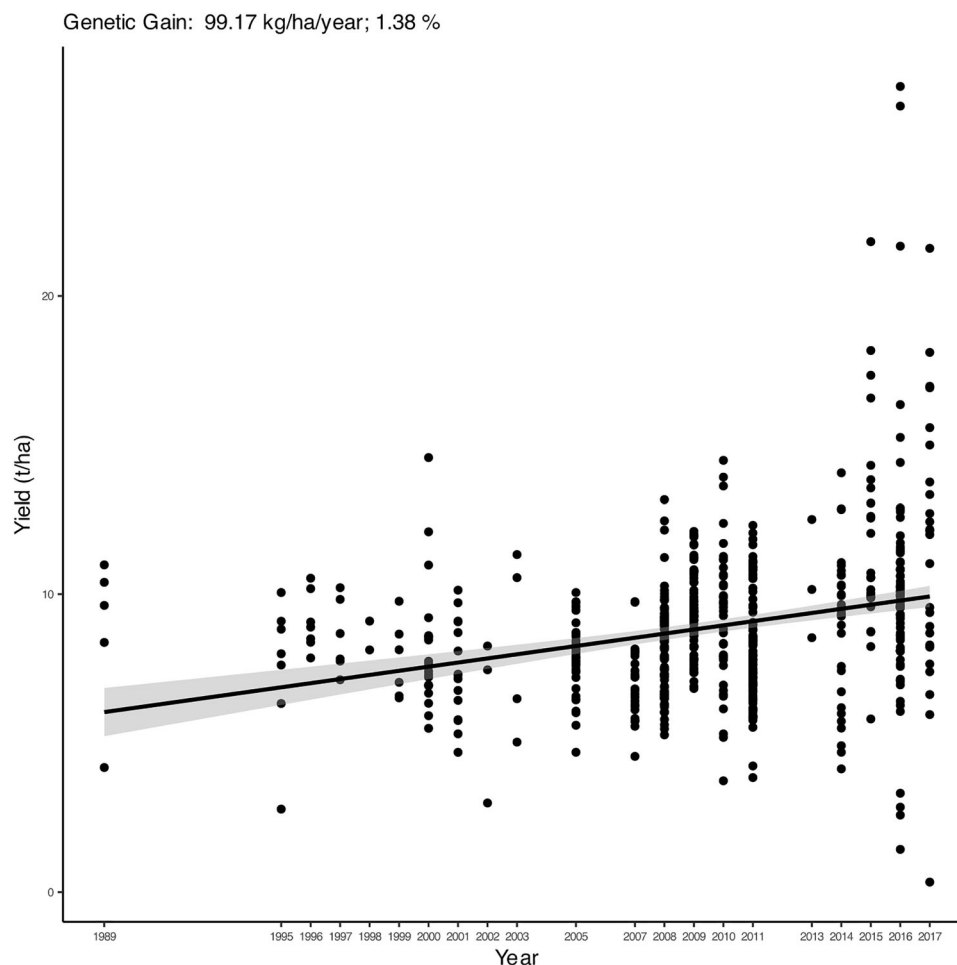


FIGURE 5 Trends of genetic gain in white yam breeding pipeline for fresh tuber yield using stages 3 and 4 historical trial data. The x-axis shows the year of origin of the genotypes and the y-axis shows the adjusted mean yield.

is important to note that the genetic gain for yam may not be directly comparable to other crops due to differences in breeding strategies, available genetic resources, and target traits, the genetic gain for fresh tuber yield in the IITA's breeding program is comparable to that of cassava fresh root yield reported in Nigeria. Okechukwu and Dixon (2008) reported a genetic gain of 1.3% per year for fresh root yield over 30 years of cassava breeding in Nigeria.

Extending the analysis from the traditional linear regression method to the segmented linear regression method in our study has provided valuable insights into the temporal dynamics of genetic gain for fresh tuber yield in both white and water yam breeding pipelines. In the case of white yam, a temporal trend of 0.52% per annum before 2011 as the year of origin of the clone and a substantial 2.19% per annum rate after that period were recorded. Likewise, a notable temporal trajectory was observed in the water yam breeding pipeline with an increase in the rate of genetic gain from 0.70% per annum pre-2011 to an impressive 15.82% per annum post-2011 as a year of cross. Interestingly, the quantile regression method did not reveal significant devia-

tions from the linear regression outcomes, underscoring the robustness of the observed trends. These results collectively emphasize the robustness of the observed genetic gain trends and their temporal dynamics that corresponded with outcomes of different breeding strategies employed for years in the IITA yam breeding program. Before mid-2010, the program operated an open population development strategy with fixed recycling parents and donors. After that, in the preceding years, the focus shifted toward a recurrent selection strategy employing closed population improvement with rapid recycling parents, where parents are selected based on their high genetic merits in crosses. The breeding program has routinely implemented a genomic-assisted prediction model to ascertain cross-performance at early generation and optimize its application for best integration into an existing yam breeding scheme.

Tuber dry matter and disease resistance represent other key yam traits in targeted product profiles for breeding (Darkwa et al., 2020). In our study, we observed negative trends in genetic gain for tuber dry matter content in both yam breeding pipelines, indicating a lack of consistent improvement in dry

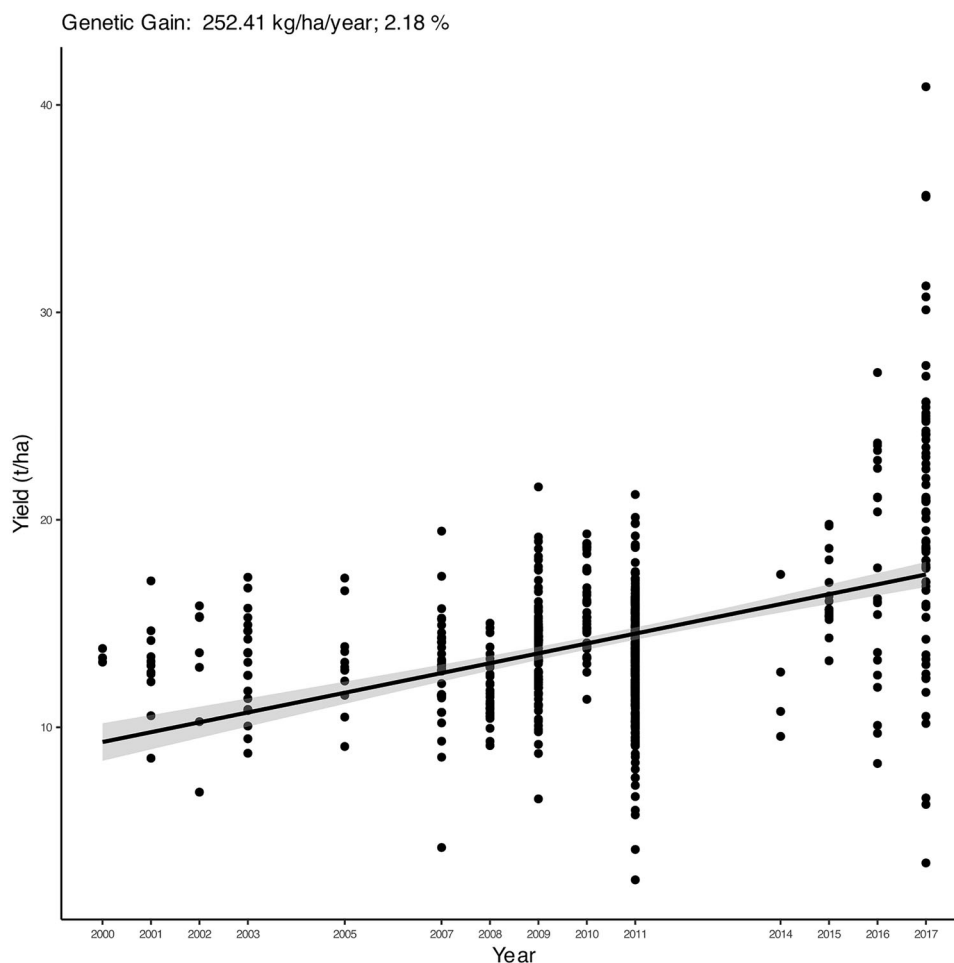


FIGURE 6 Trends genetic gain in water yam breeding pipeline for fresh tuber yield using stages 3 and 4 historical trial data. The x-axis shows the year of origin of the genotypes and the y-axis shows the adjusted mean yield.

matter content over time. This could potentially impact the nutritional value of the produce and its overall quality. Likewise, the IITA breeding efforts in improving yam varieties for disease-resistance traits have yet to achieve a significant genetic gain except for YMV resistance in water yam. This could be a significant concern, as no genetic gain for important diseases of the crop can lead to increased vulnerability to pests and diseases, potentially affecting crop yields and quality. Several factors contribute to these traits' observed trends in non-substantial genetic gain. The availability of diverse germplasm, advances in breeding techniques, and improved understanding of the genetics underlying essential traits have all played crucial roles. Yam is susceptible to various diseases, including viral and fungal infections, and the lack of a true source of resistance in the yam breeding collection always poses a challenge to improving tolerance against these diseases through selective breeding. This highlights the importance of monitoring genetic gain to ensure breeding programs' effectiveness and identify potential challenges and areas for improvement.

The present study provides a baseline for future yam breeding efforts in Africa. Overall, our findings indicate that while the breeding program has succeeded in enhancing fresh tuber yield, it might have unintentionally led to decreased quality (lower dry matter content) and compromised disease resistance in the genotypes being developed. These trade-offs are not uncommon in breeding programs, as different traits are often interconnected, and improving one trait might inadvertently affect others. It is important for breeding programs to strike a balance between various traits, ensuring that increased yield does not come at a cost to food quality or disease resistance. This might involve a more comprehensive analysis of the breeding strategy, considering factors such as genetic diversity, trait interdependencies, and the potential for unintended consequences. It is also crucial to continually monitor and assess the performance of the breeding pipelines to make informed decisions about future breeding efforts.

It is important to note that yam breeding is a complex and long-term process. Genetic gain depends on factors such as the genetic diversity available, the breeding

methods employed, and the challenges posed by specific stresses in different regions. Advances in breeding technologies and methodologies, as well as the availability of high-quality historical trial data, continue to drive improvements in yam varieties for tuber yield and disease resistance traits. In addition, sustained investments and collaborative efforts are required to continue the desired trend of genetic gain, ensuring the development of high-yielding and disease-resistant yam varieties to meet present and future demands and ensure food security.

AUTHOR CONTRIBUTIONS

Asrat Asfaw: Conceptualization; data curation; formal analysis; funding acquisition; investigation; writing—original draft; writing—review and editing. **Paterne A. Agre:** Data curation; investigation; writing—review and editing. **Ibnou Dieng:** Data curation; formal analysis; methodology; writing—review and editing. **Patrick Adebola:** Project administration; writing—review and editing. **Jude E. Obidiegwu:** Investigation; writing—review and editing. **Emmanuel Chamba:** Investigation; supervision; writing—review and editing. **Kwabena Darkwa:** Investigation; writing—review and editing. **Emmanuel Otoo:** Investigation; writing—review and editing. **Alexandre Dansi:** Investigation; writing—review and editing. **Konan Evrard Brice Dibi:** Investigation; writing—review and editing. **Amani Michel Kouakou:** Investigation; writing—review and editing. **Robert Asiedu:** Funding acquisition; investigation; project administration; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used for analyses are available on <http://datadryad.org> (Dryad. <https://doi.org/10.5061/dryad.2ngf1vhxk>) or can be obtained upon request by the corresponding author.

ORCID

Asrat Asfaw  <https://orcid.org/0000-0002-4859-0631>
 Ibnou Dieng  <https://orcid.org/0000-0002-1051-9143>
 Konan Evrard Brice Dibi  <https://orcid.org/0000-0002-9703-3866>

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