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| RESEARCH ARTICLE

Genetic Uniformity and Residual Divergence in Apomictic Mangosteen *Garcinia mangostana* L.) Revealed by RAPD Markers

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| ABSTRACT
Mangosteen (*Garcinia mangostana* L.) is a high-value tropical fruit whose genetic improvement is constrained by obligate apomictic reproduction, which limits meiotic recombination and narrows detectable diversity. This study assessed the genetic uniformity and residual divergence among mangosteen accessions to support objective mother-tree selection and germplasm management. Twenty local accessions from Bulukumpa District, Bulukumba Regency (South Sulawesi, Indonesia), and two commercial reference genotypes (Kali Gesing and Lotan) were evaluated using five RAPD primers (OPA-01, OPA-04, OPB-01, OPB-04, and OPB-18). Genomic DNA was extracted using a modified CTAB protocol, amplified under optimized RAPD-PCR conditions, and electrophoresed on a 2% agarose gel. To ensure robustness, each primer–accession combination was amplified in duplicate; only clear, consistently reproducible bands were scored in a binary matrix (1/0), with no-template controls included to monitor for contamination. Genetic similarity was estimated using Jaccard's coefficient and clustered using UPGMA (SAHN) in the NTSYS-pc 2.1. All primers produced clear and reproducible banding patterns, yielding two to six loci per primer. However, the polymorphism was highly limited: four primers generated exclusively monomorphic profiles, whereas primer OPA-04 produced five loci with one polymorphic locus. Overall polymorphism was ~20%, with moderate marker informativeness indicated by PIC and expected heterozygosity values of approximately 0.40 for OPA-04. Similarity coefficients were very high (0.95–1.00), reflecting a strongly homogeneous genetic structure. UPGMA clustering resolved two groups at a similarity threshold of 0.95: a major cluster containing most accessions, along with Kali Gesing and Lotan, and a minor sub-cluster comprising four accessions (MGS_9, MGS_13, MGS_17, and MGS_18) differentiated by the single polymorphic locus. These findings confirm an extremely narrow genetic base consistent with apomictic reproduction, while highlighting a small set of relatively distinct accessions that may be prioritized for conservation and evidence-based parent selection in mangosteen improvement programs.

| KEYWORDS
Apomixis, genetic uniformity, residual genetic variation, RAPD markers, genetic similarity, mangosteen, germplasm management.

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1. Introduction

Mangosteen (*Garcinia mangostana* L.) is a high-value tropical fruit cultivated predominantly in Southeast Asia and is widely recognized for its substantial economic contribution and rich bioactive composition. The economic implications of mangosteen go beyond the fruit's market value, supporting farmers' livelihoods and rural economies, as well as the increasing use of its extracts in the pharmaceutical and cosmetic industries through more efficient extraction techniques (Herawati et al., 2020; Zamarudin et al., 2023). The fruit is highly valued in both domestic and international markets owing to its distinctive flavor, premium positioning, and the presence of health-promoting compounds, particularly xanthones. Despite its long history of cultivation and steadily increasing global demand, the genetic improvement of mangosteen has progressed far more slowly than

that of other major horticultural crops. This stagnation is not primarily due to agronomic neglect or lack of interest, but rather to inherent biological constraints that fundamentally limit genetic variability and breeding flexibility (Mursyidin & Maulana, 2020; Susilo, 2023).

Recent studies have highlighted the potential of Garcinia mangostana in treating various other conditions, including COVID-19. Compounds from mangosteen have been identified as candidates for blocking viral protein interactions, indicating their potential in the development of antiviral strategies (Suhandi et al., 2023; Ansori et al., 2022). Additionally, its use as a natural antibiotic growth promoter in animal feed is gaining increasing attention, with implications for improving poultry welfare and reducing antibiotic resistance (Herawati et al., 2020; Rusli et al., 2024).

From a biological standpoint, mangosteen is an obligate apomictic species that reproduces clonally through seeds without fertilization. This reproductive mechanism suppresses meiotic recombination and genetic segregation, which are essential for generating new genetic combinations in sexually reproducing crops. Consequently, progeny are genetically identical or nearly identical to the maternal plant, resulting in extremely low levels of genetic variability within cultivated populations (Susilo, 2023; Mursyidin et al., 2024). Consequently, mangosteen accessions frequently exhibit high genetic uniformity, even when sampled across broad geographic regions, diverse agroecological conditions, or long-established cultivation centers. This biological uniformity presents major challenges for conventional breeding programs aimed at improving yield stability, tolerance to biotic and abiotic stresses, and resistance to pests and diseases.

Consistent with these biological characteristics, molecular studies have repeatedly reported a narrow genetic base for mangosteen. Genetic divergence among accessions is often considerably lower than expected based on morphological variation or geographic origin (Susilo, 2023; Malviya & Agrawal, 2022). Molecular studies indicate that the genetic diversity of mangosteen is very limited and does not correspond to its morphological variation, a common pattern in cultivated plants due to environmental influences and human practices, as evidenced by SSR and SRAP analyses (Lācis et al., 2022; Zafeiriou et al., 2021; Gao et al., 2020; Mansilla et al., 2021).

Limited genomic resources remain a common constraint across crops; however, unlike barley, wheat, or cotton, where genomics has enabled robust breeding and trait discovery, mangosteen still lacks sufficient genomic tools. This deficiency restricts the effective use of genetic diversity and modern biotechnological approaches in breeding programs (Riaz et al., 2021; Kushanov et al., 2021). This lack of genomic resources hampers the efficiency of breeding programs because breeders cannot leverage genetic diversity or effectively employ modern biotechnological tools. Such approaches increase the risk of redundancy in germplasm collection and reduce the overall efficiency of conservation and utilization efforts (Mursyidin & Maulana, 2020; Salgotra & Chauhan, 2023). Consequently, molecular marker systems play a crucial role in objectively characterizing genetic relationships and assessing the true extent of diversity within the mangosteen germplasm, particularly under conditions of restricted genetic variation.

Among the available molecular tools, Random Amplified Polymorphic DNA (RAPD) markers remain relevant as an exploratory approach for species with narrow genetic bases. RAPD markers have been widely applied to detect genetic uniformity and residual divergence in apomictic or clonally propagated crops, offering a practical and cost-effective means of genetic assessment when detailed genomic information is unavailable (Koffi et al., 2022; Rosmaina et al., 2022; Malviya & Agrawal, 2022). Although RAPD often reveals low levels of polymorphism in such species, even limited and reproducible variation can provide valuable insights into the genetic structure, clonal differentiation, and presence of unique or divergent accessions.

Therefore, understanding both the high genetic uniformity and existence of relatively divergent accessions is essential for developing realistic and biologically informed mangosteen improvement strategies. Identifying genetically distinct materials supports more rational parent tree selection, enables targeted conservation of unique germplasms, and facilitates breeding approaches that explicitly acknowledge the biological constraints imposed by apomixis (Mursyidin et al., 2024; Susilo, 2023). Ultimately, integrating molecular genetic information with agronomic evaluation provides a robust scientific foundation for optimizing the utilization, conservation, and long-term improvement of mangosteen as an economically and nutritionally important.

2. Materials and Methods

2.1. Plant Materials and Sampling

This study evaluated the genetic similarity between 20 mangosteen (Garcinia mangostana L.) accessions selected as candidate mother trees and two reference accessions of the commercially recognized Kali Gesing and Lotan genotypes. All mangosteen accessions were collected from the Bulukumpa District and Bulukumba Regency, South Sulawesi Province, Indonesia. The sampled trees were approximately 10–15 years old and represented mature and productive individuals that were generally considered suitable for selection as parent trees.

Young, healthy leaf tissues were collected from each accession to ensure high-quality genomic DNA. Leaf samples were handled using sterile tools to minimize cross-contamination and were immediately processed for DNA extraction. Each accession was assigned a unique code (MGS-1 to MGS-20), including the commercial accession Kali Gesing, and was consistently labeled with the same code throughout the laboratory procedures and data analysis.

2.2. Genomic DNA Extraction

Genomic DNA was extracted using a modified cetyltrimethylammonium bromide (CTAB) method following Porebski et el. (1997). Approximately 100 mg of fresh leaf tissue was ground in extraction buffer containing 2% CTAB, 100 mM Tris-HCl (pH 8.0), 1.4 M NaCl, 20 mM EDTA (pH 8.0), 2% polyvinylpyrrolidone (PVP), and 0.3% sodium bisulfite to reduce oxidation by phenolic compounds.

The homogenate was incubated at 65 °C for 15 min with gentle mixing at regular intervals, followed by purification using chloroform:isoamyl alcohol (24:1). DNA was precipitated using cold isopropanol in the presence of sodium acetate, washed with 70% ethanol, air-dried, and resuspended in Tris-ethylenediaminetetraacetic acid (TE buffer. The DNA stock solutions were stored at −20 °C until further analysis. The extracted DNA consistently showed adequate quality and concentration for PCR amplification.

2.3 RAPD Amplification and PCR Conditions

Random Amplified Polymorphic DNA (RAPD) analysis was performed using five decamer primers (OPA-01, OPA-04, OPB-01, OPB-04, and OPB-18). Polymerase chain reactions were conducted in a total reaction volume of 10 µL, containing 2 µL genomic DNA (10 ng μL^{-1}), 5 µL of 2× MyTaq HS polymerase mix, 1 µL primer (10 pmol), and nuclease-free water.

PCR amplification was performed in a thermal cycler under the following conditions: initial denaturation at 94 °C for 4 min; 45 cycles of denaturation at 94 °C for 1 min, annealing at 35 °C for 1 min, and extension at 72 °C for 2 min; and a final extension at 72 °C for 5 min. The annealing temperature followed standard RAPD conditions and was pre-optimized to ensure stable amplification profiles.

Amplification products were separated by electrophoresis on 2% agarose gels in 1× TAE buffer at 90 V for 65 min. The DNA fragments were stained with ethidium bromide and visualized under ultraviolet light using a gel documentation system. Fragment sizes were estimated using a 100 bp DNA ladder.

Table 1. List of RAPD primers used

Number	Name of Primers	Sequences
1	OPA-01	5′- CAGGCCCTTC-3′
2	OPA-04	5′-AATCGGGCTG-3′
3	OPB-01	5′-GTTTCGCTCC-3′
4	OPB-04	5′-GGACTGGAGT-3′
5	OPB-18	5′-CCACAGCAGT-3′

2.4 Reproducibility and Quality Control

To ensure reproducibility, all PCR amplifications were performed in duplicate for each primer–accession combination. Only DNA bands that appeared consistently across replicate reactions were considered reliable and were included in subsequent analyses. Each PCR run included a no-template control to monitor for potential contamination. Inconsistent, faint, or ambiguous bands were excluded from the scoring to minimize scoring bias, which is critical in RAPD-based analyses.

Reproducibility and reliability of the RAPD analysis were ensured by performing duplicate PCR amplifications for each primer–accession combination and scoring only consistently reproducible DNA bands, thereby minimizing spurious polymorphisms (Penner et al., 1993; Saunders et al., 2001). Negative controls were included in each PCR run to monitor for contamination. Given the sensitivity of RAPD to minor PCR variations, reactions were conducted under optimized conditions using a calibrated thermal cycler with uniform temperature profiles. Faint or ambiguous bands were excluded to improve the data reliability (Devos and Gale, 1992; Tingey and Del Tufo, 1993).

2.5 Band Scoring and Data Matrix Construction

Clear and reproducible DNA bands were scored manually as present (1) or absent (0) to generate a binary data matrix. Bands with identical electrophoretic mobility were considered to represent the same locus. Missing or non-amplified reactions were treated as missing data and explicitly coded as missing values in the data matrix, rather than as numerical alleles, to prevent bias during similarity calculations. Clear and reproducible DNA bands were manually scored as present (1) or absent (0) to produce a binary data matrix. Bands with identical electrophoretic mobility were considered to represent the same locus. Missing or non-amplified reactions were treated as missing data and explicitly coded as missing values in the data matrix, rather than as numerical alleles, to avoid bias during similarity calculations. Binary scoring systems derived from molecular markers effectively simplify complex genetic data for diversity analysis, as demonstrated using ISSR in pineapple and RAPD in agronomic trait studies, enabling detailed and efficient assessment of genetic variation (Harahap et al., 2021; Vanmathi et al., 2022).. Bands that migrate identically on electrophoresis gels are considered to represent the same genetic locus, allowing comparison between samples.

Explicitly treating missing or non-amplified reactions as missing data, rather than coding them as present or absent alleles, is crucial to avoid introducing bias in similarity calculations and further analysis. This approach ensures that missing bands do not artificially increase or decrease similarity coefficients between samples (Fan et al., 1995; Fekete et al., 1992). This practice has become standard in fingerprinting techniques such as arbitrarily primed PCR (AP-PCR) and other PCR-based genomic fingerprinting methods, which generate reproducible banding patterns to assess genetic relationships by calculating similarity coefficients based on the binary matrix (Fekete et al., 1992; Sosinski & Douches, 1996). Therefore, manual scoring combined with careful treatment of missing data is a robust procedure for representing PCR banding patterns in genetic studies.

2.6 Genetic Similarity and Cluster Analysis

Genetic similarity among mangosteen accessions was estimated using the Jaccard similarity coefficient, which is appropriate for dominant marker data based on presence–absence scoring. The resulting similarity matrix was analyzed using the Sequential Agglomerative Hierarchical and Nested (SAHN) clustering algorithm with the Unweighted Pair-Group Method with Arithmetic Mean (UPGMA) implemented in NTSYS-pc version 2.1.

Cluster relationships were visualized as a dendrogram illustrating the genetic relatedness among accessions and the reference genotype. Pairwise similarity values were further summarized in a genetic similarity matrix to support the interpretation of clustering patterns.

2.7 Data Presentation

Genetic relationships among accessions were presented through dendrograms derived from UPGMA clustering, representative agarose gel electrophoresis images highlighting polymorphic primers, and a genetic similarity matrix. In addition, primer performance was summarized to facilitate interpretation of RAPD marker informativeness..

3. Result

3.1 RAPD Marker Performance and Polymorphism

Amplification using five RAPD primers (OPA-01, OPA-04, OPB-01, OPB-04, and OPB-18) generated clear and reproducible banding patterns across all evaluated mangosteen accessions and reference genotypes. The number of loci detected per primer ranged from two to six. However, the level of polymorphism varied substantially among primers.

The polymorphic RAPD amplification profile (primer OPA04), which illustrates the differences in band patterns among 22 mangosteen DNA samples, is shown in Figure X, highlighting primer-specific variation in the number of loci and polymorphism.

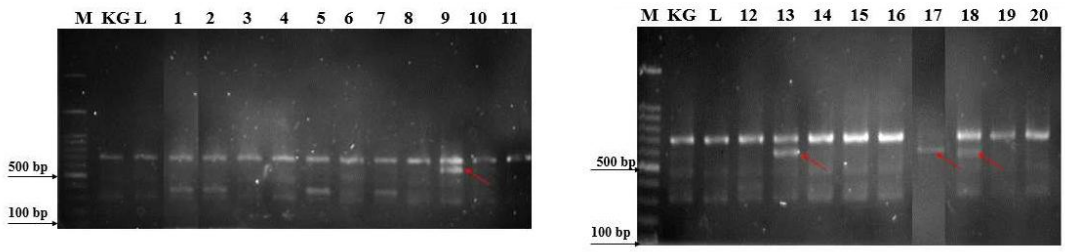

Figure 1. RAPD banding patterns produced by primer OPA-04 across 22 mangosteen DNA samples showing locus polymorphism

Figure 1 shows clear and reproducible RAPD banding patterns across all 22 mangosteen DNA samples (local accessions and reference genotypes). The OPA-04 primer produced five reproducible loci, with one locus being polymorphic (indicated by an arrow), while the other loci were monomorphic. The polymorphic band appeared in some accessions and was absent in others, indicating limited but evident genetic variation among the samples. The polymorphic band reflects allelic differences between accessions, which are essential for revealing genetic variability and supporting breeding selection, whereas monomorphic bands indicate genetic uniformity; RAPD studies on eggplants affirm the role of polymorphic loci in distinguishing cultivars (Hasan et al., 2023).

These findings confirm that OPA-04 is the most informative primer among those tested, while the other primers tend to be monomorphic—consistent with the apomictic nature of mangosteen, which limits detectable genetic variation.Four primers (OPA-01, OPB-01, OPB-04, and OPB-18) produced exclusively monomorphic banding profiles across all 22 samples, resulting in zero polymorphic loci, zero polymorphic information content (PIC), and zero expected heterozygosity (He). In contrast, primer OPA-04 produced five reproducible loci, of which one locus was polymorphic. This resulted in an overall

polymorphism rate of approximately 20%, with estimated PIC and He values of about 0.40, indicating moderate marker informativeness.

Monomorphic RAPD profiles indicate identical loci across samples, resulting in zero polymorphic loci, PIC, and He, and thus provide limited information for assessing genetic diversity despite high reproducibility. In contrast, polymorphic profiles reveal allelic variation and contribute to estimates of polymorphism rate, PIC, and expected heterozygosity. For instance, primer OPA-04 showed 20% polymorphism with moderate PIC and He (~0.40), indicating reasonable marker informativeness.

Overall, polymorphic primers are essential for meaningful genetic diversity, population structure, and breeding analyses, whereas monomorphic primers have limited utility (Elmeer et al., 2011; Wong et al., 2001; Tingey & Tufo, 1993)

A comparative summary of amplification quality, polymorphism level, and overall marker informativeness across all primers is presented in Table 3, providing an integrated evaluation of primer performance for genetic diversity analysis in mangosteen.

Meanwhile, the values for the number of alleles, the number of polymorphic loci, the PIC values, and the heterozygosity values for each primer can be seen in Table 4..

Table 4 shows that the five RAPD primers used were able to amplify 2–6 alleles per primer, indicating successful amplification and adequate DNA quality. However, the level of detected polymorphism was very low, as only primer OPA-04 produced a single polymorphic locus out of a total of five amplified loci. This is reflected in the PIC value and expected heterozygosity (He) of around 0.40, which indicates moderate informativeness. Only primer OPA-04 produced a single polymorphic locus among five amplified loci, indicating low polymorphism likely due to close genetic relatedness or primer–genome mismatch, consistent with reports that RAPD effectiveness varies with species genetic background (Kufee & Thamir, 2023; Slameto, 2023).

Conversely, primers OPA-01, OPB-01, OPB-04, and OPB-18 showed completely monomorphic banding patterns, with PIC and He values of 0.00, even though the number of detected alleles varied relatively. These findings confirm that the number of alleles does not always correlate with genetic diversity, as most loci are conserved.

The results of genetic diversity analysis of mangosteen accessions showed low diversity, in line with the apomictic reproductive system of mangosteen. Apomixis is asexual reproduction through seeds that produces clonal offspring genetically identical to the parent, resulting in minimal genetic variation among mangosteen accessions (Ramage et al., 2004; Whitton et al., 2008). A study using Randomly Amplified DNA Fingerprinting (RAF) molecular marker technique on 37 mangosteen accessions revealed that most accessions (70%) showed no genetic marker variation, and the remainder showed only a very low level of variation, supporting the existence of a single well-conserved mangosteen genotype (Ramage et al., 2004).

Table 3. Performance evaluation of RAPD primers used for genetic diversity analysis of mangosteen accessions

Primers	Amplification Quality	Polymorphics	Informativeness
OPA-01	Good–Very Good	Low–Medium	Medium
OPA-04	Good	Low	Low
OPB-01	Very Good	High	Very high
OPB-04	Good	Medium–High	high
OPB-18	Very Good	Very Low	Low

Table 4. Genetic diversity parameters (allele number, polymorphic loci, PIC, and He) revealed by RAPD primers across mangosteen accessions

Primer	**Number of alleles**	**Polymorphic loci**	**PIC**	**He**
OPA-01	3	0	0.00	0.00
OPA-04	5	1	~0.40	~0.40
OPB-01	6	0	0.00	0.00
OPB-04	5	0	0.00	0.00
OPB-18	2	0	0.00	0.00

3.2 Analysis Genetic Similarity and Cluster Analysis

Based on genetic similarity analysis using the NTSYS software, the 20 mangosteen accessions used in this analysis were separated into two clusters at a similarity coefficient of 0.95 (Figure 2). The dendrogram, constructed using the Jaccard similarity coefficient, showed that most local mangosteen accessions and two commercial genotypes (Kali Gesing and Lotan) grouped together at the maximum similarity level (J = 1.00), forming a single, highly homogeneous main cluster. This pattern indicated identical RAPD profiles among the majority of the accessions analyzed. However, four accessions (MGS_9, MGS_13, MGS_17, and MGS_18) separated to form a minor subcluster at a slightly lower similarity value (J ≈ 0.952). This separation reflects differences at a single RAPD locus, consistent with the limited polymorphism detected by the OPA-04 primer. Overall, the

dendrogram confirmed a highly homogeneous genetic structure with low yet detectable genetic variation, consistent with the apomictic reproductive system of mangosteen.

The presence of Kali Gesing and Lotan within the main cluster along with local accessions indicates a very close genetic relationship between commercial and local materials, supporting the assumption of a narrow genetic base resulting from apomictic reproduction and clonal propagation. In summary, this dendrogram confirms low genetic diversity with limited differentiation, but still provides indications of relatively distinct candidate accessions to be considered in mother tree selection and germplasm conservation. The first cluster consisted of 16 mangosteen accessions grouped together with the reference accession Kali Gesing. The second cluster contained four accessions that were separate from the other mangosteen accessions, namely MGS-9, MGS-13, MGS-17, and MGS-18.

To partially determine the level of similarity among accessions, a matrix table was created (Table 5). The genetic similarity matrix based on the Jaccard coefficient demonstrated that the 20 local mangosteen accessions and the two commercial accessions (Kali Gesing and Lotan) had a very high level of genetic similarity, with coefficient values ranging from 0.95 1.00. The majority of accession pairs, including comparisons between local and commercial accessions, displayed maximum similarity values (J = 1.00), indicating identical RAPD band profiles with no detectable locus differences.

Nevertheless, several accessions, particularly MGS_9, MGS_13, MGS_17, and MGS_18, showed slightly lower similarity values (J ≈ 0.95) than the other accessions. This value reflects a difference at one RAPD locus, which is consistent with the finding that only one primer produced a polymorphic locus. Although this difference was relatively minor, its presence indicated limited but detectable genetic variation among the analyzed mangosteen accessions.

The overall high genetic similarity values confirmed that the genetic base of the mangosteen population in this study was relatively narrow, both in local and commercial accessions. This pattern aligns with the apomictic reproductive system and the long-term practice of clonal propagation in mangosteen, which tends to maintain genetic uniformity among plants. Thus, this similarity matrix confirms the results of the PIC/He and UPGMA dendrogram analyses, while also highlighting a small group of accessions that are relatively more distinct and potentially valuable for parent tree selection and germplasm conservation.

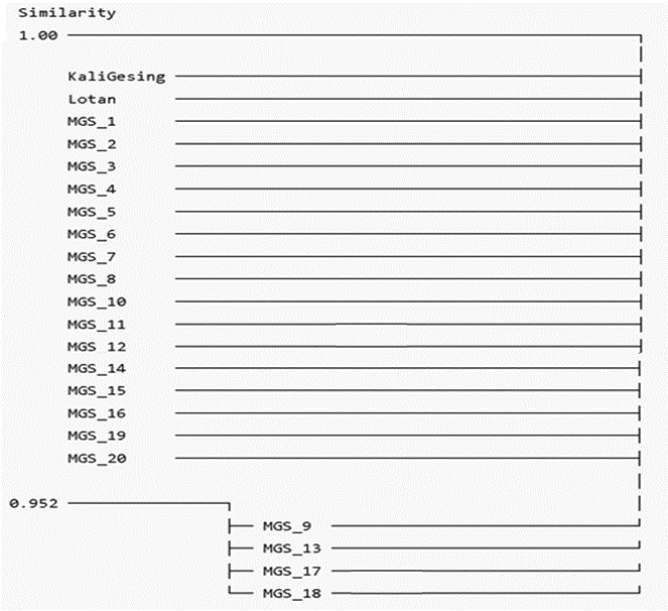

Figure 2. Dendrogram showing the genetic similarity relationships among the mangosteen accessions used in this analysis

4. Discussion

4.1 Reliability of RAPD Data and Methodological Robustness

The reliability of RAPD-based genetic analysis depends strongly on DNA quality, PCR reproducibility, and rigorous band scoring. In this study, the use of a modified CTAB protocol produced high-quality genomic DNA, as reflected by clear and reproducible amplification patterns without smearing. Duplicate PCR amplifications and exclusion of non-reproducible bands ensured analytical robustness, aligning with the current recommendations for dominant marker systems in plant genetic diversity studies (Kumar et al., 2021; Salgotra & Chauhan, 2023). The quality of DNA extraction is crucial in RAPD studies because secondary metabolites can inhibit amplification. CTAB-based protocols have been proven to yield pure DNA with clear and reproducible banding patterns, supporting reliable genetic diversity analysis (Rahmadara et al., 2022). The inclusion of negative

controls further confirmed that the observed banding patterns represent genuine genetic variation rather than technical artifacts.

The inclusion of negative controls in every PCR run ensured that the observed RAPD banding patterns were not influenced by contamination or nonspecific amplification. This procedural safeguard strengthens the reproducibility and reliability of RAPD data, which is particularly critical for dominant markers and has been consistently recommended in recent molecular diversity studies as a standard quality-control measure (Kumar et al., 2021; Salgotra & Chauhan, 2023).

4.2 Performance of RAPD Primers and Marker Informativeness

Primer-specific performance differences were evident, with four primers producing monomorphic profiles and only OPA-04 revealing polymorphisms. Such variability among RAPD primers has been widely reported, particularly in crops with narrow genetic bases, where only a subset of primers can detect informative loci (Rani et al., 2023; Su et al., 2025). Primer-specific performance differences were evident, with four primers yielding monomorphic profiles and only OPA-04 detecting polymorphisms. Such variability among RAPD primers is common in crops with narrow genetic bases, where only a limited subset of primers captures informative loci, reflecting the underlying genomic uniformity rather than methodological bias (Rani et al., 2023; Salgotra & Chauhan, 2023). The predominance of monomorphic bands across the four primers indicates high genetic homogeneity and limited allelic variation. Similar challenges in detecting RAPD polymorphisms have been reported in genetically narrow crops such as soybean and Lactuca indica, where only a few primers revealed informative loci (Nkongolo et al., 2020; Pham et al., 2022).This apomixis-driven primer behavior is directly reflected in the low overall PIC and expected heterozygosity values, as well as the highly compressed UPGMA clustering, where most accessions grouped at very high similarity levels, indicating a narrow genetic base with limited but detectable residual variation.

The moderate PIC and He values (~0.40) observed for OPA-04 indicated sufficient discriminatory power for preliminary diversity assessment, supporting the continued relevance of RAPD as a screening tool under resource-limited conditions (Salgotra & Chauhan, 2023). The moderately high PIC value (~0.40) for the OPA-04 primer indicates adequate discriminatory ability for the rapid assessment of genetic variation, especially in crops with low diversity, as reported in Eruca sativa cultivars (Kufee & Thamir, 2023).

The moderate PIC and expected heterozygosity values (~0.40) observed for primer OPA-04 indicated sufficient discriminatory power for preliminary genetic diversity assessment. Such marker performance supports the continued relevance of RAPD as a cost-effective screening tool in species with limited genomic resources, particularly for baseline germplasm characterization and early stage selection under resource-constrained conditions (Rani et al., 2023; Salgotra & Chauhan, 2023).

Table 5. Genetic similarity matrix of 20 mangosteen accessions and two commercial accessions

Aksesi	Kali Gesing	Lotan	MGS 1	MGS 2	MGS 3	MGS 4	MGS 5	MGS 6	MGS 7	MGS 8	MGS 9	MGS 10	MGS 11	MGS 12	MGS 13	MGS 14	MGS 15	MGS 16	MGS 17	MGS 18	MGS 19	MGS 20
Kali_Gesing	1.00																					
Lotan	1.00	1.00																				
MGS_1	1.00	1.00	1.00																			
MGS_2	1.00	1.00	1.00	1.00																		
MGS_3	1.00	1.00	1.00	1.00	1.00																	
MGS_4	1.00	1.00	1.00	1.00	1.00	1.00																
MGS_5	1.00	1.00	1.00	1.00	1.00	1.00	1.00															
MGS_6	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00														
MGS_7	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00													
MGS_8	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00												
MGS_9	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	1.00											
MGS_10	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00										
MGS_11	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00									
MGS_12	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00								
MGS_13	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	1.00	0.95	0.95	0.95	1.00							
MGS_14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.95	1.00						
MGS_15	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.95	1.00	1.00					
MGS_16	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.95	1.00	1.00	1.00				
MGS_17	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	1.00	0.95	0.95	0.95	1.00	0.95	0.95	0.95	1.00			
MGS_18	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	1.00	0.95	0.95	0.95	1.00	0.95	0.95	0.95	1.00	1.00		
MGS_19	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.95	0.95	1.00	
MGS_20	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.95	0.95	1.00	1.00

4.3 Reliability of RAPD Data and Methodological Robustness

The reliability of RAPD-based genetic analysis depends strongly on DNA quality, PCR reproducibility, and rigorous band scoring. In this study, the use of a modified CTAB protocol produced high-quality genomic DNA, as reflected by clear and reproducible amplification patterns without smearing. Duplicate PCR amplifications and exclusion of non-reproducible bands ensured analytical robustness, aligning with the current recommendations for dominant marker systems in plant genetic diversity studies (Kumar et al., 2021; Salgotra & Chauhan, 2023). The quality of DNA extraction is crucial in RAPD studies because secondary metabolites can inhibit amplification. CTAB-based protocols have been proven to yield pure DNA with clear and reproducible

banding patterns, supporting reliable genetic diversity analysis (Rahmadara et al., 2022). The inclusion of negative controls further confirmed that the observed banding patterns represent genuine genetic variation rather than technical artifacts.

The inclusion of negative controls in every PCR run ensured that the observed RAPD banding patterns were not influenced by contamination or nonspecific amplification. This procedural safeguard strengthens the reproducibility and reliability of RAPD data, which is particularly critical for dominant markers and has been consistently recommended in recent molecular diversity studies as a standard quality-control measure (Kumar et al., 2021; Salgotra & Chauhan, 2023).

4.4 Performance of RAPD Primers and Marker Informativeness

Primer-specific performance differences were evident, with four primers producing monomorphic profiles and only OPA-04 revealing polymorphisms. Such variability among RAPD primers has been widely reported, particularly in crops with narrow genetic bases, where only a subset of primers can detect informative loci (Rani et al., 2023; Su et al., 2025). Primer-specific performance differences were evident, with four primers yielding monomorphic profiles and only OPA-04 detecting polymorphisms. Such variability among RAPD primers is common in crops with narrow genetic bases, where only a limited subset of primers captures informative loci, reflecting the underlying genomic uniformity rather than methodological bias (Rani et al., 2023; Salgotra & Chauhan, 2023). The predominance of monomorphic bands across the four primers indicates high genetic homogeneity and limited allelic variation. Similar challenges in detecting RAPD polymorphisms have been reported in genetically narrow crops such as soybean and Lactuca indica, where only a few primers revealed informative loci (Nkongolo et al., 2020; Pham et al., 2022).This apomixis-driven primer behavior is directly reflected in the low overall PIC and expected heterozygosity values, as well as the highly compressed UPGMA clustering, where most accessions grouped at very high similarity levels, indicating a narrow genetic base with limited but detectable residual variation.

The moderate PIC and He values (~0.40) observed for OPA-04 indicated sufficient discriminatory power for preliminary diversity assessment, supporting the continued relevance of RAPD as a screening tool under resource-limited conditions (Salgotra & Chauhan, 2023). The moderately high PIC value (~0.40) for the OPA-04 primer indicates adequate discriminatory ability for the rapid assessment of genetic variation, especially in crops with low diversity, as reported in Eruca sativa cultivars (Kufee & Thamir, 2023).

The moderate PIC and expected heterozygosity values (~0.40) observed for primer OPA-04 indicated sufficient discriminatory power for preliminary genetic diversity assessment. Such marker performance supports the continued relevance of RAPD as a cost-effective screening tool in species with limited genomic resources, particularly for baseline germplasm characterization and early stage selection under resource-constrained conditions (Rani et al., 2023; Salgotra & Chauhan, 2023).

4.5 Genetic Uniformity and the Role of Apomictic Reproduction

The predominance of monomorphic loci and high similarity coefficients (0.95–1.00) are consistent with the obligate apomictic reproductive system of mangosteen. Apomixis restricts meiotic recombination, leading to genetically uniform progeny over successive generations. Recent studies on apomictic and clonally propagated fruit crops have similarly reported low detectable molecular variation despite their broad geographic distribution (Mansyah et al., 2021; Suksathan et al., 2022). Recent studies on apomictic and clonally propagated fruit crops have reported low detectable molecular variation despite broad geographic distribution. High genetic similarity has been observed between micropropagated plants and vegetatively propagated garlic, reflecting reproductive strategies that maintain genetic fidelity across regions (Alwahibi et al., 2022; So et al., 2021). Thus, the genetic uniformity observed in this study reflects inherent biological constraints rather than methodological limitations.

Thus, the genetic uniformity observed in this study reflects inherent biological constraints rather than methodological limitations. In apomictic species such as mangosteen, genetic recombination is bypassed, producing clonal offspring with minimal variation. Even across broad environments, recent research on clonally propagated fruits, such as Garcinia species, confirms that detectable diversity is naturally limited (Mansyah et al., 2021; Suksathan et al., 2022). Consequently, low polymorphism or monomorphic markers do not imply flaws in RAPD or sampling but are an accurate depiction of the genetic architecture, highlighting the need for complementary approaches to explore deeper variation (Salgotra & Chauhan, 2023).

4.6 Residual Genetic Variation and Its Biological Significance

Although the overall diversity was low, several accessions showed slightly reduced similarity values, indicating residual genetic variation. Such limited divergence in apomictic species is often attributed to somatic mutations, epigenetic changes, or rare historical recombination events (Kumar et al., 2021; Salgotra & Chauhan, 2023). Even minimal variation can be biologically meaningful, as it represents the remaining genetic reservoir available for conservation and selective utilization in long-lived perennial crops.

Even minimal genetic variation can be biologically meaningful, particularly in long-lived perennial crops such as mangosteen. This residual diversity represents the remaining genetic reservoir that can support adaptation to environmental changes, disease pressure, and long-term sustainability. Recent studies have emphasized that small but consistent molecular differences in clonally propagated or apomictic crops may originate from somatic mutations or rare recombination events, and can be strategically valuable for conservation prioritization and selective utilization. Therefore, preserving and characterizing such

limited variation is critical to avoid genetic erosion and enable informed parent selection and germplasm management in perennial fruit crops (Galeano et al., 2021; Salgotra & Chauhan, 2023; Su et al., 2025). The characterization of genetic variation is essential for informed parent selection and effective germplasm management. Preserving diverse cultivated and wild genetic stocks enhances breeding efficiency, mitigates genetic erosion, and supports the improvement of key agronomic traits in crops with limited diversity (Gangtire et al., 2021; El-Abeid et al., 2023; Susilo, 2023).

4.7 Interpretation of Jaccard Similarity Matrix and UPGMA Clustering

The Jaccard similarity matrix and UPGMA dendrogram revealed a single major cluster with a small sub-cluster at slightly lower similarity values, confirming a highly homogeneous genetic structure. Jaccard's coefficient is particularly suitable for RAPD data because it ignores shared absences and emphasizes the presence of informative bands (Kumar et al., 2021). Similar clustering patterns have been reported in other tropical fruit species characterized by clonal propagation and restricted genetic bases (Rani et al., 2023).

The overall structure depicted by the dendrogram demonstrates pronounced genetic homogeneity within the analyzed mangosteen population. This similarity may have serious implications for conservation strategies and crop improvement programs. Although a monomorphic genetic landscape may facilitate the achievement of certain breeding objectives, it also poses risks concerning species resistance to diseases and environmental fluctuations. As shown in various studies on other crops, genetic uniformity can lead to vulnerability, thereby underscoring the importance of maintaining genetic diversity for crop sustainability (Helen & Bency, 2023; SINGH et al., 2021; Islam et al., 2020).

Similar clustering patterns have been reported in several tropical fruit species, characterized by clonal propagation and narrow genetic bases. Recent molecular studies on clonally propagated fruits, such as banana, date palm, and apomictic Garcinia species, have consistently revealed highly compact dendrograms with limited sub-structuring, reflecting strong genetic uniformity across accessions. These patterns are commonly attributed to long-term vegetative propagation, restricted recombination, and founder effects, which collectively reduce detectable molecular variation despite the wide geographic distribution. Such findings reinforce that tight clustering in similarity-based analyses is a biologically expected outcome in clonally maintained perennial fruit crops, rather than an artifact of marker choice or sampling strategy (Mansyah et al., 2021; Suksathan et al., 2022; Salgotra & Chauhan, 2023).

Consequently, mangosteen improvement programs should prioritize the identification, conservation, and strategic use of the few genetically distinct accessions detected, rather than relying on conventional recombination-based breeding approaches, which are inherently constrained by apomictic reproduction.

4.8 Implications for Parent Tree Selection and Germplasm Management

From a breeding and conservation perspective, high genetic similarity among accessions indicates potential redundancy in planting materials, whereas accessions in minor subclusters may warrant priority for conservation. Molecular identification of such accessions supports more objective parent tree selection and reduces reliance on phenotypic assessment alone (Mansyah et al., 2021; Salgotra & Chauhan, 2023). This molecular approach helps mitigate the risks associated with relying solely on phenotypic traits, which may not accurately reflect genetic variation, particularly in apomictic species such as mangosteen. As demonstrated in the characterization of various fruit crops, reliance on molecular assessments has enabled more precise selection of parent trees that can lead to successful hybridization and improved cultivars (Moura et al., 2020). Integrating molecular data with agronomic traits is increasingly recommended to optimize germplasm utilization strategies.

Integrating molecular data with agronomic traits is a crucial strategy for optimizing germplasm utilization for crop improvement. Molecular markers, such as SSRs and SNPs, provide objective insights into genetic diversity and complement phenotypic evaluations, enabling the development of representative core collections that capture both genetic and agronomic variation, as demonstrated in soybean germplasm studies (Wang et al., 2006; Bunjkar et al., 2024). This integration facilitates the identification of quantitative trait loci (QTLs) and SNPs associated with key agronomic traits, including yield components, stress tolerance, and phenology, particularly through genome-wide association studies (GWAS) (Han et al., 2024). Furthermore, combining molecular and phenotypic data using multivariate statistics, population structure analysis, and bioinformatics tools improves parent selection and genetic gain (Bunjkar et al., 2024; Mohammadi & Prasanna, 2003). Advances in high-throughput genotyping, phenotyping, and artificial intelligence further strengthen genotype–phenotype associations, supporting precision breeding strategies, such as genomic selection and genome editing, for sustainable crop improvement (Dwivedi et al., 2017; Nguyen & Norton, 2020; Khan et al., 2022).

Integrating molecular marker data with agronomic and phenotypic traits is increasingly recommended to optimize germplasm utilization strategies in crop improvement programs. Molecular information provides an objective assessment of genetic relationships and redundancy, whereas agronomic traits capture adaptive performance and economic value in specific environments. Recent studies have emphasized that combining these datasets enables more accurate parent selection, reduces bias in germplasm evaluation, and enhances the efficiency of conservation and breeding decisions, particularly in crops with narrow genetic bases or clonal reproduction systems. Such integrative approaches support evidence-based management of

plant genetic resources and facilitate the identification of elite yet genetically distinct materials for sustainable crop improvement (Galeano et al., 2021; Salgotra & Chauhan, 2023; Su et al., 2025).

4.9 Study Limitations and Future Research Directions

The dominant nature of RAPD markers and the limited number of polymorphic loci constrain the resolution of fine-scale genetic structures. Recent advances in SSR- and SNP-based approaches have demonstrated higher sensitivity in detecting subtle variations in clonally propagated crops (Kumar et al., 2021; Su et al., 2025). Future studies incorporating higher-resolution markers, broader sampling, and multi-locus analyses would provide deeper insights into mangosteen genetic diversity.

Future studies incorporating higher-resolution molecular markers, broader geographic sampling, and multi-locus analyses are essential to gain deeper insights into mangosteen genetic diversity. Marker systems, such as SSRs and SNPs, offer greater allelic resolution and codominant inheritance, enabling finer discrimination among closely related genotypes than RAPD. Expanding sampling across regions and production systems would further capture rare or localized variants that may be overlooked in limited datasets. Recent advances have demonstrated that integrative multi-locus and genome-informed approaches substantially improve the detection of subtle genetic structures in clonally propagated and apomictic crops, thereby strengthening inferences for conservation, parent selection, and long-term breeding strategies (Salgotra & Chauhan, 2023; Su et al., 2025). Understanding genetic diversity using advanced molecular approaches is essential for effective conservation and mitigation of genetic erosion in perennial crops. Integrating such techniques enables the accurate identification and preservation of diverse genetic resources, supporting sustainable conservation and future breeding programs (Dementieva et al., 2022).

Taken together, these results indicate that the limited polymorphism detected is a true biological feature of mangosteen shaped by apomictic reproduction, whereas the small but consistent genetic divergence observed among a few accessions remains biologically and practically relevant.

Integrating molecular data with agronomic traits is a crucial strategy for optimizing germplasm utilization for crop improvement. Molecular markers, such as SSRs and SNPs, provide objective insights into genetic diversity and complement phenotypic evaluations, enabling more representative core collections that capture both genetic and agronomic variation, as demonstrated in soybean germplasm studies (Wang et al., 2006; Bunjkar et al., 2024). This integration facilitates the identification of quantitative trait loci (QTLs) and SNPs associated with key traits, including yield components, stress tolerance, and flowering time, particularly through genome-wide association studies (GWAS) (Han et al., 2024). Furthermore, combining molecular and phenotypic data using multivariate statistics, population structure analysis, and bioinformatics tools enhances parent selection and genetic gain (Bunjkar et al., 2024; Mohammadi & Prasanna, 2003). Advances in high-throughput genotyping, phenotyping, and artificial intelligence have further strengthened genotype–phenotype associations, supporting precision breeding approaches, such as genomic selection and genome editing, for sustainable and climate-resilient crop improvement (Dwivedi et al., 2017; Nguyen & Norton, 2020; Khan et al., 2022).

5. Conclusion

Mangosteen (Garcinia mangostana L.) exhibits a highly homogeneous genetic structure, as indicated by its predominantly monomorphic RAPD profiles, high Jaccard similarity coefficients, and compact UPGMA clustering across local accessions and commercial genotypes. This uniformity is consistent with obligate apomictic reproduction and long-term clonal propagation. Nevertheless, limited but reproducible genetic variation was detected using a single informative RAPD primer, yielding moderate PIC and expected heterozygosity values. Although minimal, this residual variation is biologically meaningful and represents a valuable genetic reservoir for germplasm conservation and informed parent tree selection. Practically, improvement programs should prioritize conserving and strategically utilizing the few genetically distinct accessions identified, rather than relying on recombination-based breeding approaches. Overall, RAPD markers provide a reliable baseline.

Declaration of generative AI in scientific writin

During the preparation of this work, the authors used ChatGPT to enhance the clarity of the writing. After using ChatGPT, the authors reviewed and edited the content as needed and take full responsibility for the publication's content.

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