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GENETIC DIVERSITY OF *ANACARDIUM OCCIDENTALE* L. FROM SULAWESI ISLAND, INDONESIA, BASED ON ISSR AND MORPHOLOGICAL TRAITS

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SUMMARY

Cashew (*Anacardium occidentale* L.) is a tropical plant that originated in South America and later spread to Africa and Asia, including Indonesia. Sulawesi Island in Indonesia is one of the primary production centers of cashew nuts. The insufficient superior planting material is one of the major hindrances in developing cashew nut production in Indonesia. Therefore, the presented research aimed to explore and identify the diversity and kinship of cashew nuts on Sulawesi Island, Indonesia. For cashew characterization and identification, the morphological traits and molecular analysis employed the inter-simple sequence repeat (ISSR) method. Data analysis on morphological traits phenetically also used the unweighted pair group method (UPGMA) in the multivariate statistical package (MVSP) programs. Polymorphic allele data obtained from ISSRs incurred assessment using the principal coordinate analysis (PCoA) with the GenAlEx ver. 6.5 program. The results revealed genetic diversity among cashew populations, and some populations exhibited higher heterozygosity and diversity indices. The clustering pattern disclosed the considerable relationship between specific populations, while others appear isolated, demonstrating genetic divergence resulting from geographical isolation and environmental adaptation. This discovery underscores the importance of conserving populations with high genetic diversity as a potential resource for future breeding.

Keywords: Cashew (*A. occidentale* L.), genetic diversity, morphology, molecular analysis, ISSR

Key findings: The results provided a clear understanding of the genetic diversity of cashew (*A. occidentale* L.) genotypes in Indonesia and provide a scientific basis for future conservation policies and the development of superior cashew cultivars.

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INTRODUCTION

Cashew (*Anacardium occidentale* L.) is a tropical perennial species belonging to the family Anacardiaceae and is native to South America (Savadi *et al.,* 2020). It gained greater importance through wide utilization and economic values worldwide (Aluko *et al.,* 2023; De-Vasconcelos *et al.,* 2024). In Indonesia, cashew cultivation has concentrated in the eastern regions, particularly in Sulawesi Island, where it holds considerable potential to support both local and national demands and economic development. However, increased cashew productivity mainly depends upon the availability of superior planting material generated through systematic breeding programs. The success in such breeding programs and conservation efforts, however, crucially relies on the comprehensive understanding of the species' genetic diversity (Singh and Behera, 2022; Ozbek, 2024).

Previous studies have reported substantial morphological variations among cashew populations in several districts of Southeast Sulawesi, including South Konawe, Konawe, and West Kolaka, Indonesia (Boer *et al.,* 2021; Nawir *et al.,* 2022). These morphological variations were evident in both generative traits (inflorescence length and fruit thickness) and vegetative traits (leaf size, branch development, petiole angle, leaf shape, leaf apex, branching pattern, and leaf aroma). However, morphological traits individually do not always reflect the true genetic diversity because such types of traits receive considerable influences from environmental factors (Yuan *et al.,* 2025).

Overcoming these limitations has widely employed molecular markers to assess the genetic diversity in crop plants. Among markers, microsatellite-based markers, such as inter-simple sequence repeats (ISSRs), have proven effective in detecting and authenticating genetic variations in cashew, enabling apparent differentiation among the genotypes based on their genetic profiles (Carneiro *et al.,* 2019). Moreover, ISSR-based studies revealed genetic clustering of cashew accessions does not always correlate with their geographical origins (Borges *et al.,* 2018).

Despite these advances, no previous comprehensive study has integrated both morphological and molecular approaches to evaluate the genetic diversity of cashew in Sulawesi, Indonesia. Most molecular investigations to date have focused on populations from Brazil, India, and Africa, while Indonesian populations remain understudied. This gap underscores the need for future research through an integrative approach of morphological and molecular studies in this region. Therefore, the subsequent study, based on morphological characterization and ISSR-marker analysis, aimed to assess the genetic diversity of cashew populations in Sulawesi, Indonesia. Such a type of approach sought to provide a more profound understanding of cashew's genetic structure in Indonesia, ultimately supporting conservation strategies, breeding programs, and the development of locally adapted superior cultivars.

MATERIALS AND METHODS

Plant material

The collection of cashew (*A. occidentale* L.) accessions totaled 36 from different provinces across Sulawesi Island, Indonesia (Figure 1). The sampling sites included Southeast Sulawesi (Konawe/Wawonii Island: 5 samples, West Muna: 3 samples, and Central Buton: 4 samples), South Sulawesi (Selayar Island: 4 samples and Bulukumba: 3 samples), West Sulawesi (Polewali: 4 samples and Majene: 4 samples), Central Sulawesi (Morowali: 3 samples), and Gorontalo (Pohuwatu: 6 samples). Morphological characterization of cashew accessions, including various generative and vegetative traits (stem, leaf, flower, fruit, and seed traits), proceeded following the descriptors of the International Board for Plant Genetic Resources (IBPGR, 1986), with modifications made by Boer *et al*. (2021).

DNA extraction

Genomic DNA extraction continued from young frozen leaves of 36 cashew accessions using

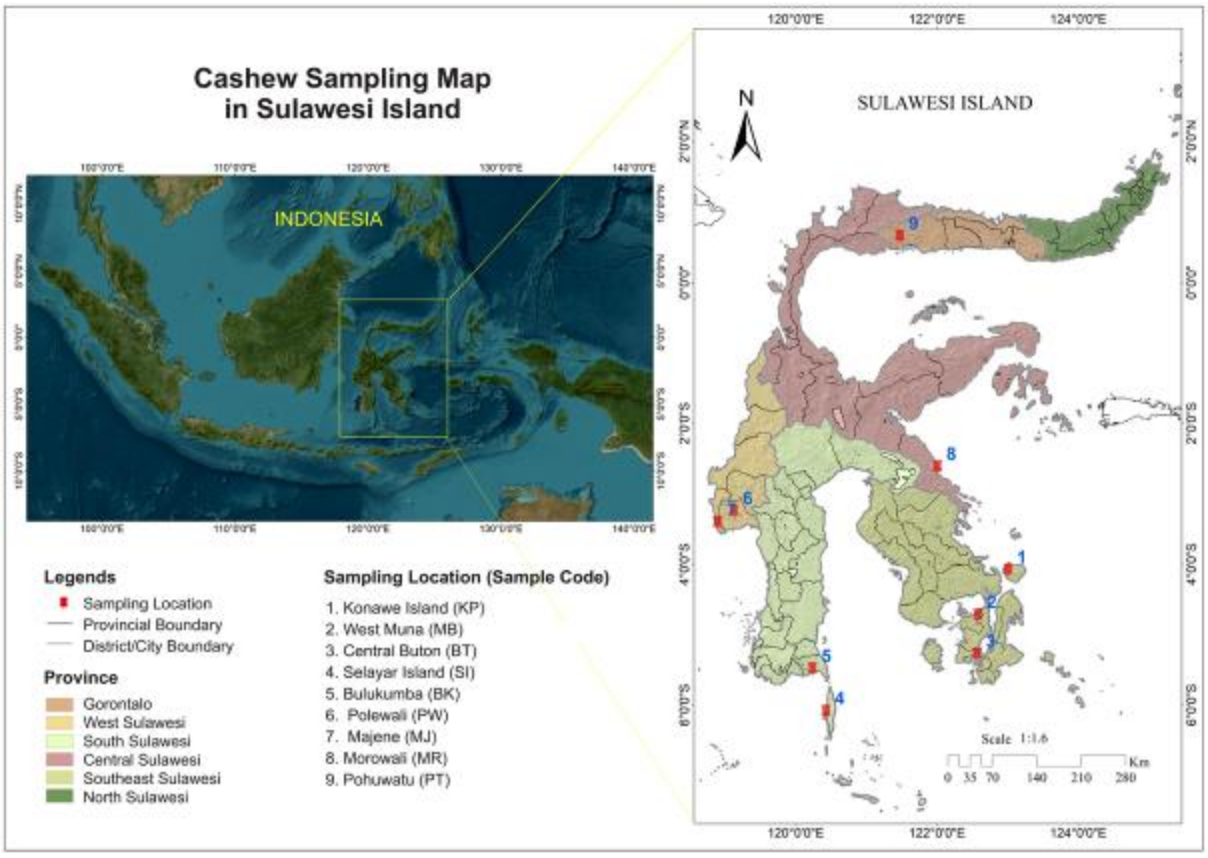

Figure 1. Geographic distribution of cashew samples in Sulawesi Island.

the Genomic DNA Mini Kit Plant (Geneaid, Taiwan). The study used approximately 100 mg of leaf tissue for each extraction. The DNA concentration and purity underwent assessment with a NanoDrop Lite Plus spectrophotometer (Thermo Fisher Scientific, USA), with the samples having an A260/A280 ratio between 1.8 and 2.0 considered for downstream analyses.

ISSR analysis

Polymerase chain reaction (PCR) amplification commenced using MyTaq HS RedMix (Bioline, USA) in a final reaction volume of 20 µL containing 10 µL of MyTaq HS RedMix, 2 µL of primer, 2 µL of genomic DNA template (50 ng/µL), and 6 µL of nuclease-free water. The PCR amplifications progressed in a T100 Thermal Cycler (Bio-Rad, USA) with the following conditions: an initial denaturation at 95 °C for 3 min; 40 cycles of denaturation at 95 °C for 45 s; annealing at 45 °C–50 °C for 30 s and extension at 72 °C for 1 min; followed by a final extension at 72 °C for 5 min. ISSR primers employed in this study totaled 14 (Table 1).

Agarose gel electrophoresis

Amplified PCR products were successful in separating by horizontal electrophoresis on 2% agarose gels (1st BASE, Singapore) prepared with FloroSafe DNA intercalating dye (1st BASE, Singapore). Electrophoresis ensued in 2% TBE buffer at 50 V for 60 min. A 100 bp DNA ladder (Geneaid, Taiwan) served as a molecular size standard. Gels entailed visualization under UV light, and documentation used a GelDoc-UV transilluminator system.

Table 1. Polymorphism statistics from 14 ISSR primers used in this study.

No.	ISSR Primer	Motifs	Primer length (bp)	Annealing Temperature (°C)	NB	PB	PR (%)	PIC	RP
1	UBC 807	$(AG)_8T$	17	50.3	6	1	16.67	0.04	0.17
2	UBC 808	$(AG)_8C$	17	51.3	11	5	45.45	0.10	4.78
3	UBC 825	$(AC)_8A$	17	48	7	0	0.00	0	0.00
4	UBC 826	$(ACA)_5$ CC	17	51	6	4	66.67	0.20	5.67
5	UBC 834	$(AG)_8YT$	18	51	10	1	10.00	0.05	1.05
6	UBC 840	$(GA)_8YT$	18	49.4	3	0	0.00	0	6.57
7	UBC 841	$(GA)_8TC$	18	51	9	5	55.56	0.12	5.05
8	UBC 842	$(GA)_8YG$	18	48.8	5	1	20.00	0.11	0.06
9	UBC 847	$(CA)_8RC$	18	55	6	4	66.67	0.18	6.33
10	UBC 855	$(ACA)_5$ CYT	18	53	6	2	33.33	0.09	0.83
11	UBC 856	$(ACA)_5$ CYA	18	52.8	8	6	75.00	0.27	4.28
12	UBC 857	$(ACA)_5CYG$	18	51	9	6	66.67	0.18	5.72
13	UBC 864	$(ATG)_5$	15	49	8	3	37.50	0.13	1.5
14	UBC 873	$(GACA)_4$	16	49	10	7	70.00	0.12	1.67
Total					104	45			
Means					7.43	3.21	40.25	0.11	3.12

Notes: NB = Number of scored bands; PB = Number of polymorphic bands; PR = polymorphic rate; PIC = polymorphic information content; RP = resolving power

Data analysis

Morphological trait scores and binary scoring of ISSR banding patterns underwent multivariate statistical analyses. Cluster analysis also engaged the multivariate statistical package (MVSP) software based on the unweighted pair group method with arithmetic mean (UPGMA) and Jaccard's coefficient. The principal coordinate analysis (PCoA) had the study use GenAlEx version 6.5 for the molecular data.

RESULTS AND DISCUSSION

Morphological diversity of cashew accessions

This study successfully revealed substantial morphological variation among 36 cashew (*Anacardium occidentale L.*) accessions collected from nine sampling stations on Sulawesi Island. Observations of 55 morphological characters, encompassing both vegetative and generative organs, indicate the cashew population in Sulawesi possesses phenotypic diversity beneficial as a source of germplasm for plant breeding programs. This finding aligns with the view of Pessoni (2007), who stated the highest genetic diversity in cashew occurs within populations, while variation among populations tends to be lower.

The observed morphological variation among cashew accessions in Sulawesi reflects the phenotypic plasticity of this species in response to diverse environmental conditions. Quantitative traits, such as the pseudofruit, nut, and inflorescence dimensions, exhibit a relatively extensive variation between accessions. Reports of similar results from Ramteke *et al*. (2020), who found quantitative traits in cashew, particularly nut weight and size, contribute significantly to genotype differentiation. Likewise, Matos-Filho *et al*. (2023) confirmed quantitative morphological traits, such as leaf length and width and pseudofruit weight, are reliable descriptors for cashew accession identification.

Cluster analysis using the UPGMA method based on 55 morphological characters grouped the 36 accessions into two main clusters, with a similarity coefficient ranging from 0.72 to 0.88 (72%–88%) (Figure 2). The similarity values indicate the morphological relationships among the Sulawesi cashew accessions are relatively close. This finding contrasts with that of Chipojola *et al*. (2009) in Malawi, who reported a lower similarity index

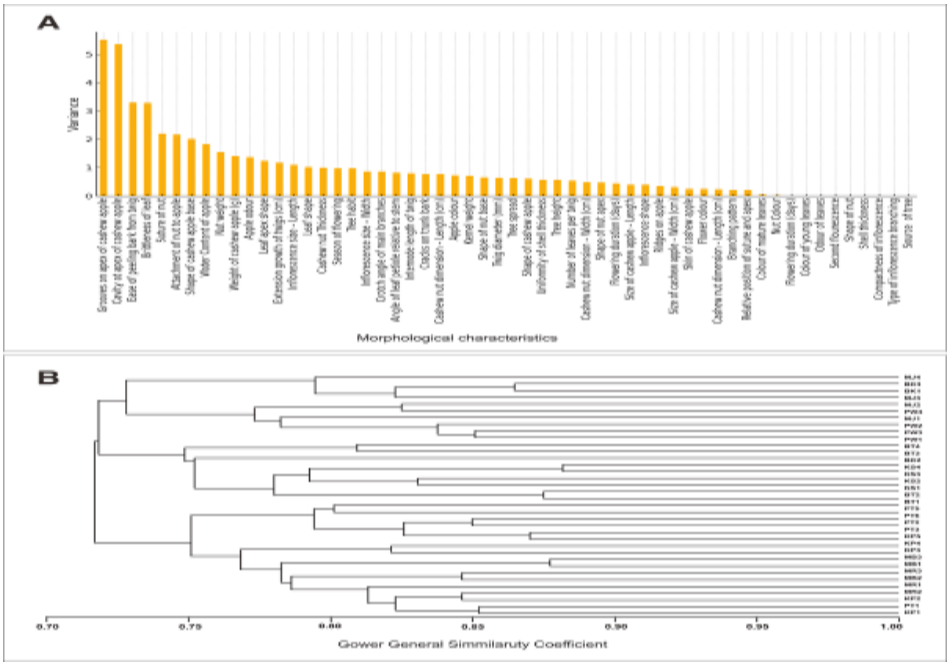

Figure 2. Variance (A) and UPGMA dendrogram (B) of cashew accessions from Sulawesi Island based on morphological characteristics.

of 35%–66%, and Aliyu and Awopetu (2007) in Nigeria, with a similarity range of 22%–100%. These differences suggest that geographical conditions and the history of plant introduction influence the genetic diversity of cashew in a given region. The high morphological homogeneity reflects the significant influence of domestication, local breeding practices, and consistent cultivation methods maintained over generations (Gepts, 2014; Martínez-Ainsworth and Tenaillon, 2016). In Sulawesi, Indonesia, the farmers often select cashew seedlings based on advantageous morphological traits, a practice that reduces the genetic variation while increasing morphological uniformity.

The clustering of accessions based on morphological characters showed a tendency for grouping by geographical origin, although this was not entirely consistent. Group I showed a predominant composition of accessions from Central Buton (BT) and Selayar Islands (KS), Polewali (PW), Bulukumba (BK), and Majene (MJ), while group II consisted of accessions from various locations, including the Konawe Islands (KP), West Muna (MB), Morowali (MR), and Pohuwatu (PT). This phenomenon can be because of the concept of geographical isolation proposed by Douaihy *et al*. (2012), which posits that geographically isolated populations tend to develop distinct morphological characteristics in response to local environmental selection pressures.

Molecular diversity of cashew accessions

Fourteen ISSR primers generated 104 scorable DNA fragments, in which 45 were polymorphic, with an average of 3.21 polymorphic fragments per primer (Table 1). The number of polymorphic bands per primer ranged from 1 to 7. Notably, the primers UBC 825 and UBC 840 yielded no polymorphic bands (0% polymorphism), whereas the primer UBC 856 produced the highest polymorphism information content (PIC = 0.27) and resolving power (RP = 4.28). Across all studied primers, the mean RP and PIC values were 3.12 and 0.11, respectively, confirming the informativeness of ISSR markers for assessing genetic variation in cashew (*A. occidentale*). These results also emphasize ISSR efficiency

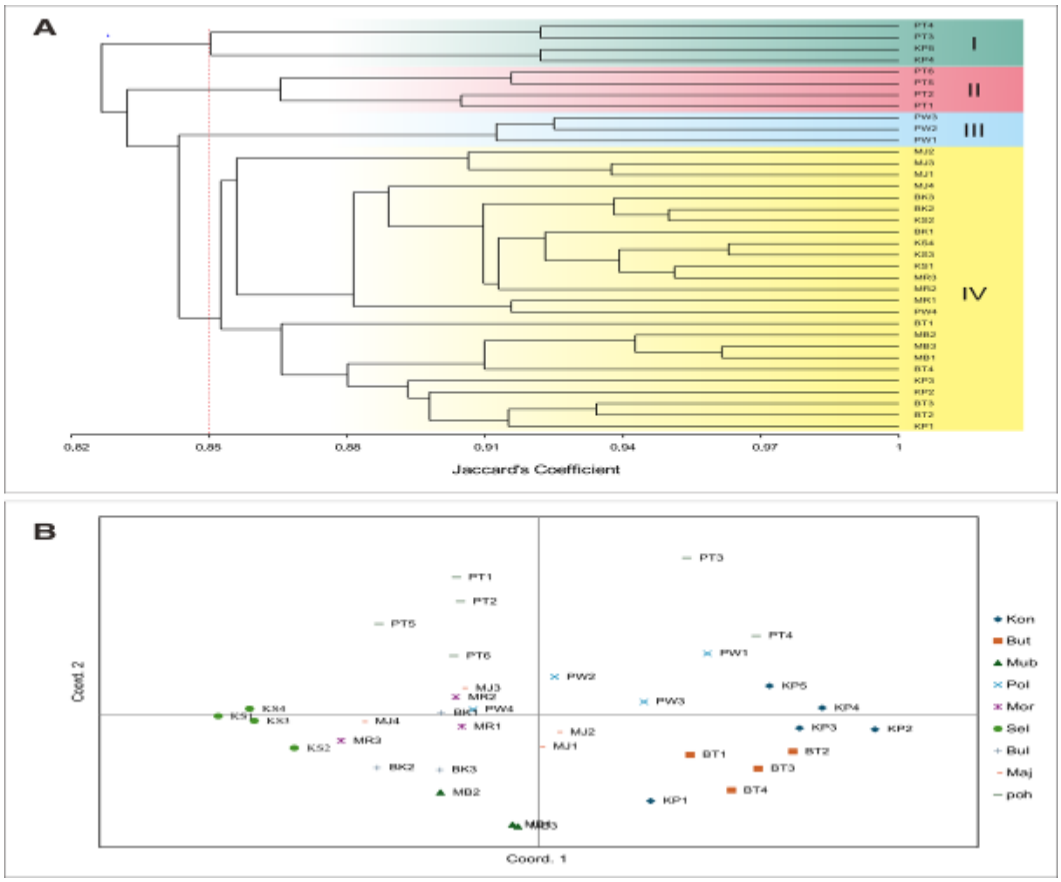

Figure 3. UPGMA dendrogram (A) and principal coordinate analysis (B) of the studied cashew accessions based on inter-simple sequence repeat.

depends on primer-genome compatibility, as also previously reported in various cashew studies (Abdelaziz *et al.,* 2020; Konate *et al.,* 2022).

The UPGMA dendrogram based on ISSR data revealed moderate to high genetic similarity among cashew accessions, with Jaccard's coefficients ranging from 0.82 to 86 (Figure 3A). Four major clusters identified had some grouping according to diverse geographic origins. The cashew accessions obtained from Morowali (MR), Selayar (KS), and Bulukumba (BK) came together within Cluster IV, showing a close genetic relationship. Such characterization patterns suggested cashew accessions from the same locality were often genetically similar, shaped by shared agronomic practices and eco-geographic factors (Chiumbi and Mangosongo, 2024). The results show a slight discrepancy when compared with genetic diversity based on morphological characteristics. Such a phenomenon is a common encounter in plant taxonomic studies and can refer to several factors. First, morphological traits gained influences from environmental factors (Mondini *et al*., 2009; Dasmohapatra *et al*., 2014), whereby accessions with different genotypes can exhibit similar phenotypes under identical environmental conditions, and vice versa. Second, ISSR markers only represent a small portion of the total genome, meaning not all the genetic variation underlying morphological traits could be detected (Salsabila *et al.,* 2025; Tunç *et al.,* 2025).

Interestingly, the cashew accessions from certain populations were split across the different clusters, such as Polewali (PW), Pohuwatu (PT), and Konawe Island (KP). For instance, PT4 and PT5 were grouped in Cluster

I, while PT1–PT3 placed into Cluster II. Such discrepancies may be explained by gene flow, which facilitates genetic exchange among the populations and contributes to within-population heterogeneity (Serrote *et al.,* 2019). This phenomenon has also been reported in wild cashew populations in Brazil, where high genetic heterogeneity was observed even within small geographic areas due to extensive gene flow (Dos-Santos *et al.,* 2019).

The principal coordinate analysis (PCoA) provided additional insight into the genetic structure of 36 cashew accessions obtained from nine different populations (Figure 3B). Accessions from West Muna (Mub), Bulukumba (Bul), Selayar (Sel), and Central Buton (But) showed spatial clustering, reflecting the highest genetic similarity within these populations. In contrast, populations from Konawe Island (Kon), Pohuwatu (Poh), Majene (Maj), and Polewali (Pol) had wider dispersion, indicating considerable inter-population divergence. This type of pattern suggested some cashew populations (Mub and Sel) maintained relatively homogeneous genetic pools, while others (Kon, Poh, and Pol) revealed greater intra-population variability. Such differentiation was often driven by geographic isolation, ecological adaptation, and historical domestication events (Archak *et al*., 2009; Kouakou *et al*., 2020; Pitono *et al*., 2024).

Genetic diversity indices

Genetic diversity parameters estimated through ISSR markers enunciated that the Pohuwatu cashew population expressed the highest Nei's gene diversity (He), Shannon's information index (I), and percentage of polymorphic loci (%P). It indicates this population harbors substantial genetic variation and may represent a valuable genetic reservoir for future breeding and conservation with tangible results (Table 2). The cashew populations obtained from the Konawe, Polewali, and Majene displayed moderate diversity levels (He = 0.060–0.072; I = 0.087–0.105; P = 14%–17%), consistent with their intermediate clustering in PCoA. In contrast, the cashew populations from Buton, Morowali, Bulukumba, and Selayar exhibited a lower genetic diversity (He = 0.037–0.056; I = 0.055–0.082; P = 9.62%–13.46%), suggesting reduced effective population sizes with considerable genetic drift. The lowest genetic diversity resulted in the West Muna population, consistent with its isolated position in the PCoA.

These results highlighted that cashew populations with higher He and I values contribute disproportionately to overall species diversity, with the same also reported in past ISSR/SSR-based studies (Abd-dada *et al.,* 2023; He *et al.,* 2024). Conversely, reduced diversity often reflects restricted gene flow and

Table 2. Genetic diversity indices of cashew accessions in Sulawesi based on ISSR markers.

Populations	Na	Ne	I	He	%P
Kon	1.173±0.037	1.129±0.029	0.105±0.023	0.0723±0.016	17.31%
But	1.137±0.034	1.100±0.026	0.082±0.021	0.057±0.014	13.46%
Mub	1.058±0.023	1.046±0.018	0.037±0.015	0.027±0.010	5.77%
Pol	1.173±0.037	1.115±0.026	0.101±0.022	0.068±0.015	17.31%
Mor	1.115±0.031	1.092±0.025	0.073±0.020	0.051±0.014	11.54%
Sel	1.096±0.029	1.062±0.019	0.055±0.017	0.037±0.011	9.62%
Bul	1.115±0.031	1.092±0.025	0.073±0.020	0.051±0.014	11.54%
Maj	1.144±0.034	1.106±0.026	0.087±0.021	0.060±0.015	14.42%
Poh	1.231±0.041	1.168±0.032	0.138±0.025	0.095±0.017	23.08%
Means	1,138±0,034	1,101±0,025	0.084±0.020	0.057±0.014	13.46%

Note: Na = Number of observed alleles, Ne = number of effective alleles, I = Shannon's information index, He = Genetic diversity and %P = percentage of polymorphic loci

demographic hindrances (Vaishnav *et al.,* 2023). The observed consistency between molecular indices and clustering patterns further validates the ISSR as an effective tool for uncovering cashew genetic diversity.

The average genetic diversity of the cashew population in Sulawesi (He = 0.057; I = 0.084; PBB = 13%) attained a low to moderate classification compared with similar studies on other plant species. For comparison, a study by Thimmappaiah *et al*. (2009) on 100 cashew accessions in India, using a combination of RAPD and ISSR markers, reported a polymorphism rate of over 85%. The low genetic diversity in the Sulawesi cashew population has a likely relation to the limited genetic foundation of the initial introduction of this plant to Indonesia, as brought by the Portuguese in the 16th century. Moreover, it could be due to cultivation practices that have not undergone systematic selection.

CONCLUSIONS

The cashew populations in Sulawesi show a low to moderate genetic diversity based on morphological and ISSR-marker analyses. Phylogenetic relationships from both approaches generally reflect geographic clustering, although not always consistently. The Pohuwatu population exhibits the highest genetic diversity and should become a priority for conservation and breeding programs. Populations, such as West Muna, show lower diversity, likely due to geographic isolation and genetic drift. These findings provide a scientific basis for germplasm conservation and breeding strategies in Indonesia. Accessions with high diversity and superior traits should be choices for parental material. Further research recommendations are using high-resolution molecular markers and agronomic trait evaluation to improve cashew germplasm characterization and breeding outcomes.

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