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Agro-morphological and molecular characterization of Gamma-induced cocoyam mutants using simple sequence repeat (SSR) markers

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Cocoyam (*Xanthosoma sagittifolium*) is a key staple food in Ghana. However, its limited genetic diversity has constrained breeding progress, contributing to low yields and declining production trends. To broaden its genetic diversity, gamma irradiation was applied to three improved cocoyam varieties (CRI-Akyede, CRI-Ma ye yie, and CRI-Gye me di), producing mutant lines now advanced to the M5 generation. This study assessed the genetic diversity and population structure of three parental genotypes and their 26 mutants using 13 agro-morphological traits and simple sequence repeat (SSR) markers. Significant phenotypic variation was observed in the 13 phenotypic traits studied. A total of sixty-seven polymorphic alleles were detected, with a mean of 8.38 alleles per locus. The mean polymorphic information content (PIC) was 0.46, indicating high marker informativeness. Observed heterozygosity (0.53) exceeded expected heterozygosity (0.48), suggesting an abundance of heterozygotes and absence of inbreeding. Cluster analyses (UPGMA) grouped accessions into six, with several mutants retaining close genetic identity with their parents, while others showed distinct genetic divergence. Analysis of molecular variance (AMOVA) revealed that most of the variation occurred within populations (82%) as opposed to among populations (18%). The PhiPT and FST values of 0.18 and 0.09, respectively, coupled with moderate gene exchange (Nm = 2.69), confirmed measurable genetic divergence within some mutants but partial retention of parental genetic background in other lines. These results demonstrate that gamma irradiation effectively induced new allelic diversity in the cocoyam mutants, providing valuable resources for the crop's improvement.

Key words: Cocoyam, gamma irradiation, genetic diversity, simple sequence repeat (SSRs), mutation breeding, mutants.

INTRODUCTION

Cocoyam [*Xanthosoma sagittifolium* (L.) Schott] is a vital root and tuber crop that serves as a major source of food and income, particularly in the tropics and developing countries (Aremu et al., 2024; Siqueira et al., 2023). It is known to have originated from South and Central America, introduced to Africa during the slave trade, and

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Table 1. List of the three cocoyam varieties used for the study and their respective gamma-irradiated mutants.

Improved variety	Mutant
CRI-Gye me di	GM06, GM07, GM16, GM17, GM18
CRI-Ma ye yie	ME21, ME21B, ME24A, ME29, ME32, ME32B, ME35, ME36
CRI-Akyede	AD38, AD41, AD43, AD43B, AD46, AD46B, AD47, AD86, AD86B, AD88, AD88B, AD89, AD96

is now commonly grown in the tropics and developing countries (Offei et al., 2004). In West Africa, cocoyam is most popular in Ghana, Nigeria, and Cameroon (Boakye et al., 2018). In Ghana, its cultivation provides substantial livelihood and support for rural communities, contributing to household food security, employment, and income generation for smallholder farmers, helping in poverty alleviation and food security (Acheampong et al., 2018; Boakye et al., 2018; Offei et al., 2004). Beyond local consumption, cocoyam is also gaining recognition as an emerging export commodity with significant potential for value addition and agribusiness development (Acheampong et al., 2018). Cocoyam is a nutrient-dense crop valued for its edible leaves and cormels (Boakye et al., 2018; Aremu et al., 2024). It is rich in dietary fiber, resistant starch, and key minerals such as potassium, manganese and copper, offering numerous health benefits (Aremu et al., 2024; Wada et al., 2019). Additionally, its antioxidant and phenolic compounds contribute to disease prevention and overall well-being (Eleazu, 2016).

Despite its nutritional and economic significance, cocoyam production and utilization in Ghana have declined in recent decades (Acheampong et al., 2018; Owusu-Darko et al., 2014). Being a vegetatively propagated crop, cocoyam suffers from a narrow genetic base, which limits genetic variation and poses challenges to conventional breeding efforts. In Ghana, three improved cocoyam varieties; CRI-Gye me di, CRI-Akyede, and CRI-Ma ye yie, were released in 2012 by the Council for Scientific and Industrial Research–Crops Research Institute (CSIR-CRI) with support from the West African Agricultural Productivity Programme (WAAPP) (CRI, 2025; Ministry of Food and Agriculture [MOFA], 2019). No other improved cocoyam varieties have since been released. For orphaned and neglected, but opportunity crop such as cocoyam, breeding and selection efforts can be accelerated through beneficial mutations that alter the crop's genetic architecture (Riviello-Flores et al., 2022). Mutation breeding offers an effective strategy for rapid crop improvement, introducing genetic variability and enhancing stress resilience while reducing time and costs compared to conventional methods (Bharat et al., 2024; Shetgaonkar et al., 2024). Gamma and X-rays, which are key examples of ionizing radiation, use ionization energy to shift molecules or atoms from a neutral to an ionized state (Riviello-Flores et al., 2022). Gamma irradiation has been widely applied to develop crop varieties with improved agronomic traits, higher yields, and enhanced disease resistance (Bharat et al., 2024; Mba, 2013; Ulukapi et al., 2018). In Ghana, gamma irradiation has been utilized to induce beneficial mutations in cocoyam, aiming to enhance genetic diversity and disease resistance, particularly against root rot and leaf blight. Although initial evaluations showed limited morphological variation and suboptimal yield performance (Blay et al., 2004; Danquah et al., 2006), this approach holds promise for broadening the crop's genetic base. Currently, gamma irradiation has been applied to the three released cocoyam varieties, producing mutant lines advanced from the M1 to the M5 generation. However, further research is needed to characterize genetic relationships among these mutant lines.

Previous studies on cocoyam diversity and genetic relationships have utilized various molecular markers, including Random Amplified Polymorphic DNA (RAPD) (Arhin et al., 2014; Johnson et al., 2015; Offei et al., 2004), Amplified Fragment Length Polymorphism (AFLP) (Mwenye et al., 2016), and simple sequence repeats (SSRs) (Agarwal et al., 2008; Bammite et al., 2021; Cathebras et al., 2014; Wada et al., 2021). Among these, SSR markers are particularly informative as they have co-dominant inheritance, reproducibility, and capacity to detect multi-allelic polymorphisms across loci (Ellegren, 2004; Gupta et al., 1996). They are also effective for distinguishing closely related genotypes and providing reliable estimates of population structure and genetic diversity (Agarwal et al., 2008). The objective was to use agro-morphological traits and SSR markers to evaluate the genetic diversity and population structure among 26 cocoyam mutants and their three parental genotypes, with the goal of identifying promising mutants for crop improvement.

MATERIALS AND METHODS

Plant

In all, 29 cocoyam samples, comprising three improved varieties (CRI-Gye me di, CRI-Ma ye yie, and CRI-Akyedie) and 26 gamma-ray-induced mutants (five from CRI-Gye me di, eight from CRI-Ma ye yie, and 13 from CRI-Akyede) (Table 1) were used.

Agro-morphological characterization

The 26 mutants and their respective parental genotypes were planted at the CSIR-CRI research field at Fumesua in April, 2023 in a single role at a planting distance of 1 m x 1 m and harvested 12 months after planting. Phenotypic characterization was done using 13 agro-morphological traits based on International Board for Plant Genetic Resources (IBPGR, 1989) descriptors and end-user preferred traits in Ghana. The list of descriptor traits used are cormel dry matter content, harvest index, number of plants, number of plants with cormels, top weight, cooking quality, cormel flesh colour, cormel skin colour, number of marketable cormels, number of unmarketable cormels, total cormels weight, weight of marketable cormels, and weight of non-marketable cormels.

Mutation induction by Gamma irradiation

The three released cocoyam varieties (CRI-Akyede, CRI-Ma ye yie and CRI-Gye me di) were irradiated using gamma radiations at the Biotechnology and Nuclear Agricultural Research Institute, Ghana Atomic Energy Commission (GAEC), Kwabenya, Accra. Minisett cormels and corms (~50 g) bearing at least a single bud were prepared from each parental line. The cocoyam samples were then exposed to defined gamma-ray doses within a Category IV wet storage cobalt-60 multipurpose gamma irradiator (model CoS43HH). The irradiation treatment was at a dose rate of 0.162 KGy/h (162 Gy/h) and doses (5, 10, 15, and 20) Gy delivered were confirmed using an Ethanol-chlorobenzene dosimetry system. The samples were irradiated at each dose for each variety in triplicate after the dosimetry studies for field evaluation. Mutant lines were advanced through generations to the M5 generation from 2020 before characterization using SSR markers.

Genomic DNA extraction

Approximately 200 mg of young tender leaves were sampled into liquid nitrogen from the CSIR-Crops Research Institute Cocoyam experimental field at Kwadaso, Kumasi, Ghana. The leaves were ground in a 2 ml Eppendorf tube before a modified Cetyl trimethyl Ammonium Bromide (CTAB) protocol was followed (Doyle and Doyle, 1990). Under a fume hood, 1 ml of freshly prepared CTAB buffer [1.0 M Tris-HCl at pH of 8, 0.5 M EDTA, 5.0 M NaCl, 2% CTAB (w/v), 3% β-Mercaptoethanol (v/v)] was added and vortexed for 1 min. The samples were incubated in a water bath at 65°C for 30 min (tubes were gently inverted every 5 min). The tubes were removed and placed on the working bench to cool for 5 min, then 500 µl of chloroform: isoamyl alcohol (24:1) was incorporated and mixed by inversion until the mixture turned milky. The upper layer phase was moved into a clean 2 ml Eppendorf tube, and 1.5 times the volume of ice-cold absolute ethanol (900 µl), and 0.5 µl of 3 M sodium acetate were added. The tubes were then inverted 10 times and centrifuged at 9000 rpm for 10 min. 1 ml of 70% ethanol was added after the supernatant was removed and centrifuged at 9000 rpm for 10 min. The ethanol was removed, and the pellet was subsequently dried at room temperature for 30 min. The pellet was resuspended in 500 µl low-salt Tris EDTA buffer, and 6 µl RNase A (20 mg/ml) was added. The solution was incubated at 37ºC for 45 min, and 50 µl of 7.5 M ammonium acetate was added. It was mixed and kept cold on ice for 5 min, after which it was centrifuged at 9000 rpm for 10 min. The supernatant was transferred into a new 1.5 ml tube, 700 µl of isopropanol was added, mixed by inversion, and incubated at -20°C for 1 h. This mixture was centrifuged at 13000 rpm for 5 min. The supernatant was discarded; the pellet was washed twice with 1 ml 80% ethanol, centrifuged at 13000 rpm for 5 min and dried at room temperature for 30 min. The genomic DNA was dissolved in 100 µl low salt TE buffer.

DNA quality was checked on 0.8% agarose gel, and its concentration (ng/µl) and purity (260/280) were analyzed using the NanoDrop Spectrometer 2000C (ThermoScientific, USA). The final DNA concentration was normalized to 50 ng/µl for the polymerase chain reaction (PCR) analysis.

Simple sequence repeat amplification

A total of fourteen SSR markers were used to genotype the 29 cocoyam samples (Table 2) (Cathebras et al., 2014). PCR was carried out in a Veriti PCR thermal cycler (Life Technologies, Singapore) in a 10 µl reaction volume, comprising 50 ng DNA, 2x DreamTaq Hot Start Master Mix (ThermoScientific), 10% OneTaq GC Enhancer (Biolabs), 10 µM each of forward and reverse primers and nuclease-free sterile water. The PCR protocol began with an initial denaturation at 95ºC for 5 min, followed by 42 cycles of denaturation at 95ºC for 20 s, annealing (44 to 50ºC) for 1 min depending on the primer (Table 2), and elongation at 72ºC for 2 min. The procedure concluded with a final extension phase at 72ºC lasting 20 min and a 4ºC hold. Products of the PCR were run on a 6% acrylamide gel (10x TBE, 40% Acrylamide, 10% APS, TEMED, and distilled water) and amplicons generated were visualized using a UV transilluminator (Alpha Imager).

Data analysis

The 13 agro-morphological data were subjected to Principal Component Analysis (PCA), biplot analysis and Cluster Analysis using Genstat version 9.2.0.152 (Genstat, 2007). The PCA was done based on the correlation matrix. The biplot was constructed to depict the phenotypic relationships among the mutants and their parental genotypes, based on their correlation with the traits significant for PC1 and PC2. Dendrogram for the agro-morphological traits was constructed using R (vers. 4.4.2, R Core Team, 2025). Amplicons generated from the SSR markers were recorded as binary data (presence = 1 and absence = 0) using AlphaImager HP software version 3.4. The binary data were analyzed using PowerMarker version 3.25 (Liu and Muse, 2005), GenAlEx version 6.0 (Peakall and Smouse, 2006), and NTSYSpc version 2.2 (Rohlf, 1988). PowerMarker was used to generate summary statistics for each SSR locus, including allele frequencies, the number of polymorphic loci, and polymorphic information content (PIC). The binary dataset was standardized in NTSYSpc, and a pairwise similarity matrix was computed using the Simple Matching Coefficient (SMC) to estimate genetic relatedness among the genotypes. This similarity matrix served as the basis for constructing an unweighted pair group method with arithmetic mean (UPGMA) dendrogram to determine the relationships among the samples. Furthermore, Principal Coordinates Analysis (PCoA) was conducted in GenAlEx to visualize patterns of genetic variation and to determine the proportion of total variance explained by the first few principal coordinates. AMOVA-based Phi (Φ) PT statistics and Wright's fixation index (FST) were also used to assess population differentiation and structure.

RESULTS AND DISCUSSION

Genetic diversity based on 13 agro-morphological traits

Variability was observed in all the 13 agro-morphological

Table 2. SSR markers used for the study.

No	Marker	Marker sequence	Expected band size (bp)	Annealing temperature (°C)
1	MXsCIR11	F: AATTCTTAGCAGCATTGTTA R: CATTCGTATCAACTTCCTTT	204-236	44
2	MXsCIR22	F: CGTGAGAAACACCTGAATTA R: AATTTGCTCTGTCATTGTG	216-226	44
4	MXsCIR27	F: TGCATGAATTGAAGAAAT R: AACAAAGAGTCTCACCACAT	217-245	44
5	MXsCIR13	F: GTTTCCTTTATTCGTTGATG R: GTAGTGGCTGAGAATTGAAA	223-244	48
6	MXsCIR7	F: GGACTGGGAGTCTGAGTAG R: CCTTTCCCCTCACTATAAA	224-241	48
7	MXsCIR14	F: TACCCTACATTTGGGATCT R: TTTTGGCTTTAGGTCTATTC	190-216	47
8	MXsCIR16	F: CTTATTGATGCCGAGAATAC R: TTCCTCACAATATGTTCTCAT	202-205	47
9	MXsCIR12	F: TACATTTCCATTGCCATC R: CAAATTAAAGAGGGAGACAG	223-282	44
10	MXsCIR23	F: TGTAGGTATGGACACATGG R: TTAAGACAAACCCTCAGC	176-184	46
11	MXsCIR10	F: GATGTCTGTAGTGGCCTAGT R: AATTAAGTTGGGTGGTAGAT	208-251	49
12	MXsCIR5	F: GCGCATTATTAACGAATATC R: GTCATCTATGGCTATCACCT	212-216	46
13	MXsCIR20	F: CCCTTATTGCTGTTTTCA R: CATATCTCTTCCTCTCACCA	226-247	49
14	MXsCIR21	F: CTTAACCTTGTCAGCCTCT R: GAGCGGTATAACAATTCATC	194-226	46

Source: Cathebras et al. (2014).

traits. The first four principal components (PCs) with eigenvalues greater than 1.0 jointly explained 84.23% of the total phenotypic variation in the mutants and their parental genotypes (Table 3). The traits of importance for the first component were the number of plants with cormels, the number of marketable cormels, the number of unmarketable cormels, the total weight of cormels, and the weight of marketable cormels. Top weight, cooking quality, cormel flesh colour, and cormel skin colour were of importance for PC2. Scores on the first two PCs accounted for 60.47% of the total phenotypic variation, and were related to top weight, cormel yield, colour traits, and cooking quality. The distribution produced by PC1 and PC2 (Figure 1) had CRI-Gye me di grouped closely with most of the mutants, CRI-Ma ye yie in close proximity with AD86B, while CRI-Akyede is distantly

Table 3. Principal Component Analysis of the agro-morphological traits of the cocoyam mutants and their parental genotypes.

Morphological trait	PC1	PC2	PC3	PC4
Cormel dry matter content	-0.111	0.078	0.465	-0.444
Harvest index	0.100	0.230	0.427	0.465
Number of plants	0.220	0.129	-0.488	-0.005
Number of Plants with cormels	0.367	0.080	-0.189	0.200
Top weight	0.278	-0.388	-0.129	-0.181
Cooking quality	0.059	0.310	0.226	0.478
Cormel flesh colour	-0.163	-0.501	0.197	0.158
Cormel skin colour	-0.163	-0.501	0.197	0.158
Number of marketable cormels	0.416	-0.163	0.006	0.076
Number of unmarketable cormels	0.335	0.083	0.278	-0.334
Total cormel's weight	0.381	-0.215	0.129	0.100
Weight of marketable cormels	0.378	-0.222	0.124	0.107
Weight of unmarketable cormels	0.298	0.200	0.271	-0.312
Latent roots (Eigen values)	5.216	2.645	1.813	1.275
Variance (%)	40.12	20.35	13.95	9.81
Cumulative (%)	40.12	60.47	74.42	84.23

*Values in bold indicate the most relevant characters (>0.3) that contributed most to the variation of the particular component.

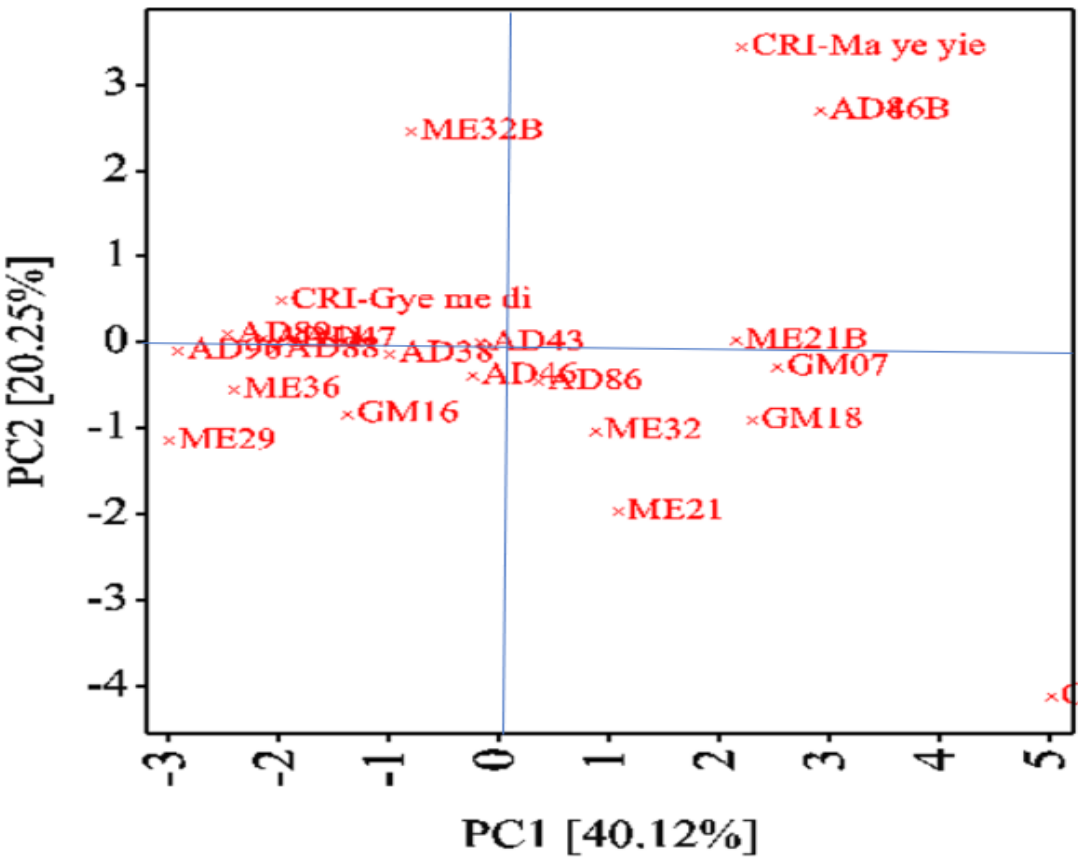


Figure 1. A biplot of PC1 and PC2 showing the distribution of the cocoyam mutants and their parental genotypes.

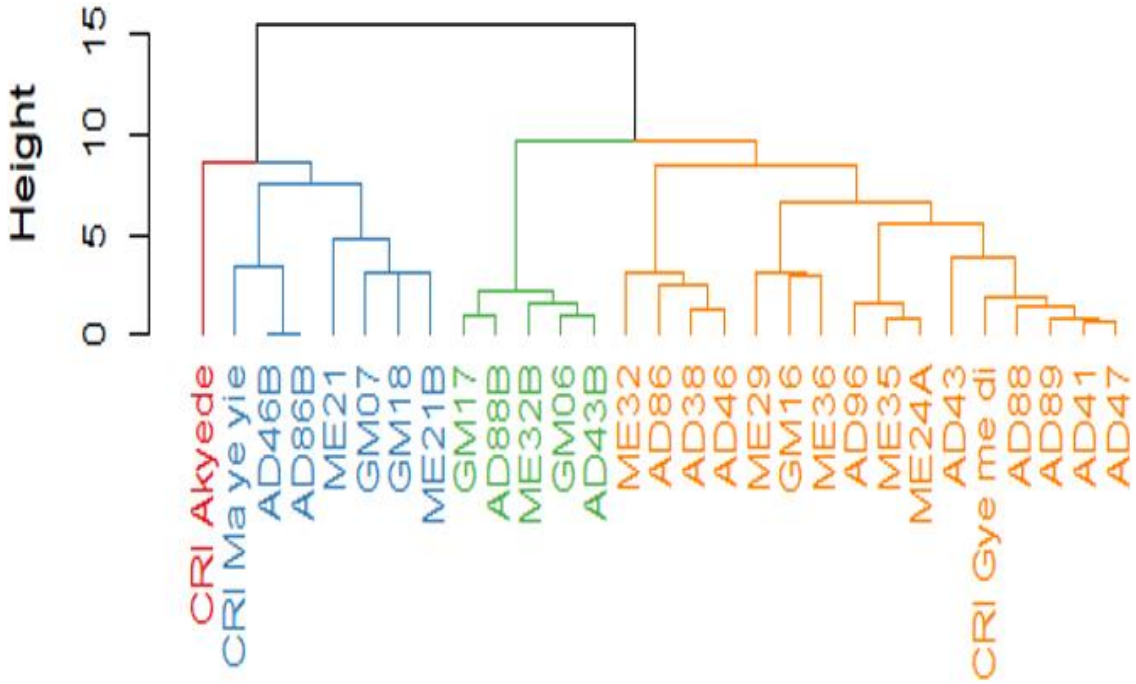


Figure 2. Dendrogram showing grouping of the 26 cocoyam mutants and their parental genotypes based on 13 agro-morphological markers.

away from all of the mutants. The dendrogram separated the 26 mutants and the three parental genotypes by a distance of 0 to 15 into four clusters (Figure 2). Cluster 1 had 17 mutants consisting of nine mutants of CRI-Akyede, four mutants of CRI-Ma ye yie, and one mutant of CRI-Gye me di clustering with CRI-Gye me di. Cluster 2 is composed of five mutants, which were mutants of CRI-Akyede (AD43B, AD88B), CRI-Gye me di (GM06, GM17), and CRI-Ma ye yie (ME32B). Cluster 3 is made up of six mutants (two each from each of the parental genotypes) clustering with CRI-Ma ye yie. Cluster 4 had CRI-Akyede as a unique outlier. The distribution of the mutants and the parental genotypes in the biplot and the dendrogram affirms the variation observed in the PCA analysis. This shows existence of a high degree of agro-morphological polymorphism among the mutants and their respective parental genotypes for the traits studied.

Genetic diversity based on eight SSR markers

Out of the fourteen SSR markers used to screen the 29 cocoyam samples, six produced fragments significantly larger than the expected amplification range, suggesting non-specific primer binding, and were therefore excluded from further analysis. Eight of the 14 SSR markers amplified within the expected range and formed the basis of our analysis. An image of PCR amplicons visualized on 6% Polyacrylamide gel electrophoresis (PAGE) is shown in Figure 3. A total of 67 polymorphic alleles were detected across all loci, ranging from 3 (MXsCIR 22) to 13 (MXsCIR 20, 26) per locus, with a mean of 8.38 alleles per marker (Table 4). The major allele frequency (MAF) ranged from 0.47 to 0.88, with a mean of 0.70 (Table 4). This indicates a high level of allelic richness and moderate allelic dominance among the parental lines and their derived mutants. The allelic richness observed here is markedly higher than values reported in previous cocoyam and taro studies. Cathebras et al. (2014), who utilized the same set of markers to analyze cocoyam accessions, reported two to six alleles per locus (mean = 3.70). Similarly, Wada et al. (2021) observed two to five alleles per locus (mean = 3.27), and Bammite et al. (2021) obtained mean alleles per locus of 3.15 for taro and 3.0 for cocoyam accessions. Compared to these SSR-based studies, our study shows more than a two-fold increase in mean allelic richness. In contrast, Offei et al. (2004) reported a mean observed number of alleles of 1.99 (effective alleles ~1.54) using dominant RAPD markers, which is substantially lower than the SSR-based alleles reported, likely due to the greater polymorphism detected by SSRs compared to RAPDs. The MAF observed in this study (mean = 0.70) is comparable to previous reports on *Xanthosoma* and related *Colocasia* species, with Bammite et al. (2021) reporting a mean MAF of 0.62 in taro and 0.83 in cocoyam, with ranges of

Table 4. Genetic diversity in 29 cocoyam samples using SSR markers. He: expected heterozygosity, Ho: observed heterozygosity, PIC: Polymorphic information content.

Marker	Major allele frequency	Allele No.	Gene diversity (*He*)	Observed Heterozygosity (*Ho*)	PIC
MXsCIR 27	0.88	6.0	0.22	0.24	0.22
MXsCIR 22	0.84	3.0	0.27	0.31	0.26
MXsCIR 10	0.62	12.0	0.60	0.76	0.59
MXsCIR 20	0.57	13.0	0.66	0.86	0.64
MXsCIR 23	0.72	8.0	0.46	0.55	0.45
MXsCIR 26	0.47	13.0	0.75	0.66	0.74
MXsCIR 11	0.79	7.0	0.36	0.34	0.35
MXsCIR 13	0.71	5.0	0.47	0.55	0.45
Mean	0.70	8.38	0.48	0.53	0.46

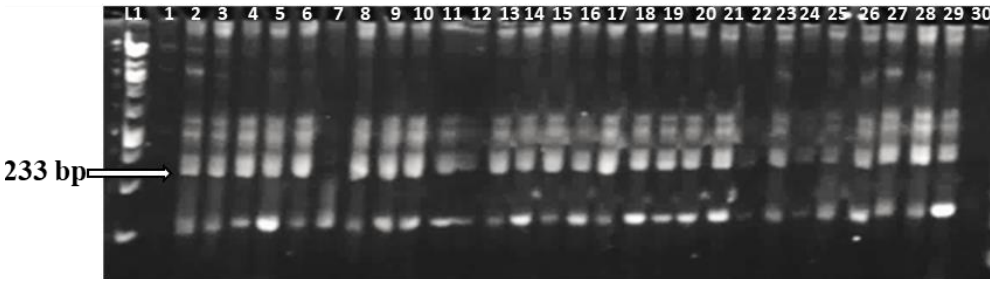


Figure 3. PCR amplicons of 29 cocoyam samples with SSR marker MXsCIR13 visualized on 6% PAGE gel. L1=100bp ladder, 1-29 = test samples, 30 = negative control.

0.38 to 0.88 and 0.47 to 0.97 for taro and cocoyam, respectively. The higher allelic richness observed in this study, coupled with the balanced distribution of alleles reflected by the moderate MAF, depicts an increase in polymorphism and reduced allele dominance, likely due to induced mutagenesis, which can create novel alleles and alter/modify existing loci, thereby broadening the genetic variation detected by SSRs. This is beneficial for enhancing the pool of genetic variation available for selection and cocoyam improvement.

PIC establishes the informativeness of molecular markers according to allele counts and their distribution across genotypes. PIC values obtained ranged from 0.22 (MXsCIR 27) to 0.74 (MXsCIR 26), with an average of 0.46, which demonstrated that among the accessions analyzed, a moderate degree of genetic diversity exists. Botstein et al. (1980) noted that markers with PIC values > 0.50 indicate high informativeness, while values between 0.25 and 0.50 suggest moderate informativeness. This implies that the markers used in this study collectively showed a strong capacity for genetic differentiation. Our PIC values align with previous studies. Reported ranges include 0.10 - 0.75 for cocoyam (mean = 0.48) (Cathebras et al., 2014), and 0.2 to 0.65 (mean = 0.43) and 0.06 to 0.62 (mean = 0.25) for taro and cocoyam, respectively (Bammite et al., 2021). Olasupo et al. (2018) similarly found PIC values ranging from 0.33 to 0.63 (mean 0.51) in irradiated cowpea mutants using SSR markers. This comparatively suggests that the SSR markers employed in the present study are sufficiently informative for detecting polymorphism levels comparable to those observed in related studies, thereby confirming their suitability for genetic diversity analysis in this germplasm.

Gene diversity

Gene diversity (expected heterozygosity (*He*)) indicates the potential genetic variation within a population by quantifying the chance that two randomly selected alleles from a population are distinct (Nei, 1987). In this study, *He* values ranged from 0.22 (MXsCIR 27) to 0.75 (MXsCIR 26), with a mean of 0.48, indicating a moderate level of genetic diversity among the accessions analyzed (Table 4). The corresponding observed heterozygosity (*Ho*) values ranged from 0.24 to 0.86, with a mean of 0.53, suggesting a slightly higher proportion of heterozygotes than expected under Hardy–Weinberg equilibrium. These results are consistent with those

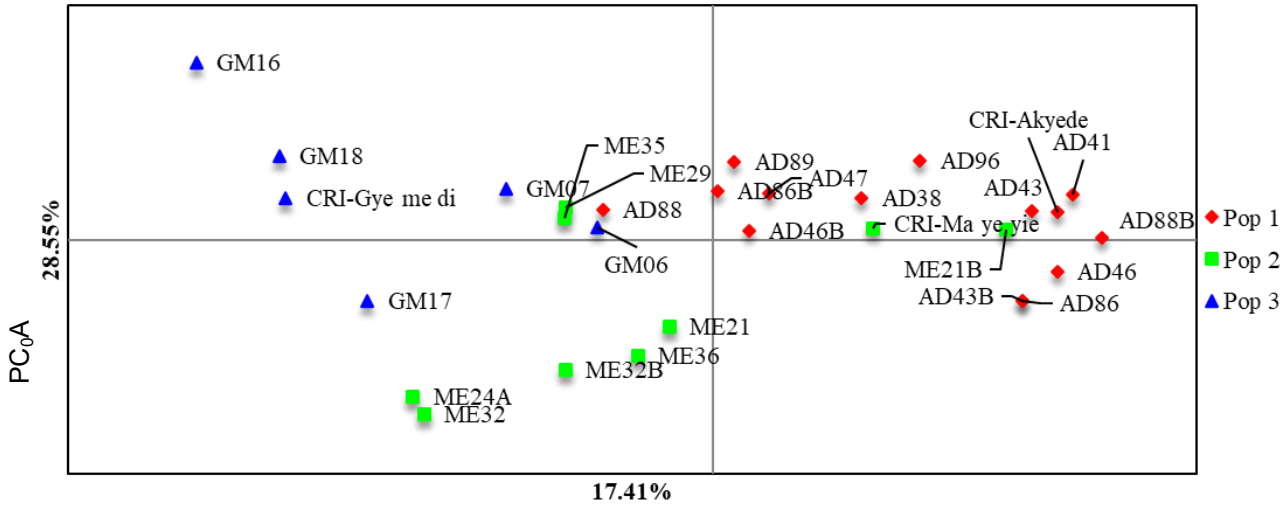


Figure 4. PCoA showing the genetic relationships among parental cocoyam genotypes and their gamma-irradiated mutants based on eight SSR markers. Each color represents a distinct parental genotype and its corresponding mutant derivatives. *Pop*: population.

reported in related studies. Nei's gene diversity values, ranging from 0.21 to 0.71 (mean = 0.49) for taro and 0.06 to 0.67 (mean = 0.28) for Togolese cocoyam accessions, have been reported (Bammite et al., 2021). Cathebras et al. (2014) similarly recorded *He* values ranging from 0.09 to 0.78 and *Ho* from 0.00 to 0.97. Similarly, *He* values between 0.29 and 0.73 (mean = 0.57), with a mean *Ho* of 0.51 was recorded among Ethiopian cocoyam accessions (Wada et al., 2021). Conversely, the mean gene diversity among Ghanaian cocoyam accessions using RAPD markers was 0.32 (Offei et al., 2004). The moderate level of gene diversity (mean *He* = 0.48) observed in this study indicates that the parental genotypes and their induced mutants possess considerable genetic variation. The slightly higher observed heterozygosity (Ho = 0.53) relative to the expected heterozygosity suggests a mild excess of heterozygotes, which may reflect the creation of novel allelic combinations or point mutations by induced gamma irradiation. Such mutagenic treatments are known to generate random genetic changes that can enhance allelic variability, particularly in clonally propagated crops like cocoyam, where natural recombination is restrained. The results, therefore, suggest a broadening of the genetic base of the studied mutant lines, potentially increasing the probability of selection in subsequent breeding trials. The result also suggests that while induced mutations have contributed to broaden the genetic variability of the parental lines, the diversity obtained are within the range reported for other cocoyam and related aroid populations comparatively (Bammite et al., 2021; Cathebras et al., 2014; Offei et al., 2004; Wada et al., 2021), which indicates that the magnitude of change remains within biologically realistic bounds.

Principal coordinates analysis (PCoA)

The PCoA distinguished the parental cocoyam genotypes and their gamma-irradiated mutants into three main clusters corresponding to their parental origins (Figure 4). Three populations (color-coded) consisting of each improved cocoyam variety and their respective mutants were analyzed. The first two principal coordinates explained 28.55 and 17.41% of the total genetic variation, respectively, accounting for a cumulative 45.96% of the observed diversity (Figure 4). Population 1, comprising CRI-Akyede and its mutants (red diamonds), generally formed as a relatively tight cluster in the first quadrant of the ordination plot, with few exceptions. Population 2, comprising CRI-Ma ye yie and its mutants (green squares), displayed a more dispersed pattern, with the parental genotype and one mutant located in the first quadrant, while most of the mutants clustered in the third quadrant, suggesting greater allelic differentiation. On the other hand, Population 3, comprising CRI-Gye me di and its mutants (blue triangles), generally clustered in the fourth quadrant.

The PCoA clustering patterns illustrate the genetic distinctness of the parental lines and the variation generated within their mutant populations. CRI-Ma ye yie grouped closely with CRI-Akyede and its mutants in the first quadrant, whereas CRI-Gye me di was clearly separated from the other parental lines. This suggests that CRI-Akyede and CRI-Ma ye yie may share a more recent common ancestry. Within each parental group, the

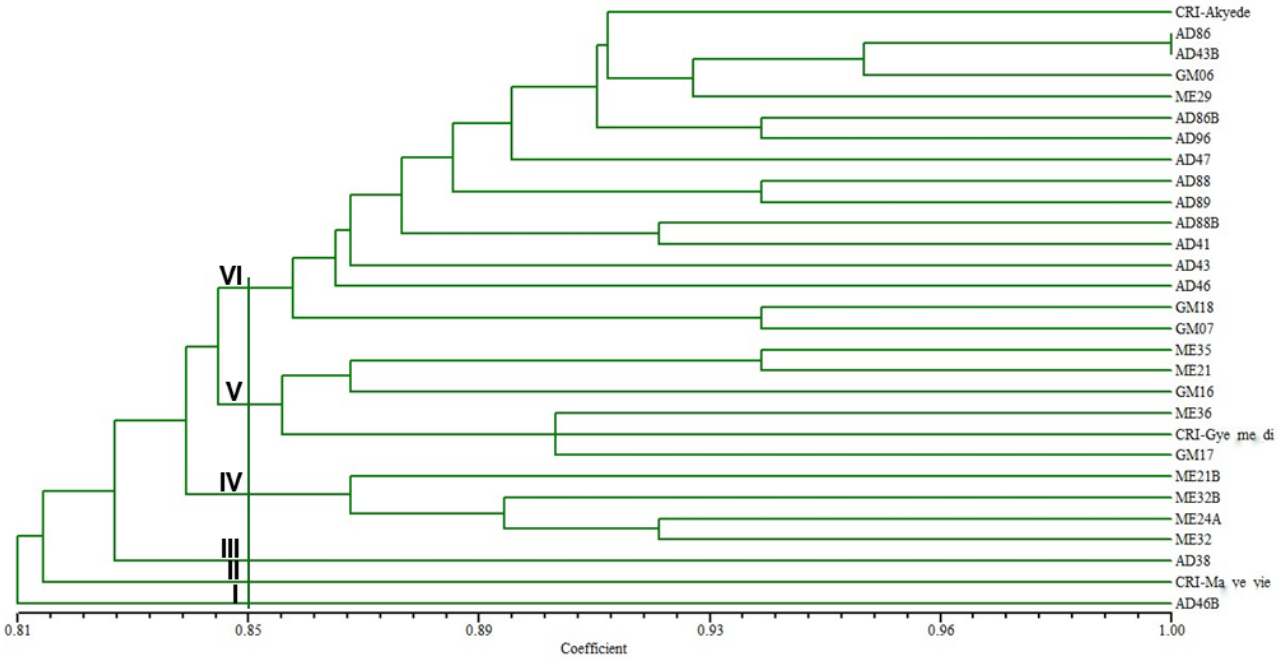


Figure 5. UPGMA dendrogram showing genetic relationships among parental cocoyam genotypes (CRI-Akyede, CRI-Ma ye yie, and CRI-Gye me di) and their gamma-irradiation-derived mutants based on SSR data. Six major clusters (I–VI) were identified at a similarity coefficient of ~0.85.

mutants generally clustered around their respective parents but showed varying degrees of internal dispersion. This pattern suggests that, while some mutants retained much of their parental genetic background, gamma irradiation introduced detectable allelic variations among some mutant lines. The tight clustering observed for CRI-Akyede and its mutants, as well as for CRI-Gye me di and its mutants, implies limited divergence and a high level of allelic retention. In contrast, the broader spread of CRI-Ma ye yie's mutants indicates stronger mutagenic effects and greater within-group variation. Induced mutations often uncover novel alleles, broadening genetic diversity beyond existing germplasm (Mba, 2013). For example, genetic diversity analyses of selected mutants of cowpea (*Vigna* species) based on SSR markers revealed that most mutants formed distinct clusters separate from their parental lines (Olasupo et al., 2018). Faba bean mutant lines genotyped together with their parental line similarly revealed a similar pattern, where some mutants displayed distinct clustering separated from the parental lines (Khazaei et al., 2024). Clustering of mutants separate from parents infers that crossing mutants with parental lines remains feasible for introgression of desirable traits through genetic hybridization, making mutants usable as parents in breeding programs (Ulukapi et al., 2018). Collectively, these findings confirm successfully induced genetic changes in some mutant lines while maintaining the core genetic identity of each parental background, a desirable outcome for mutation breeding programs aimed at broadening genetic diversity within parental genotypes.

Cluster analysis (UPGMA Dendrogram)

UPGMA dendrogram revealed the genetic relationships among the parental cocoyam genotypes (CRI-Akyede, CRI-Ma ye yie, and CRI-Gye me di) and their corresponding mutants (Figure 5). The similarity coefficient among the cocoyam accessions ranged from 0.81 to 1.00, with an average of 0.91, indicating generally high genetic relatedness among the accessions. The highest similarity (1.00) was observed between two CRI-Akyede mutants (AD86 and AD43B), suggesting near-identical genetic profiles at the analyzed SSR loci for these two lines. At a similarity coefficient of ~0.85, the accessions were grouped into six major clusters (I–VI) (Figure 5). Cluster I comprised a single CRI-Akyede mutant (AD46B), while Cluster II contained the parental genotype CRI-Mayeyie. Cluster III included another single CRI-Akyede mutant (AD38). Cluster IV consisted entirely of four CRI-Ma ye yie-derived mutants (ME21B, ME32B, ME24A, and ME32), showing their close intra-group relationship. Cluster V grouped the parental genotype CRI-Gye me di with two of its mutants (GM16,

Table 5. AMOVA (based on ΦPT) showing genetic differentiation among and within three cocoyam populations as analyzed by SSR markers. Each population is made up of a parental genotype and its derived mutants.

Source	Df	Sum of squares	Mean of squares	Estimated variance	% variation
Among pops	2	18.35	9.17	0.68	18
Within pops	26	78.14	3.01	3.01	82
Total	28	96.48		3.68	100

Statistics	Value	P value
PhiPT	0.18	0.001

GM17) and three CRI-Ma ye yie mutants (ME35, ME21, ME36). The largest group, Cluster VI, included the parental genotype CRI-Akyede along with 11 of its mutants (AD86, AD43B, AD86B, AD96, AD47, AD88, AD89, AD88B, AD41, AD43, and AD46), three CRI-Gye me di mutants (GM06, GM18, GM07), and one CRI-Ma ye yie mutant (ME29) (Figure 5). The UPGMA clustering pattern supports the PCoA results, confirming that gamma irradiation induced measurable but controlled genetic variation within each parental lineage.

The distinct clustering of the mutants of CRI-Akyede, CRI-Ma ye yie, and CRI-Gye me di revealed both conserved and novel allelic patterns, such that while several mutants retained the genetic identity of their parental lines, others acquired new allelic combinations because of mutagenic induction. The separation of two CRI-Akyede mutants (AD46B and AD38) into unique clusters suggests radiation-induced allelic changes sufficient to distinguish them from both their parents and sibling mutants. CRI-Ma ye yie's mutants exhibited broader dispersion across clusters, consistent with the PCoA results showing higher within-group differentiation. This pattern points to stronger mutational effects and enhanced allelic diversity within the CRI-Ma ye yie lineage. Nonetheless, the formation of a distinct cluster (Cluster IV) containing only CRI-Ma ye yie mutants also shows strong intra-line relatedness coupled with divergence from the parental genotype. In contrast, the relatively tight clustering of CRI-Akyede and CRI-Gye me di mutants, particularly within the large composite Cluster VI, suggests more conservative mutational effects and retention of most parental alleles.

The presence of CRI-Gye me di and CRI-Ma ye yie mutants within this Cluster VI suggests partial genetic overlap, likely resulting from shared ancestral alleles or convergent mutations at SSR loci just as was observed by Olasupo et al. (2018). The clustering pattern in our study similarly confirms successfully induced measurable genetic variation by gamma irradiation without the disruption of the fundamental parental genetic architecture, which emphasizes the reliability of SSR markers in detecting subtle mutational shifts. It also confirms the variation observed using the 13 agro-morphological traits.

Genetic structure

Analysis of Molecular Variance (AMOVA) based on PhiPT (ΦPT) and fixation index (FST) evaluates the population differentiation and provides insights into the population structure (Excoffier et al., 1992). AMOVA based on ΦPT statistics (Table 5) revealed significant genetic differentiation among the three cocoyam populations (ΦPT = 0.18, p = 0.001). Most of the total genetic variation occurred within populations (82%), while 18% of the variation was attributed to differences among populations. The estimated variance components were 3.01 within populations and 0.68 among populations, giving a total molecular variance of 3.68 (Table 5). These indicate that most of the genetic diversity resides within the individual populations rather than between, suggesting substantial allelic variability among genotypes derived from the same parental background.

The significant ΦPT value confirms a moderate but meaningful level of genetic differentiation among the cocoyam populations. The high within-population genetic variation suggests that most of the detectable diversity is due to individual differences among the mutants rather than between population groups. The low among-population variation suggests that the three parental genotypes (CRI-Akyede, CRI-Ma ye yie, and CRI-Gye me di) share a narrow genetic background. Thus, the genetic divergence among mutants of the same parent and the observed within-group variability reinforce the value of gamma irradiation in inducing the detected changes.

Similarly, AMOVA based on fixation index (FST) revealed moderate but statistically significant genetic differentiation in the analysed cocoyam populations (Table 6). The FST observed was 0.09 (p = 0.004), showing that about 9% of the total genetic variation is due to differences between populations, while the remaining 91% exists within populations. Furthermore, a higher genetic variation (93%) was attributed to differences within individuals, while 7% occurred among

Table 6. AMOVA (based on Wright's Fixation Index (FST)) shows genetic differentiation among and within three cocoyam populations as analyzed by SSR markers. Each population is made up of a parental genotype and its derived mutants.

Source	Df	Sum of squares	Mean of squares	Estimated variance	% variation
Among population	2	9.17	4.59	0.17	7
Among Individuals	26	39.07	1.50	0.00	0
Within individuals	29	62.00	2.14	2.14	93
Total	57	110.24		2.31	100

F-statistics	Value	P value
Fst	0.09	0.004
Fis	-0.18	1.000
Fit	-0.08	0.963
Fst max	0.54	
F'st	0.16	
Nm	2.69	

Df: Degree of freedom. FST: Fixation Index, FIS: Inbreeding Coefficient within Subpopulations, FIT: Total Inbreeding Coefficient, Nm: Gene Flow.

populations and 0% among individuals within populations (Table 6). The inbreeding coefficients among individuals within populations (FIS = –0.18, p = 1.000) and across the total samples (FIT = –0.08, p = 0.963) were both negative, suggesting an absence of inbreeding and a tendency toward heterozygosity among individuals. The standardized fixation index (F′ST = 0.16) further supports a moderate degree of population differentiation, consistent with the partitioning of variation observed in the AMOVA. The absence of inbreeding (negative FIS) and the predominance of heterozygosity among individuals suggest that the cocoyam populations maintain a high degree of genetic mixing, with individuals carrying diverse allelic combinations rather than being genetically uniform. This pattern indicates that the gamma irradiation process did not cause allelic fixation or loss of heterozygosity but instead promoted the retention or creation of new heterozygous loci through induced mutations.

Varying levels of within- and among- population genetic differentiation are commonly reported in cocoyam diversity studies and are often influenced by factors such as species composition, geographical distribution, and the extent of morphological variation among test samples. For example, Wada et al. (2021) reported that 14% of the molecular variance occurred among populations, 18% among individuals, and 68% within individuals when 100 cocoyam accessions (65 green, 35 purple) from Ethiopia were analysed using SSR markers. They attributed the high within-population variance in part to the coexistence of green and purple morphotypes within the populations. Like our findings, Bammite et al. (2021) also reported greater genetic variation within than among populations in both *Colocasia esculenta* (Taro) and *Xanthosoma mafaffa* (Cocoyam). Their analysis revealed 83% within-population and 17% among-population molecular variance between the two taro populations - Dasheen (characterized by large mother corms) and Eddoe (with small mother corms), and 64% within-population and 36% among-population variance between the two new cocoyam populations distinguished by petiole colour (green vs. purple). It is obvious that morphological differences associated with corm size and petiole pigmentation contributed to partial population differentiation while substantial genetic variation remained distributed within populations in their study. In contrast, Mwenye et al. (2016) reported higher genetic variation among populations (79.2%) and lower variation within populations (20.8%) among *C. esculenta* and *X. sagittifolium* accessions from Malawi using AFLP markers. Their pronounced among-population differentiation is attributable to the presence of two genetically distinct species with contrasting leaf morphologies - peltate in *C. esculenta* and sagittate in *X. sagittifolium*. While the low among-population variance depicts the close genetic relatedness among the three parental genotypes, the observed higher within-population variation, coupled with the significantly moderate genetic differentiation detected by FST and ΦPT, thus depicts measurable divergence between parental genotypes and mutants, which implies the successful induction of new polymorphisms within each varietal group. Cocoyam (*X. sagittifolium*) is predominantly vegetatively propagated, which restricts natural recombination and limits inter-varietal genetic differentiation over time. Random mutations introduced by gamma radiation, therefore, offer a useful approach to expand the genetic variation and create new allelic

variants.

The number of migrants per generation (Nm), an indirect estimate of gene flow, was 2.69, suggesting considerable genetic exchange or shared alleles among the mutants and their parental lines. In comparison, Offei et al. (2004) reported a mean Gst of 0.086 and Nm of 5.31 among naturally occurring Ghanaian cocoyam accessions, indicating extensive gene exchange across natural populations. While gene flow typically implies allelic exchange through hybridization or outcrossing, in this study, where variation was induced through mutation breeding rather than through natural recombination, it more appropriately reflects the degree of allelic similarity or shared polymorphisms among the groups. The Nm value, which exceeds the critical threshold of 1.0, suggests that gamma irradiation generated novel allelic combinations while maintaining substantial genetic relatedness between mutants and their parental genotypes.

Conclusion

Molecular characterization of mutants is essential for understanding the extent of induced genetic variation and guiding breeding strategies aimed at identifying superior traits and conservation. In this study, twenty-nine cocoyam accessions comprising three parental genotypes and their gamma-irradiated mutants were analysed using SSR markers. Significant agro-morphological diversity was observed among the cocoyam mutants and their parental genotypes, with the first four principal components accounting for 84.23% of the total phenotypic variation. Yield-related traits, particularly the number and weight of cormels, together with top weight, cooking quality, and colour attributes, were the major contributors to this variation. The agro-morphological clustering into four distinct groups revealed clear phenotypic differentiation and reflected the broad spectrum of traits generated through induced mutagenesis, highlighting the potential for selecting desirable traits for improvement. The SSRs demonstrated high polymorphic information content and heterozygosity, effectively capturing both natural and induced genetic variation. The mutant populations showed slightly higher allelic richness compared to previously reported natural cocoyam accessions and moderate marker allele frequencies. Cluster analysis grouped the accessions into six distinct clusters, distinguishing several mutants from their parental genotypes while preserving partial genetic overlap among lineages. This pattern, supported by the PCoA, demonstrated that most mutants diverged genetically from their parents while some retained shared alleles. AMOVA based on both F-statistics and ΦPT analysis confirmed the moderate genetic differentiation with high within-population variation and substantial genetic exchange. The close genetic similarity between some mutants and their parental lines reflects retained ancestral polymorphisms, indicating that induced mutagenesis introduced new variation while preserving parental genome integrity. Although gamma irradiation introduced novel allelic combinations and moderate population differentiation, the overall genetic diversity and heterozygosity of the cocoyam populations were maintained. In essence, the induced mutants remain genetically integrated with their parental backgrounds, paralleling the moderate-to-high allelic differentiation reported in naturally diverse cocoyam populations. Collectively, these results indicate that gamma irradiation effectively broadened the genetic variability of the cocoyam breeding lines by introducing new allelic variants while preserving the overall genetic coherence of the parental gene pool. Overall, our results emphasize gamma irradiation as an effective tool for broadening the genetic base of cocoyam accessions. The mutant lines produced serve as valuable genetic resources for selection and improvement within the CSIR-CRI cocoyam breeding program to support sustainable cocoyam improvement in Ghana and beyond.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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