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GENETIC DIVERSITY OF LOCAL SHALLOT (*ALLIUM CEPA* L.) BASED ON MORPHOLOGICAL TRAITS AND ISSR MARKERS

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SUMMARY

Shallot (*Allium cepa* L.) is a strategic horticultural commodity, facing considerable pressure from enhanced domestic demand and declining production in Indonesia. This research aimed to identify morphological traits, analyze genetic diversity, and identify the potential genotypes for promising parent selection. Shallot accessions totaled 57, evaluated for genetic diversity through 18 morphological traits and molecular analysis based on 17 inter-simple sequence repeat (ISSR) markers. Morphological characterization revealed broad diversity and grouped the bulb skin color into eight distinct colors, along with considerable variation in bulb diameter. The molecular analysis using 17 ISSR primers recognized the highest level of genetic diversity (91.70%). The analysis of molecular variance (AMOVA) showed most of the genetic variation (98%) appeared within populations, with a weak differentiation among populations (2%), which confirmed a high rate of gene flow among geographical regions. Based on phenotypic performance, the shallot accessions with the highest number of bulbs, heaviest bulb weight, and ideal bulb length were notably the promising parental genotypes. The optimal breeding strategy involves utilizing these high-yielding and genetically divergent accessions to optimize heterosis and enhance the adaptive stability in shallot. This research significantly contributes to optimizing the utilization of Indonesia's local genetic resources to support national shallot seed security.

Keywords: accessions, *Allium cepa*, gene flow, genetic diversity, ISSR markers, morphological traits

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Key findings: The highest level of morphological diversity within shallots (*Allium cepa*) supported in the identification of promising accessions. The ISSR marker analysis revealed the maximum genetic diversity among shallot accessions. However, the low genetic differentiation among the regions suggests the intensive gene flow across the geographical boundaries.

INTRODUCTION

The shallot (*Allium cepa* L.) is a crucial horticultural crop, utilized as culinary spice and in traditional medicines in Indonesia. The National Socio-Economic Survey revealed shallot consumption is continuously increasing each year, reaching 2.85 kg/capita/year in 2024 and rising to 3.32 kg/capita/year in 2025, confirming an enhancement of approximately 16.49% in Indonesia (BPS, 2026). However, this rising consumption has not attained balance from a proportional surge in production. Indonesia's shallot production reached 2,085,720 tons in 2024 and experienced only a minor increase to 2,179,734 tons in 2025 (BPS, 2026). This widening gap between demand and production poses a serious challenge to maintain stable supply in the domestic market.

The development of high-yielding cultivars is essential for enhanced and stable shallot productivity. However, this strategy requires detailed knowledge of genetic diversity as the foundation for plant breeding. Indonesia also possesses considerable potential for genetic diversity in local shallot germplasm distributed across various regions, originating from both elite cultivars officially released. From the local accessions, a total of 25 local shallot cultivars has succeeded development from the research system (Directorate of Horticulture Seed Production, 2026). Indigenous germplasm always serves as a genetic resource for developing new cultivars with promising traits, including high yield, resistance to biotic and abiotic stress factors, and optimum bulb quality. Therefore, the collection and characterization of germplasm appeared to be crucial steps in plant breeding program aiming the development of high-yielding cultivars. Information regarding genetic relationships is necessary to facilitate the determination of

potential lines for use as parental genotypes in developing new populations (Syukur *et al.*, 2012).

Genetic diversity analysis can take place by using two approaches: morphological qualitative and quantitative traits, such as plant height, the number of bulbs, the number of leaves, and bulb weight, have long been beneficial to identify plant diversity and relatedness (Syukur *et al.*, 2012). However, morphological trait markers emerged to be inconsistent due to environmental influence and genotype-by-environment interactions. Overcoming this inconsistency of morphological markers revealed molecular markers can better address these weaknesses due to their consistency and with no effect from environmental factors. Among the various available molecular markers, inter-simple sequence repeat (ISSR) markers proved more effective, with frequent usage to identify plant genetic diversity. ISSR markers function by targeting non-coding DNA sequences located between two simple sequence repeats (SSR). The use of morphological markers combined with molecular markers has proven effective in mapping genetic variability across various commodities, as demonstrated in *Zoysiagrass* (Rahayu *et al.*, 2025). The ISSR markers have shown to be effective in identifying genetic diversity and relatedness among the shallot accessions (Akter *et al.*, 2015).

Therefore, the integration of morphological and ISSR markers can provide a better solution and get an accurate picture of the shallot genetic profile. Most of the previous studies on Indonesian shallot genetic relatedness were predominantly reliant on morphological traits. Based on the above discussion, this research aimed to analyze the genetic diversity of Indonesian local shallot accessions by the combination of morphological and ISSR markers. Although morphological traits can incur environmental

influences, they offer practical field identification that complements the stable genotypic data from ISSR markers.

MATERIALS AND METHODS

Genetic materials

The shallot plant genetic materials comprised 57 shallot bulb accessions originating from nine different populations. The sample codes' assigning was according to the abbreviation of each population's geographic origin followed by an accession number. The shallot accessions used were the result of collections from the Research Center for Standardization of Vegetable Instruments and independent exploration in several regions across Indonesia.

Morphological characterization

The observations on shallot morphological traits were dependent on the plant's phenotypic traits, which were the observable and directly measurable physical traits. The study followed the International Plant Genetic Resources Institute (IPGRI, 2001) and International Union for the Protection of New Varieties of Plants, or UPOV (2008) descriptors with some modifications. Morphological characterization underwent evaluation based on several key traits, including plant height, the number of leaves, leaf stiffness, the number of bulbs, bulb skin color, bulb diameter, bulb length, flowering time, and harvesting time. Key adjustments included expanding the bulb skin color scale (adding light brown, yellowish-brown, and white) and including fresh plant weight. Overall, the shallot accessions entailed evaluation on 18 morphological traits.

ISSR marker analysis

Total DNA isolation came from the 57 shallot genotypes using a modified cetyl trimethyl ammonium bromide (CTAB) method (Pambudi *et al.*, 2023), with the addition of 2% polyvinylpyrrolidone (PVP) and 2% β -

mercaptoethanol to bind polyphenols and prevent DNA degradation. Fresh leaf samples of shallot accessions reached homogenization using liquid nitrogen and subsequent incubation in CTAB buffer at 65 °C. Sequential extraction that proceeded used chloroform:isoamyl alcohol (C: I) and phenol:chloroform:isoamyl alcohol (P:C: I) solutions, followed by precipitation with isopropanol, washing with 70% ethanol, and drying, after which re-dissolving the DNA pellet in ddH₂O. The quality and quantity of the DNA entailed assessment via 1% agarose gel electrophoresis in 1x TAE buffer, with the inclusion of λ DNA marker, to ensure the integrity of the obtained DNA for subsequent analysis.

The DNA amplification proceeded using 17 ISSR primers in a 15 μ L polymerase chain reaction (PCR) reaction volume, consisting of 6 μ L master mix, 1 μ L ISSR primer (5 μ M), 2 μ L DNA template (100 ng/ μ L), and 6 μ L ddH₂O. The PCR process included pre-denaturation at 95 °C for 3 min, followed by 35 cycles (denaturation at 95 °C for 30 s, annealing at 44 °C–56 °C for 45 s, and extension at 72 °C for 45 s). The process concluded with a final extension at 72 °C for 10 min. The PCR products' separation continued by electrophoresis on a 1% agarose gel in 1x TAE buffer at 80–100 V for 30 min. Then, the results sustained visualization using a UV transilluminator and documentation with a digital camera.

Data analysis

Morphological and ISSR marker data entailed scoring as multistate and binary (1 for presence, 0 for absence), respectively. Genetic diversity parameters, including the number of observed alleles (N_a), the number of effective alleles (N_e), expected heterozygosity (H_e), Shannon's Information index (I), and percentage of polymorphic loci (PPL), underwent analysis using GenAlEx 6.5. Genetic dissimilarity calculation used appropriate distance matrices, followed by the unweighted pair group method with arithmetic mean (UPGMA)-based cluster analysis in RStudio to construct a dendrogram. Additionally, principal

component analysis (PCA), as performed, sought to determine genetic structure and identify the key traits contributing to genetic diversity.

RESULTS AND DISCUSSION

Morphological traits-based genetic diversity

Genetic diversity analysis based on 57 local shallot accessions for morphological traits revealed significant variations, as evidenced by 18 distinct traits. The presented evaluation identified several unique accessions, including those with varied bulb diameters, leaves tending toward dark green, and bulb skin colors, ranging from white to yellowish-brown (Figure 1). Morphological observations based on shallot accessions disclosed diversity both at the plant and bulb levels, as authenticated by variations in various morphological traits (Pratiwi *et al.*, 2020; Sari *et al.*, 2016).

The cluster analysis, based on morphological traits of the local Indonesian shallot accessions originating from nine populations, yielded four main clusters at a dissimilarity coefficient of 0.7 (Figure 2). The shallot accessions in Cluster I, represented by the turquoise color, demonstrated high morphological uniformity. Accessions included in this cluster sustained merging by the low dissimilarity distance. This cluster represents the shallot accessions with internal morphological diversity among individuals. Cluster II and Cluster III comprised the

accessions that showed robust morphological relatedness. In Cluster III, the accessions, such as RSE1 and RSE2, became separated at the highest dissimilarity value. This revealed that these accessions possess morphological traits distinct from the shallot accessions in other clusters, Cluster I in particular. These results align with past findings of Cramer *et al.* (2021), who reported that shallot cultivars' diversity does not always have an association with geographical distribution and environmental conditions. Agronomic traits, such as plants' structure, size, and color, gained assessment phenotypically, undergoing observations with significant variations in onion (*A. cepa* L.) ecotypes (Brahimi *et al.*, 2022).

Cluster IV showed a distinct grouping compared with the three preceding clusters. In this cluster, the shallot accessions exhibited greater dissimilarity distance, confirming that accessions in this group possess heterogeneous individual characteristics compared with the entire population studied in three preceding clusters. The diversity observed within each group can serve as a genetic source for morphological traits, appearing to be beneficial in shallot development (Pratiwi *et al.*, 2020). Asili *et al.* (2010) reported that Persian onions exhibited considerable differences across morphological traits; based on the UPGMA cluster analysis, 16 ecotypes received classification into six major groups. Similarly, cluster analysis categorized 66 garlic genotypes into five primary groups based on the genetic distance measured from 15 agro-morphological traits (Benke *et al.*, 2018).

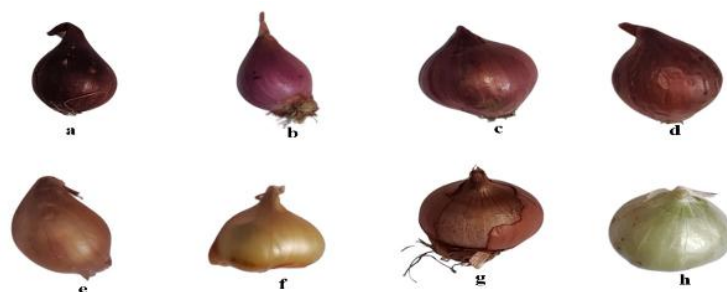


Figure 1. Variation of shallot bulb color: a) red, b) pink, c) purplish red, d) dark red, e) reddish brown, f) light brown, g) yellowish brown, and h) white.

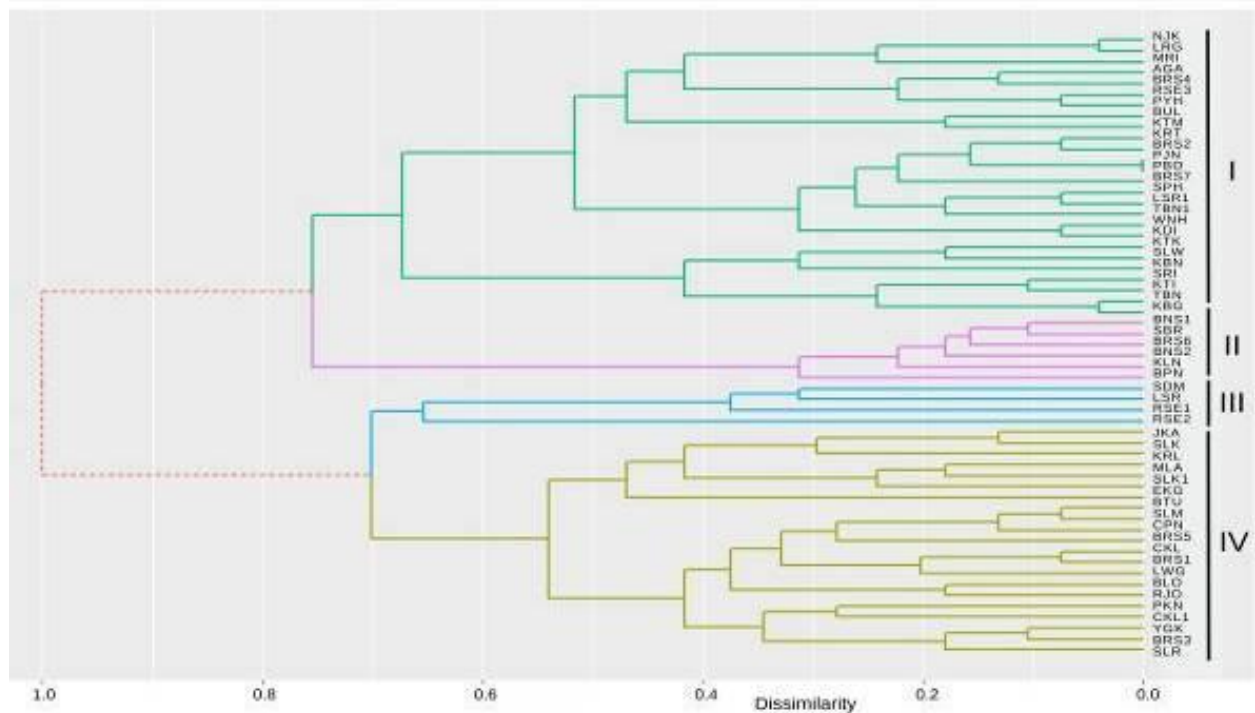


Figure 2. Dendrogram of 57 local Indonesian shallot accessions based on morphological data.

ISSR-based genetic diversity

Genetic diversity analysis of 57 local Indonesian shallot accessions distributed across nine populations was successful using 17 ISSR primers (Table 1). The average percentage of polymorphic loci (PPL) was 91.7%, revealing the highest genetic diversity. These results were consistent with the findings of Sari *et al.* (2016), who reported 89.57% polymorphism in Indonesian shallot genotypes, and Lyngkhai *et al.* (2021), who confirmed the effectiveness of SSR in evaluating shallot diversity in India. By comparing with other plant species, the genetic diversity was relatively higher than *Euphorbia resinifera* (74.81%) (Abd-Dada *et al.*, 2023) and *Pityrocarpa moniliformis* (88%) (Felix *et al.*, 2020), thereby demonstrating the superiority of the Indonesian local shallot genetic resources. Other genetic parameters, such as the number of observed alleles ($N_a = 1.85$), the number of effective alleles ($N_e = 1.70$), Shannon's Index ($I = 0.56$), and expected heterozygosity ($H_e = 0.38$), also gave the

highest level of genetic diversity. The topmost values of N_a and N_e suggested that the population's allele frequencies balanced, as evidenced by Nei's genetic diversity value showing no single allele dominates. The stable allele distribution is a biological requirement for maintaining the population's potential for adaptation and future survival (Nei, 1987). The high N_e value considerably signifies the ideal number of alleles contributing evenly to the overall observed genetic diversity (Frankham, 1996).

The AMOVA showed most of the genetic variation (98%) had a recording within populations, while only 2% of the total variation referred to variations among the populations (Table 2). The PhiPT value was 0.020, with a p-value of 0.174 (>0.05), exhibiting nonsignificant genetic variations among the populations. Biologically, this confirmed that the genetic diversity showed concentration within the accessions than among the populations. Shallots received the classification as cross-pollinating plants (Fritsch and Friesen, 2002).

Table 1. Amplification band marker profile of 57 local shallot accessions using ISSR primers.

No.	Primer	N_B	N_{PB}	N_a	N_e	I	h_e	PLP (%)
1	ISSR 810	9	9	2.00	1.80	0.62	0.43	100.00
2	ISSR 841	12	12	2.00	1.81	0.63	0.44	100.00
3	ISSR RED 4	12	12	2.00	1.83	0.64	0.45	100.00
4	ISSR RED 7	14	12	1.75	1.51	0.46	0.30	87.72
5	ISSR RED 9	11	10	1.91	1.62	0.53	0.36	92.98
6	ISSR RED 20	9	7	1.47	1.53	0.43	0.29	73.68
7	ISSR RED 25	12	12	2.00	1.77	0.61	0.42	100.00
8	PKBT 4	5	4	1.84	1.73	0.56	0.39	87.72
9	PKBT 6	9	8	1.93	1.74	0.59	0.41	96.49
10	PKBT 7	5	4	1.80	1.77	0.57	0.41	87.72
11	PKBT 9	7	6	1.87	1.72	0.57	0.40	91.23
12	PKBT 11	6	4	1.64	1.60	0.47	0.32	75.44
13	UBC 811	12	11	1.96	1.71	0.57	0.39	98.25
14	UBC 825	8	6	1.49	1.53	0.43	0.29	73.68
15	UBC 826	10	10	2.00	1.78	0.62	0.43	100.00
16	UBC 835	11	11	2.00	1.86	0.64	0.45	100.00
17	UBC 842	9	8	1.89	1.56	0.51	0.34	94.74
Average			8.82	1.85	1.70	0.56	0.38	91.74

Keys: N_B : Total number of bands, N_{PB} : Number of polymorphic bands, N_a : Average number of observed alleles, N_e : Number of effective alleles, I : Shannon's information index, h_e : Expected heterozygosity, and PLP : Percentage of polymorphic loci.

Table 2. Result of the analysis of molecular variance (AMOVA) for nine local Indonesian shallot populations.

Source of Variation	d.f.	SS	MS	VT	%
Among populations	8	300.94	37.61	0.67	2
Within populations	48	1605.82	33.45	33.45	98
Total	56	1906.77	71.06	34.12	100
PhiPT				0.02	
Prob				0.17	

Keys: d.f.: Degrees of freedom, SS: Sum of squares, MS: Mean square, and VT: Percent of total variation.

Although the propagation of shallots is primarily vegetative, the inter-regional exchange and movement of plant material by humans (human-facilitated gene flow) leads to homogenization across the geographical areas; eventually, the diversity concentration is at the individual level in a population, and the result shows high intra-population variations (98%). Hamrick and Godt (1996) reported that, on average, the vegetatively propagated plants tend to retain 83% of the variation within populations, whereas outcrossing plants revealed more than 90% of the variation residing within the population. This pattern also aligns with the findings of Sari *et al.* (2016). They reported that clustering of shallot genotypes based on ISSR markers appeared to

be not correlated with geographical origins but mostly due to influences from trade distribution and long-term cultivation.

The cluster analysis of the 57 local Indonesian shallot accessions revealed four major clusters at a dissimilarity coefficient of 0.9 (Figure 3). Shallot accessions that merged into Cluster I were the last group to join the entire population, indicating that this cluster represents a genetically distinct unit from all other populations. This highest divergence suggested this cluster separated from the main lineage long ago, possibly due to geographical isolation, which minimized the gene flow with other clusters. These results were greatly analogous to the findings of Mohanty and Prusty (2002) in their genetic diversity analysis

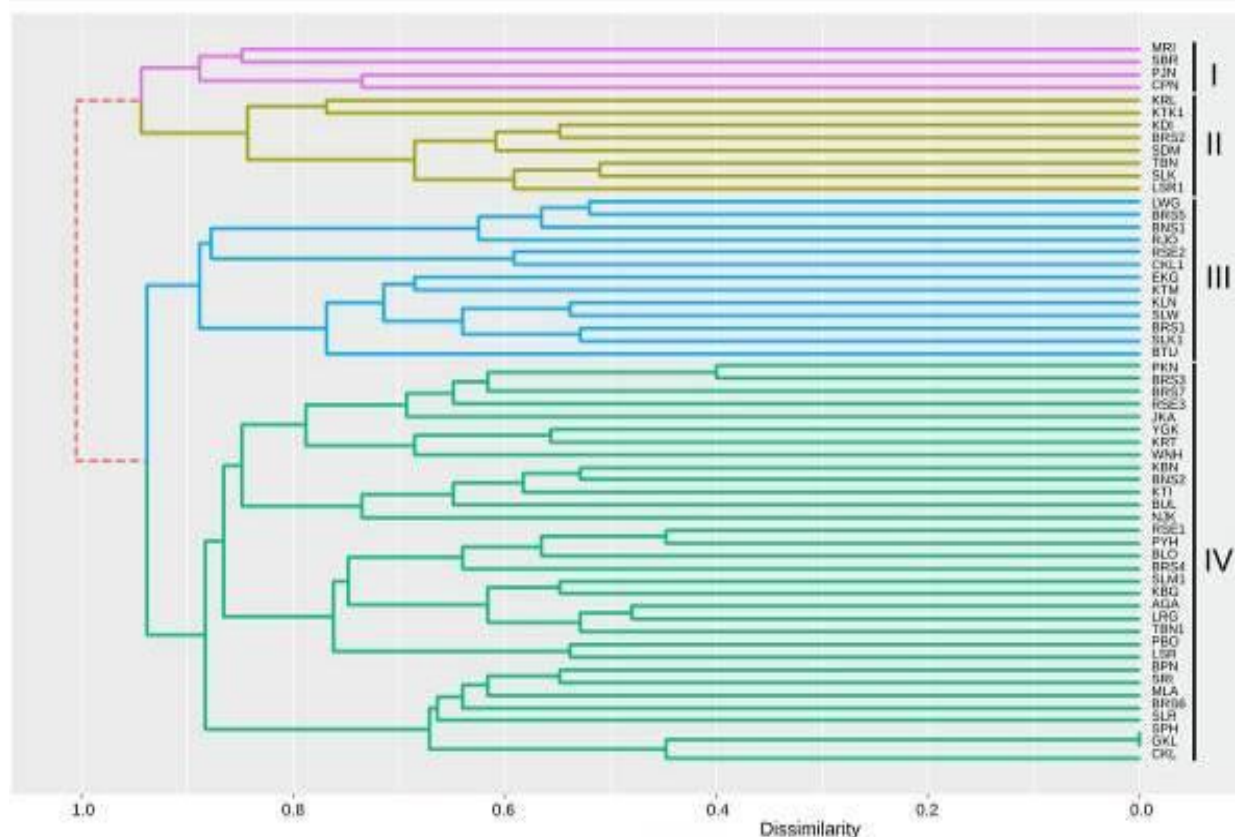


Figure 3. Dendrogram of 57 local Indonesian shallot accessions based on ISSR data.

of shallot genotypes. This consistency reinforces the reliability of ISSR in detecting genetic relatedness in onion genotypes (Grover and Sharman, 2014).

Cluster II showed a short branching distance, indicating the highest internal homogeneity. Accessions within this cluster also exhibited a high genetic resemblance. This similarity often results from inbreeding with intense local selection for specific phenotypes. Clusters III and IV relatively disclosed a broad branching, confirming that the shallot accessions within these clusters displayed the maximum genetic diversity. This implies that these clusters do not share genetic similarity with the preceding clusters; however, they comprise distinct genetic substructures, likely due to widespread population dispersal and influence of multiple distinct genetic sources. Sudha *et al.* (2019) mentioned that the ISSR markers do not always separate the onion genotypes based on their geographical

locations due to genetic admixture resulting from the exchange of planting material across different regions.

The molecular data with principal component analysis (PCA) revealed that PC1 accounted for 45.34% of the total genetic variation and served as the main axis for separating the genetic groups (Figure 4). However, the PC2 explained approximately 10.16% of the total genetic variation. The combined contribution of PC1 and PC2 explained 55.50% of the total genetic diversity, exhibiting that these two dimensions were sufficiently robust to represent the major genetic structure within the shallot sampled populations. The clustering of 34 shallot genotypes analyzed through morphological and ISSR markers appeared unrelated to their geographical origins and formed a single cluster despite originating from different locations (Sari *et al.*, 2016).

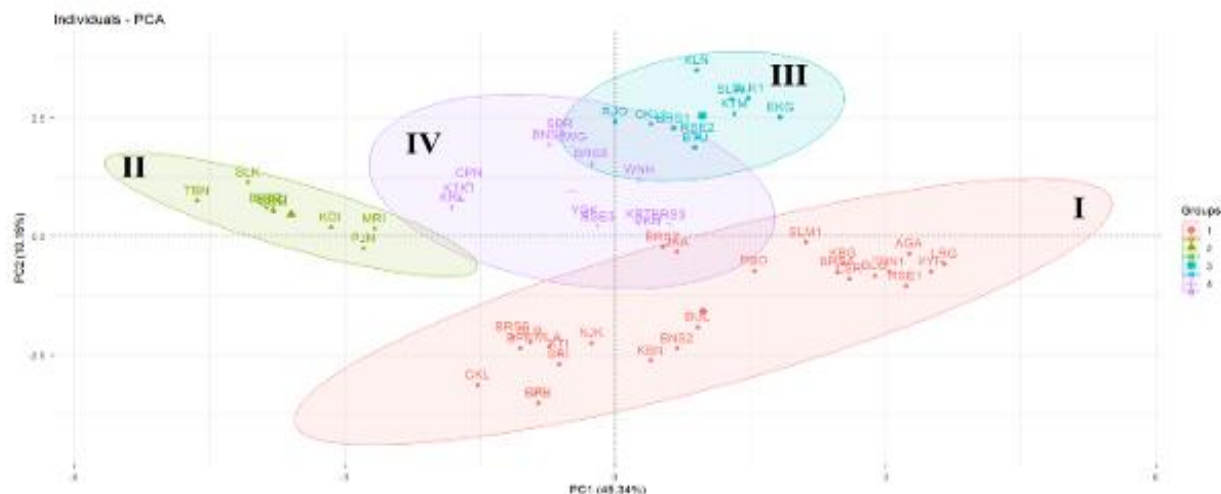


Figure 4. Matrix plot of the principal component analysis results based on the molecular ISSR traits of 57 shallot local Indonesian accessions, where the 3 letters scattered on the matrix plot represent the 57-shallot local Indonesian accession codes.

Shallot genotypes' group I had the location on the right side of PC1, suggesting the accessions within this group have a heterogeneous genetic profile and a wide distribution, denoting considerable intra-population genetic diversity. Group II was the most isolated group of the shallot genotypes, showing relatively the highest density, which suggested a moderate level of genetic homogeneity compared with the red group. Group III indicated a significant separation from Group I and comprised unique shallot genotypes that were notably distinct from other genotypes. The high density revealed a relatively homogeneous genetic profile among the accessions within the group. Group IV received an intermediate cluster classification, with a central position among the other groups, signifying the gene flow resulting from the hybridization among different genetic groups. Singh *et al.* (2020) reported the distribution pattern of shallot genotypes does not always form distinct clusters; however, it showed a continuous spread reflecting a gradient of genetic variation among accessions. The different cluster compositions between morphological and ISSR analyses are common. Morphological traits acquired high influences from environmental factors and phenotypic plasticity, whereas ISS markers

detected neutral DNA variations that are completely independent of environmental conditions.

The clustering result in this study does not show a consistent pattern between morphological characters and genetic markers. It contrasted with the findings in black pepper from Bangka Island, where accessions reached grouping based on phenotypic similarities supported by DNA profiling (Prayoga *et al.*, 2026). The research result reinforces that the characterization of shallot germplasm cannot rely on a single type of character. The discrepancy found between the morphological (describing phenotypic expression influenced by the environment) and molecular (describing differences at the DNA level) data suggested using these two approaches must be in an integrated manner to obtain comprehensive information. Utilizing multivariate analysis that combines both types of data will provide a more accurate picture of shallot genetic diversity for conservation and breeding purposes (Herlina *et al.*, 2018).

The selection of local Indonesian shallot accessions with superior traits continued based on morphological traits. Three promising shallot accessions sustained selection, namely CKL1 (Lembang, West Java), WNH (Probolinggo, East Java), and BTU

(Central Java), which also exhibited potential superiority in morphological traits contributing to bulb yield. The accession CKL1 has the potential with the highest number of bulbs per clump among all the accessions, with an expectation to further enhance the bulb yield. The accession WNH (Probolinggo) possesses the heaviest bulb weight among all accessions and proved to be an ideal candidate for achieving large bulb biomass and thus will boost the yield. The accession BTU from Central Java was distinct as a prime candidate genotype for the bulb length related to bulb shape, which can influence market aesthetics and post-harvest storage and handling. The shallot accession BTU could also contribute to specific and desired bulb dimensions for consumers.

A strategic step involves utilizing potential accessions for bulb yield (CKL1, BTU, and WNH) as parental genotypes that will serve as donor of high-yielding traits. Hybridization among these high-yielding accessions with an elite cultivar will maximize the heterotic effects. Heterosis most optimally occurs when two genetically distant parental genotypes sustains crossing, resulting in an F_1 offspring that exhibits superiority beyond the average of the two parents. Combining stable high-yield traits with broad allelic diversity can yield new cultivars with significant yield improvement and enhanced adaptive stability (Würschum et al., 2023).

CONCLUSIONS

Local Indonesian shallot accessions revealed the highest morphological diversity across 18 agronomic traits. Genetic diversity analysis using ISSR markers disclosed the highest level of genetic diversity. An analysis of molecular variance (AMOVA) showed low genetic differentiation among the populations (2%) and most of the variation occurred within populations (98%), indicating the highest gene flow. Morphological and ISSR-based cluster analyses did not group the shallot accessions with geographical origins. The accessions CKL1 (highest number of bulbs), WNH (heaviest bulb weight), and BTU (ideal bulb height) emerged

as promising parental genotypes. The optimal breeding strategy is to utilize those three high-yielding accessions as donors of yield traits in shallot. Significantly, these findings provide important genetic resource data for developing elite, high-yielding Indonesian shallot varieties.

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