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GENETIC DIVERSITY AND GERMPLASM RELATIONSHIPS OF *DURIO TESTUDINARIUS* BECC. (MALVACEAE) USING SSR MARKERS AND DNA BARCODING

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SUMMARY

Understanding the genetic diversity of *Durio testudinarius* Becc. (Malvaceae) is essential for effective germplasm conservation and genetic resource management; however, molecular information on this wild durian species remains limited. The pertinent study aimed to carry out a comprehensive assessment on genetic diversity of the species *D. testudinarius* across five populations distributed in five regencies (Sambas, Landak, Sanggau, Sekadau, and Ketapang) in West Kalimantan, Indonesia. In this study, simple sequence repeats also supported barcoding deoxyribonucleic acid of 12 taxa of *Durio* species. The highest observed and expected heterozygosity values resulted in the Sekadau population ($H_o = 0.363$ and $H_e = 0.453$, respectively), although the species exhibited an overall low level of genetic diversity. DNA barcoding analysis showed the Sambas and Ketapang taxa of *D. testudinarius* clustered together with strong bootstrap support (93%). Moreover, *D. testudinarius* formed a distinct lineage that showed a clear separation from *D. dulcis*, *D. zibethinus*, *D. oxleyanus*, *D. kutejensis*, *D. graveolens*, *D. lanceolatus*, and *D. acutifolius*. The low heterozygosity values revealed limited gene flow among the *D. testudinarius* populations. Furthermore, the DNA evidence suggested that the germplasm recognized by deoxyribonucleic acid disclosed *D. testudinarius* accessions were genetically distant from other *Durio* species in Kalimantan, Indonesia.

Keywords: *D. testudinarius*, species, DNA barcoding, morphology, SSR microsatellites

Key findings: The species *D. testudinarius* populations in Sambas and Ketapang exhibited distinct groups of Landak, Sekadau, and Sanggau. Based on DNA analysis, five accessions of the *D. testudinarius* accessions indicated obvious distinctions from seven other species, *D. dulcis*, *D. zibethinus*, *D. oxleyanus*, *D. kutejensis*, *D. graveolens*, *D. lanceolatus*, and *D. acutifolius*.

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INTRODUCTION

Durio testudinarius Becc. is a wild durian species belonging to the family Malvaceae and is endemic to the island of Borneo, where it occurs naturally in Brunei Darussalam, Indonesia (Kalimantan), and the Malaysian states of Sabah and Sarawak (Kostermans, 1958; POWO, 2023). In Indonesia, documentation of natural populations has succeeded across several regions of Kalimantan, including West, Central, and North Kalimantan (GBIF Secretariat, 2019). The species typically inhabits humid tropical lowland forests at elevations below 700 meters above sea level (masl), where it grows on fertile, well-drained soils (Fern *et al.*, 2016). As one of the wild relatives of cultivated durian, *D. testudinarius* represents an important component of Bornean tropical forest biodiversity and constitutes a valuable genetic resource for future durian improvement.

Unlike the commercially cultivated *Durio zibethinus*, *D. testudinarius* remains largely undomesticated and has experienced minimal artificial selection. The species is prominent for its cauliflorous habit, with flowers and fruits predominantly borne on the

lower trunk, together with fruit characteristics that differ markedly from cultivated durian (Figure 1). Given its relatively low economic utilization and limited cultivation, most existing populations receive maintenance under natural or semi-natural conditions. Consequently, these populations could retain substantial levels of genetic variation that are potentially valuable for breeding programs, conservation planning, and the development of improved durian cultivars possessing desirable agronomic and adaptive traits.

Understanding the extent and distribution of genetic diversity is fundamental for the effective conservation and utilization of plant genetic resources. Accurate characterization of germplasm provides the basis for identifying genetically distinct accessions, detecting duplicate collections, selecting parental materials for breeding, and formulating conservation strategies. Although morphological descriptors remain useful for preliminary germplasm evaluation, changes in their expression are often due to influences from environmental conditions and developmental stages, reducing their reliability for estimating genetic relationships among closely related individuals.



Figure 1. Map of sampling locations including rivers of the five populations of *D. testudinarius* in West Kalimantan, Indonesia.

Molecular markers provide a more robust approach for evaluating genetic variation because they are largely independent of environmental influences. Among the available marker systems, simple sequence repeats (SSRs) are particularly valuable due to their high polymorphism, codominant inheritance, reproducibility, and broad genome coverage. These make them effective for genetic diversity assessment, population structure analysis, germplasm characterization, and parentage studies (Kumar, 2018). Previous studies have demonstrated that SSR markers efficiently discriminate plant genotypes and reveal genetic relationships among cultivars and wild populations (Songnuan *et al.*, 2019). SSR markers primarily assess intraspecific genetic variation but are less suitable for confirming taxonomic identity or evaluating phylogenetic affinity.

However, these markers are highly subjective, resulting in controversial consistency, low repeatability, and complex implementation, and eventually limiting their effectiveness (Wu *et al.*, 2021). Barcoding methods, particularly short DNA sequences, were evidently useful in biodiversity research, particularly in highly diverse regions, such as the tropics, where morphological similarities among species are especially high. Barcoding analysis also assists taxonomists in identifying biodiversity and exploring potential new species (Kress and Erickson, 2012). Although DNA barcodes are the standardized sequences of short DNA segments (400–800 bp), which can facilitate rapid and accurate species identification.

Microsatellites, or simple sequence repeats (SSRs), are the short DNA sequences with a core motif that repeats twice consecutively, highly variable, and found in many organismal genomes. The SSR markers are a widely used method in various genetic studies, including genetic diversity analysis, paternity testing, population analysis, genetic traits identification, and forensic research (Kumar, 2018). Based on the above discussion, the crucial study aimed to analyze the genetic diversity of *D. testudinarius* populations based on morphological traits, carried out through specific SSR markers and DNA barcoding. These results could assist in the management and development of durian genetic resources.

MATERIALS AND METHODS

Plant materials

Twenty plant samples of the species *D. testudinarius*, procured from five places in West Kalimantan, Indonesia (Districts Sambas, Landak, Sanggau, Sekadau, and Ketapang) underwent morphological analysis based on Magandhi *et al.* (2024) (Figure 1, Table 1). Furthermore, for the SSR analysis, the plant samples selected from the five locations and each locality entailed treatment as a population, and each population comprised five individuals as samples. For DNA barcoding, the inclusion of seven *Durio* species consisted of *D. dulcis*, *D. zibethinus*, *D. oxleyanus*, *D. kutejensis*, *D. graveolens*, *D. lanceolatus*, and *D. acutifolius*, and one other species, *Theobroma cacao*, as the outgroup (submitted at the NCBI database).

Table 1. Sampling location information of the five *D. testudinarius* populations used in the research.

No.	Populations	Code	Geographical location	Elevation (meters above sea level)
1	Sambas Botanical Gardens, Sambas District	SB	01°16'21,9"N; 109°29'12,5"E	34
2	Mandor, Landak District	LD	00°14'54,4"N; 109°18'59,4"E	28
3	Tayan Hulu, Sanggau District	SG	00°15'16,8"N; 110°17'22,5"E	29
4	Nanga Taman, Sekadau District	SK	00°22'28,2"S; 110°51'03,2"E	166
5	Gunung Palung National Park, Ketapang District	KT	01°13'S ; 110°7"E	200

Table 2. The 20 SSR primers used in this study.

Primer No.	Locus ID	Primer Sequences 5'	Primer Sequences 3'	Ta (°C)
P1	dt24564	F: VIC-GTGGTCCTTCTCTGCTGCC	R: TGATCGGGCTTTTCAGGTTCT	60
P2	dt18725	F: NED-CGACAACTGGAGCTTTACA	R: TGTGGGCGATGATGAGAGTC	60
P3	dt2717	F: NED-AGCCTTTTCTTACCTCCGCT	R: CTAAACACCCTCCACTCCGC	60
P4	dt37193	F: FAM-TCCTTGAAGCTTCGGATGGT	R: TGGAGAGAGGTAGGCTGACA	60
P5	dt41585	F: VIC-TTCCGCCATATCTCCATCATCA	R: ACGATAAACTTGGAGCGTGTTT	60
P6	dt2294	F: VIC-AATCTGCCGTTTGTCCAGCA	R: GCCCAGATGCGATTTAAGGC	60
P7	dt33464	F: FAM-GCCTTGGATTATGCAACGTCA	R: GCCCAGATGCGATTTAAGGC	60
P8	dt33709	F: NED-TGGTGATGGACGGAGAGGAT	R: GCAAGGCTTTTCTTCCGCAT	60
P9	dt17599	F: NED-ATCCGCTGCTGTTCATCCAA	R: TAAGAGGGTGTCGAGGGTGG	60
P10	dt19746	F: VIC-AGGAAGTTCTCGCCGATTG	R: ACCCAACCACACCATCCATC	60
P11	dt24697	F: VIC-ATGTGCCAGCTAAGCCTGTT	R: TCCCCAAAGTTGCATCATACAGT	60
P12	dt88788	F: PET-TCTGCGACCAAAACAAAGTGAC	R: TGTAGCATCCAATGAGAAAGCAG	60
P13	dt12934	F: NED-CGTTCTCGCTTCTCATTTACAGC	R: AACCCATCACCCATGCCTTT	60
P14	dt55948	F: PET-TGACCAACCATGTGATATGCTCA	R: GCACGCATACACAAAGATCCA	60
P15	dt30243	F: FAM-TGTGGAGGAAAGGACAACGT	R: GAGAGCAAAGACCCAACCCA	60
P16	dt5254	F: FAM-AGGTGTGGAAGTTTGGACCG	R: CCAGATACCAAGACCAGCGG	60
P17	dt17930	F: FAM-ACAAGCATGCATGGACCACA	R: ACAGCTGTGCCTCTCAACAG	60
P18	dt17247	F: PET-CACCAAAGGCCTACTCTTGCT	R: TGCGCCATGAACCACTATT	60
P19	dt18696	F: PET-GGAGCAGATGACGAGTAACCC	R: ACCGAACTGTATGCTTTGCTTT	60
P20	dt126809	F: PET-TGGTGGAATTGTTCATGGGATCA	R: AGGATGCCAGTCAACACCTG	60

SSR markers

This study used a total of 20 pairs of primers and four fluorescence-labeled primers (6-FAM, VIC, NED, and PET) as tails in the forward primer sequence. In a previous study by Magandhi *et al.* (2021), microsatellite sequences derived from the whole genome data of *D. testudinarius* served as the basis for these SSR primers. We further divided the SSR primers into multiplex PCR groups, each consisting of the four fluorescence-labeled SSR primers. Detailed information about the primers is available in Table 2.

DNA extraction and amplification

A modified CTAB (cetyltrimethylammonium bromide) enabled the extraction of genomic DNA from leaf tissue of different samples. Tris-EDTA (TE) buffer served as the solvent. The quantity and quality measurement of genomic DNA, upon assessment, used the Multiskan SkyHigh Microplate Spectrophotometer. Conducting the PCR amplification utilized an Agilent SureCycler 8800, with the Type-IT PCR kit (Qiagen) used in a 10 µL reaction mixture. The reaction mixture comprised approximately 20 ng of genomic DNA, 5 µL of 2x Type-IT

Multiplex PCR Master Mix, 0.2 µM of each reverse primer, 0.1 µM of each forward primer, and 0.1 µM of each fluorescence-labeled primer. The PCR conditions were as follows: initial denaturation at 95 °C for 3 min, followed by 32 cycles at 95 °C for 30 s, annealing at 60 °C for 1 min and 30 s, extension at 72 °C for 30 s, and a final extension at 60 °C for 3 min. Allele number and size determination employed the capillary electrophoresis method and incurred manual analysis using GeneMapper Software 5 (Applied Biosystems).

Data analysis

The genetic diversity parameters' estimations included the calculations of observed heterozygosity (H_o) and expected heterozygosity (H_e) using the GenAlEx 6.5 software (Peakall and Smouse, 2012). Subsequently, a phylogenetic analysis sought to assess the genetic relationships among accessions. The dendrogram for cluster analysis of SSR markers, as performed in the study, used the PBSTAT-CL 2.1 program and Ward-based cluster analysis. The SSR analysis of a population through DNA barcoding analysis in this study continued by primers (*rbcl*, *matK*, *trnL-F*, and the ITS DNA data set

Table 3. Specimens and accession numbers deposited in NCBI GenBank used in this study.

No.	Specimens	Accession numbers in NCBI GenBank			
		<i>rbcl</i>	<i>matK</i>	<i>trnL-trnF</i> intergenic spacer	ITS
1	<i>D. testudinarius</i> SB	OR601135.1	OR601140.1	OR601145.1	OR593301.1
2	<i>D. testudinarius</i> LD	OR601136.1	OR601141.1	OR601146.1	OR593302.1
3	<i>D. testudinarius</i> SG	OR601137.1	OR601142.1	OR601147.1	OR593303.1
4	<i>D. testudinarius</i> SK	OR601138.1	OR601143.1	OR601148.1	OR593304.1
5	<i>D. testudinarius</i> KT	OR601139.1	OR601144.1	OR601149.1	OR593305.1
6	<i>D. acutifolius</i>	OR601150.1	OR601156.1	OR601162.1	OR631856.1
7	<i>D. dulcis</i>	OR601151.1	OR601157.1	OR601163.1	OR631920.1
8	<i>D. graveolens</i>	OR601152.1	OR601158.1	OR601164.1	OR631857.1
9	<i>D. kutejensis</i>	OR601153.1	OR601159.1	OR601165.1	OR631858.1
10	<i>D. lanceolatus</i>	OR601154.1	OR601160.1	OR601166.1	OR631859.1
11	<i>D. oxleyanus</i>	OR601155.1	OR601161.1	OR601167.1	OR631860.1
12	<i>D. zibethinus</i>	MG895967.1	KY860084.1	KY860055.1	AF233305.1
13	<i>Theobroma cacao</i>	LC385908.1	MZ493869.1	HM488410.1	ES440115.1

Table 4. The primers used in DNA barcoding analysis.

No.	Primer	Sequence (5'-3')	Ta (°C)	References
1.	<i>rbcl</i>	<i>rbcl</i> a-F	52	Levin <i>et al.</i> , 2003 Kress and Erickson, 2012
		<i>rbcl</i> a-R		
2.	<i>matK</i>	3F-KIM	54	Cuénoud <i>et al.</i> , 2002 Cuénoud <i>et al.</i> , 2002
		1R-KIM		
3.	<i>trnL-trnF</i> intergenic spacer	<i>eForward</i>	52	Sang <i>et al.</i> , 1997 Tate and Simpson, 2003
		<i>fReverse</i>		
4.	ITS	AB101F	58	Cheng <i>et al.</i> , 2016 Cheng <i>et al.</i> , 2016
		AB102R		

of 12 taxa of *Durio*). It included seven DNA barcoding sequence datasets from other *Durio* species (*D. dulcis*, *D. zibethinus*, *D. oxleyanus*, *D. kutejensis*, *D. graveolens*, *D. lanceolatus*, and *D. acutifolius*), along with one outgroup dataset of *Theobroma cacao* L. (Table 3) (Magandhi *et al.*, 2024). After submission, the study accessed these from the GenBank of the National Center for Biotechnology Information (NCBI, <http://www.ncbi.nlm>).

DNA barcoding analysis

The DNA barcoding markers used in this study appear in Table 4. Sequence alignments received manual examination for nucleotide ambiguities resulting from insertions, deletions, and substitutions and incurred corrections where necessary to ensure accurate sequence alignment. The edited sequences underwent further processing for dendrogram construction to establish the

phylogenetic tree. Determining the optimal model for reconstructing each marker's phylogenetic tree used the maximum likelihood method (Tamura *et al.*, 2021) (Table 4). Dendrogram construction continued using the same method. All analyses performed engaged the MEGA X software (Kumar, 2018).

RESULTS AND DISCUSSION

Allelic diversity and genetic variation

Simple sequence repeat (SSR) analysis revealed variation in allelic diversity among the five *Durio testudinarius* populations. The Sekadau population possessed the highest allelic richness, with 57 alleles (mean = 2.85 alleles locus⁻¹), whereas the Ketapang population exhibited the lowest, with 29 alleles (mean = 1.45 alleles locus⁻¹). Similarly, the Sekadau population showed the maximum

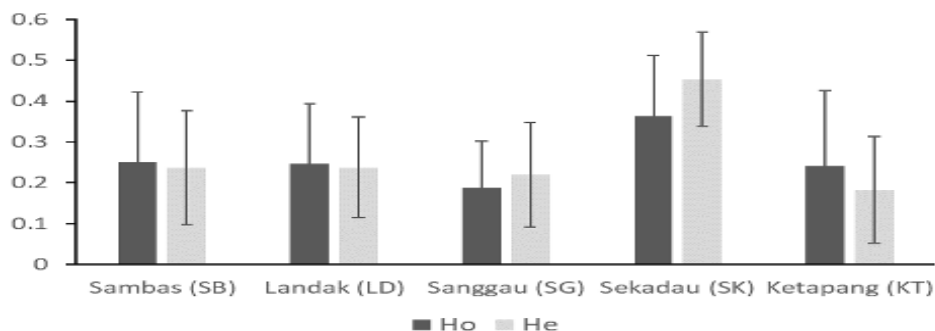


Figure 2. Mean values of the observed heterozygosity (Ho) and expected heterozygosity (He) using 20 SSR primers on five populations of the species *D. testudinarius*.

observed heterozygosity (Ho = 0.363) and expected heterozygosity (He = 0.453), while the Sanggau population expressed the lowest values (Ho = 0.188; He = 0.220) (Figure 2), indicating reduced genetic variation.

Although Sekadau harbored the greatest genetic diversity, the overall heterozygosity across *D. testudinarius* populations remained relatively low (Ho < 0.50; He < 0.50) compared with other *Durio* germplasm. Santoso *et al.* (2017), for example, reported mean Ho and He values of 0.422 and 0.431, respectively, from 11 *Durio* accessions genotyped with 11 SSR loci, whereas Siew *et al.* (2018) obtained Ho and He values of 0.390 and 0.350 from 45 accessions analyzed using seven SSR markers. These comparisons suggest that *D. testudinarius* possesses a relatively narrow genetic base.

The limited genetic diversity is likely attributable to restricted gene flow among populations. This pattern may have an association with the species' reproductive biology, particularly its cauliflorous flowering habit, in which inflorescences are borne on the lower portion of the trunk (Figure 1). Such a growth form could reduce opportunities for long-distance pollen dispersal. Moreover, Ferella *et al.* (2022) reported that *D. testudinarius* populations in Sambas exhibit a clumped spatial distribution resulting from localized seed regeneration, further promoting population isolation and genetic differentiation.

These genetic patterns are consistent with previous morphological observations. Multivariate morphological analysis showed

individuals from the Sanggau population signified an association primarily with variations in abaxial leaf glossiness, plant height, stem circumference, and leaf blade width and shape (Magandhi *et al.*, 2024). However, the extensive overlap with individuals from Sambas, Sekadau, Landak, and Ketapang indicates limited morphological differentiation, suggesting the Sanggau population does not represent a distinct morphological entity despite its relatively low genetic diversity.

Phylogenetic relationships

Phylogenetic reconstruction based on combined chloroplast DNA markers (*rbcl*, *matK*, and *trnL-F*) and the nuclear ITS region generated a dataset of 2,131 bp, comprising five *D. testudinarius* accessions, together with representative *Durio* species retrieved from GenBank (*D. dulcis*, *D. zibethinus*, *D. oxleyanus*, *D. kutejensis*, *D. graveolens*, and *D. lanceolatus*), using *Theobroma cacao* as the outgroup (Table 3; Figure 3). Bootstrap support across several internal branches was generally low (<80%), indicating limited sequence variation among closely related taxa.

The major *Durio* clade attained a strong support (BS = 99%), whereas the placement of *D. acutifolius* received only a moderate support (BS = 65%). Within *D. testudinarius*, all five accessions formed a monophyletic group, although internal relationships only gained moderate resolution (BS = 76%). Notably, the Sambas and

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