



Research article

Molecular diversity and phylogenetic relationship of native *Garcinia* (mangosteen and relatives) from Kalimantan, Indonesia

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Abstract

Importance of the work: Globally, Indonesia is one of the biggest producers of mangosteen (*Garcinia mangostana* L.), known as the “queen of fruits”.

Objectives: To determine the molecular diversity and phylogenetic relationship of mangosteen and its wild relatives (*Garcinia* spp.), native to Kalimantan, Indonesia, using the *matK* and *rbcL* markers and to compare these to other data in the GenBank database.

Materials and Methods: In total, 34 *Garcinia* samples were used, with 12 originating from Kalimantan, Indonesia. Molecular analysis began with DNA isolation using a CTAB method, with a soft modification. Next, the DNA isolates were quantified and amplified using an ultraviolet-visible spectrum spectrophotometer and a thermal cycler to perform polymerase chain reaction. The DNA targets (*matK* and *rbcL*) were sequenced using the ABI PRISM 377 sequencer at Apical Scientific Sdn. Bhd. (Seri Kembangan, Selangor, Malaysia). The molecular diversity was assessed using the nucleotide diversity index (π), while the molecular phylogeny was determined based on maximum likelihood analysis with a statistical bootstrap.

Results: Molecular analysis revealed that *Garcinia* had high molecular diversity, as indicated by π values of 0.062 for *matK* and 0.083 for *rbcL*. The phylogenetic analysis, based on the combination of the *matK* and *rbcL* markers, revealed that this germplasm could be divided into three (local scale) and six groups (global scale), with *G. mangostana* being closely related to *G. parvifolia*, *G. latissima*, and *G. dulcis*.

Main finding: This essential information could be used to enhance the future efficiency and effectiveness of the mangosteen breeding and conservation program.

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Introduction

Mangosteen (*Garcinia mangostana* L.), commonly called the ‘queen of fruits’, has an popular, exotic (delicious) fruit flavor that is preferred by many people worldwide (Seethapathy et al., 2018). Apart from its taste, some parts of this plant can also be used traditionally as medicinal raw materials (Hazarika and Lalnunsangi, 2019). For example, for some Asian people, mangosteen peel (the rind) can be used as a medicine for diabetes, obesity and liver disorders (Gogoi et al., 2021). The rind of mangosteen has been a source of bioactive compounds rich in xanthenes, which are medicinal compounds that can be used as antioxidants, anti-inflammatories, antibacterials, anti-cancers and antiviral agents (Hazarika and Lalnunsangi, 2019; Wee et al., 2022). With such potential, mangosteen is a promising horticultural commodity, with added attraction as an export commodity to enhance foreign exchange. For example, in 2020, Indonesia became the largest producer of mangosteen in the world, with production reaching more than 270,000 t and an export value of USD 75.67 million (Mursyidin et al., 2024).

However, despite being the world's largest exporter of mangosteen, Indonesia's mangosteen fruit quality still requires improvement, mainly due to the low tolerance of the fruit-bearing plants to pests, diseases and environmental changes (Murthy et al., 2018). Consequently, plant breeding efforts must be undertaken to enhance the quality of Indonesia's mangosteen. Furthermore, considering that mangosteen is a plant with a narrow genetic diversity (because it is apomictic and agamospermic, where the development of fruit and seeds occurs without gamete fusion), it is vital to expand genetic diversity (Sutthinon et al., 2019). This can be achieved by exploring and characterizing mangosteen cultivars and their wild relatives' germplasm is carried out (Mursyidin and Maulana, 2020). According to Hazarika and Lalnunsangi (2019), some mangosteen relatives carry unique (superior) genes that could be applied to improve the quality and expand the genetic diversity of mangosteen.

To date, 40 species of *Garcinia* have been classified as edible and are widely distributed, especially in Southeast Asia (Gaudeul et al., 2024). In Indonesia, it is known that as many as 64 species of *Garcinia* out of 400 species worldwide can be applied in breeding tasks (Seethapathy et al., 2018), including *Garcinia atroviridis*, *G. hombroniana*, *G. indica*, *G. multiflora*, and *G. pedunculata* (Hazarika and Lalnunsangi, 2019). According to Mursyidin and Maulana (2020),

the genetic diversity of *Garcinia* in Indonesia is spread across several large islands, including Kalimantan (25 species), Sumatra and Sulawesi (22 species), with the remaining species distributed throughout Java, Nusa Tenggara, Maluku and Papua. Conceptually, breeding tasks involve in-depth characterization of the germplasm owned, both morphologically, anatomically, biochemically and molecularly (Acquaah, 2015; Yu et al., 2022).

The current study aimed to determine the molecular diversity and phylogenetic relationships of mangosteen and its relatives (*Garcinia* spp.), native to Kalimantan, Indonesia, and to compare them to other data in GenBank, based on the combination of DNA barcoding markers, specifically *matK* and *rbcL*. According to Barthet et al. (2020), *matK* is one of the functional chloroplast genes that has a relatively high mutation rate, while substitutions (transitions) are often found more than indels (insertions and deletions) (Kar et al., 2015). *rbcL*, a functional chloroplast gene, has a lower mutation rate than *matK*. However, because *rbcL* is easily duplicated, sequenced and aligned, it is preferred in phylogenetic studies (Dong et al., 2013). In general, chloroplast genes, such as *matK* and *rbcL*, are reliable standard molecular markers in phylogenetic analyses, because they are inherited uniparentally (maternally) and have a simple structure, yet have high genetic stability (CBOL Plant Working Group, 2009; Galimberti et al., 2014).

According to Sevindik et al. (2024), *matK* and *rbcL* sequences could be utilized to determine nucleotide ratios and the genetic distance and nucleotide diversity (π) of organisms such as *Prunus armeniaca* (Rosaceae). Both markers have been successfully applied to study the diversity and taxonomy of bamboo (Bambuseae) (Awaliah and Polosoro, 2024; Yong et al., 2024) and the Burseraceae (Teklemariam et al., 2023). Hence, the application of these two markers could also improve and complement the weaknesses of PCR-based molecular markers (DNA fingerprinting), such as random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism RFLP, amplified fragment length polymorphism (AFLP) and inter-simple sequence repeat (ISSR), which have highly subjective analytical results with low reproducibility and limited cross-taxon discriminative ability (Li et al., 2011). In contrast, DNA barcoding markers, such as *matK* and *rbcL*, based on DNA sequencing, offer high resolution for identifying closely related species, and the analytical results are more standardized and can be reproduced across laboratories (CBOL Plant Working Group, 2009; Chac and Thinh, 2023). Additionally, these markers provide sequence information for direct comparison in a global database (Ho et al., 2021).

Thus, the results of the current study should be of considerable value in supporting future mangosteen breeding efforts.

Materials and Methods

Plant materials

In total, 34 *Garcinia* samples were used, with 12 collected directly from the island of Kalimantan (Borneo), Indonesia, using a purposive sampling method (Table S1 in Supplementary File). In contrast, the others were obtained from the GenBank database (Table S2 in Supplementary File). The samples collected directly were prepared and the molecular analysis carried out in the Laboratory of Genetics and Molecular Biology, Faculty of Mathematics and Natural Sciences, University of Lambung Mangkurat, Indonesia.

Molecular preparation and analysis

The molecular preparation and analysis commenced with DNA isolation using a modified CTAB method, which incorporated mercaptoethanol to remove phenolic compounds from the sample (Aboul-Maaty and Oraby, 2019). At this stage, a leaf sample weighing 0.5 g was used for each of the different samples. After obtaining pure DNA, the sample was quantified and amplified using spectrophotometry and PCR methods. In the amplification process, two *matK* and *rbcL*-specific primers were used (Table S3, Supplementary file). DNA amplification was performed using the MultiGene Optimax PCR equipment from Labnet International Inc. (Madison, NJ, USA) with a reaction volume of 25 μ L (consisting of 2 μ L of template DNA, 22.0 μ L of PCR mix (Bioline; Memphis, TN, USA) and 1 μ L of DNA primer (10 μ M). The PCR conditions according to Mursyidin and Firmanda (2024) were: initial denaturation (94°C; 5 min); 35 cycles of denaturation (94°C; 30 s), annealing (48°C; 30 s) and extension (72°C; 45 s); and a third, final extension (72°C; 7 min). Visualization of the PCR results used the electrophoresis method with fluorescence under a UV transilluminator. The DNA of the target formed (*matK* and *rbcL*) was sent to Apical Scientific Sdn. Bhd. (Seri Kembangan, Selangor, Malaysia) to be purified and sequenced using the bidirectional Sanger method on an ABI PRISM 377 sequencer (Applied Biosystems; Waltham, MA, USA).

Data analysis

All the *matK* and *rbcL* sequence data of *Garcinia* were aligned using the ClustalW software (Larkin et al., 2007). The genetic diversity was determined using the nucleotide diversity index (π), as described by Nei and Li (1979). Phylogenetic analysis was conducted using the maximum likelihood method and evaluated based on 1,000 replicates of statistical bootstrap (Mursyidin et al., 2022). All analyses were conducted using the MEGA 11 software (Tamura et al., 2021).

Results and Discussion

Genetic diversity and its importance

Native *Garcinia* had unique *matK* and *rbcL* sequence characteristics, with the germplasm consisting of different lengths of both sequences: 914 bp for *matK* and 577 bp for *rbcL* (Table 1). Further analysis revealed that *matK* and *rbcL* exhibited distinct guanine-cytosine (GC) contents, polymorphisms, transition/transversion bias values, and genetic (nucleotide) diversity. The *matK* sequence had a polymorphic site at position 323, a transition/transversion bias value of 1.03, a GC content of 32.23%, and a nucleotide diversity of 0.062. The *rbcL* sequence had 163 polymorphic sites, a transition/transversion bias value of 1.526, a GC content of 44.82 and a nucleotide diversity of 0.057 (Table 1). Based on Table 1, the combination of the two markers showed high nucleotide diversity (0.083), a GC content of 38.18%, a transition/transversion bias of 1.209 and 473 polymorphic sites. Fig. 1 illustrates the detailed evidence of polymorphisms in the *matK* and *rbcL* sequences, where substitutions (both transitions and transversions) were more prevalent than insertions and deletions (indels).

Table 1 Molecular characteristics of *matK*, *rbcL* sequences and their combination for native *Garcinia* based on Kimura 2-parameter model

Parameter	<i>matK</i>	<i>rbcL</i>	Combined
Sequence length analyzed (bp)	914	577	1491
Polymorphic sites	323	163	473
Transition/transversion bias value	1.030	1.526	1.209
Guanine-cytosine content (%)	32.23	44.82	38.18
Nucleotide diversity	0.062	0.057	0.083

(A)

Samples	Nucleotide Position																													
	1	2	5	29	31	40	141	181	182	183	184	185	186	194	195	270	278	299	322	333	335	359	384	401	403	407	478	514	532	566
Consensus	-	-	-	T	A	G	C	A	A	C	A	A	A	A	C	C	T	T	T	C	G	G	C	A	C	C	G	T	T	A
G1	-	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
G2	T	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
G3	T	C	T	.	T	.	T	.	.	.	.	.	.	G	T	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.
G4	-	-	-	C	T	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	T	.	.	.	.	A	.	.
G5	T	C	T	.	T	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	G	.	.	.	.	.	G
G6	T	T	C	.	T	A	T	.	.	.	.	.	.	-	-	A	G	.	A	A	.	T	.	.	T	.	.	.	.	.
G7	T	C	T	C	.	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	G	.	.	.	.	.	G
G8	-	-	T	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
G9	-	-	C	.	.	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	A	.	.
G10	-	-	C	.	.	A	T	.	.	.	.	.	.	-	-	A	G	.	.	A	.	.	.	.	.	.	.	.	.	.
G11	T	C	T	.	.	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	A	.	.
G12	T	T	C	.	T	.	T	T	T	T	G	T	T	G	T	.	G	C	.	.	C	.	.	.	.	T	.	.	G	.

continued ...

Samples	Nucleotide Position																												
	569	573	592	613	616	629	636	664	668	682	685	703	714	716	727	773	784	824	825	866	868	894	907	908	909	910	911	912	913
Consensus	A	C	G	C	T	C	T	G	C	T	G	A	T	G	G	A	C	G	T	T	A	A	G	A	C	T	C	-	-
G1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-	-
G2	.	.	.	A	.	.	C	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	-	-	-
G3	.	.	.	A	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	G	.	-
G4	.	.	T	A	.	T	.	A	.	G	.	.	.	.	A	.	T	.	C	.	.	C	.	T	-	-	-	-	-
G5	.	.	T	A	C	T	.	A	.	G	.	.	G	.	A	G	T	.	C	.	.	C	A	C	T	C	T	G	T
G6	G	G	T	A	.	T	.	A	G	.	.	.	.	.	A	.	T	T	C	.	.	.	A	C	T	C	G	-	-
G7	.	.	T	A	C	T	.	A	.	G	.	.	G	.	A	G	T	.	C	.	.	C	.	.	.	.	-	-	-
G8	.	.	.	A	.	.	C	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	G	T	-
G9	.	.	T	A	.	T	.	A	.	G	.	.	.	.	A	.	T	.	C	.	.	C	A	C	T	C	G	G	G
G10	.	.	T	A	.	T	.	A	.	.	.	.	.	G	A	.	T	.	C	.	.	.	A	C	T	C	G	G	G
G11	.	.	T	A	.	T	.	A	.	G	.	.	.	.	A	.	T	.	C	.	.	C	A	C	T	C	G	T	G
G12	.	.	T	A	.	T	.	A	.	.	A	C	.	.	A	.	T	.	C	C	C	C	.	.	.	.	G	-	-

(B)

Samples	Nucleotide Position											
	18	19	24	25	26	192	209	302	415	417	423	443
Consensus	A	G	G	G	A	A	G	T	C	G	A	G
G1	.	.	.	.	.	.	.	.	.	.	.	.
G2	.	.	.	.	.	.	.	.	.	.	.	.
G3	.	.	.	.	.	.	.	.	.	.	.	.
G4	.	.	T	T	T	.	.	C	.	.	.	.
G5	G	.	.	.	.	.	.	C	.	.	.	.
G6	.	.	.	.	.	.	.	C	A	T	G	A
G7	G	.	.	.	.	.	.	C	.	.	.	.
G8	.	.	.	.	.	.	.	.	.	.	.	.
G9	.	A	T	T	T	.	.	C	.	.	.	.
G10	G	.	.	.	.	G	A	C	.	T	.	A
G11	.	A	T	T	T	.	.	C	.	.	.	.
G12	G	.	.	.	.	.	.	C	A	.	.	.

■ insertion
■ deletion
■ transition
■ transversion

Fig. 1 Polymorphism in *matK* (A) and *rbcl* (B) regions of native *Garcinia* showing four mutation events: insertion (red), deletion (yellow), transition (green) and transversion (blue), where A = adenine, C = cytosine, G = guanine and T = thymine.

According to Swarup et al. (2021), genetic diversity is closely related to mutations. In this context, genetic diversity arises as a result of mutations. Mutations alone are the basis for the emergence of genetic diversity. At the population level, mutations are indispensable for forming a baseline population (Govindaraj et al., 2015). Hence, genetic diversity is important in natural selection and evolution. Furthermore, the direction of evolutionary change in response to environmental change necessitates genetic diversity parameters. According to Lloyd et al. (2016), the high genetic diversity in a population is an essential prerequisite for dealing with extreme environmental changes.

Based on the current results, the genetic diversity of *Garcinia* was relatively high, with important implications for plant conservation and breeding programs. Conceptually, germplasm with a high genetic diversity level is more adaptive and survives dramatic environmental changes than germplasm with low or narrow genetic diversity (Jackson et al., 2014). According to Mursyidin et al. (2022), the high genetic diversity of a germplasm is also valuable in increasing the efficiency and effectiveness of the conservation and breeding programs.

However, despite the high level of genetic diversity, the development or genetic expansion of *Garcinia* is still required, especially for commercial species, such as mangosteen, with strong market value based on consumer demand. Breeders have suggested several methods to expand the genetic diversity of mangosteen, including hybridization or crossing with other species, especially wild types. According to Migicovsky and Myles (2017), some wild species of *Garcinia* possess superior genes that could be introduced into commercial mangosteen, as has been recognized for most wild relatives and that can be introduced to enhance the

genetic diversity of populations (Witherup et al., 2019; Yan, 2021). Similarly, mutagenesis and introgression can be applied to the genetic expansion of mangosteen (Allier et al., 2020). Conceptually, mutagenesis is a biochemical process where the genetic information of an organism is changed by mutations, both spontaneously or artificially, especially by chemical or mutagenic agents (Zhang and Vijg, 2018). Introgression ('introgressive hybridization') is a unique process in which genetic material of an organism is transferred across species and conducted by the repeatable backcrossing of an interspecific hybrid (Neale and Wheeler, 2019).

Phylogenetic relationships and their implications

Based on the combination of the *matK* and *rbcL* markers, *Garcinia* was divided into three groups (local scale) and six groups (global scale), as shown in Fig. 2. In this case, *Garcinia mangostana*, both the 'Balangan' and 'Palembang' varieties, was closely related (one group = clade I) to *G. dulcis*, *G. porrecta*, and *G. forbesii* (Fig. 2A). Group II comprised *G. nervosa*, *G. celebica*, *G. atroviridis*, and *G. xanthochymus*, with the remainder in group III. Globally, when combined with the GenBank data, the grouping of *Garcinia* also changed, with most clustered in the same clade; however, the germplasm occupying clade II was separate from the other clades globally. In this case, *G. nervosa* occupied clade III, while *G. celebica*, *G. atroviridis* and *G. xanthochymus* belonged to clade V (see Fig. 2B). In more detail, the closest relationship was for *G. celebica* and *G. xanthochymus*, while the farthest was between *G. latissima* and *G. atroviridis* and *G. xanthochymus* (Fig. 3).

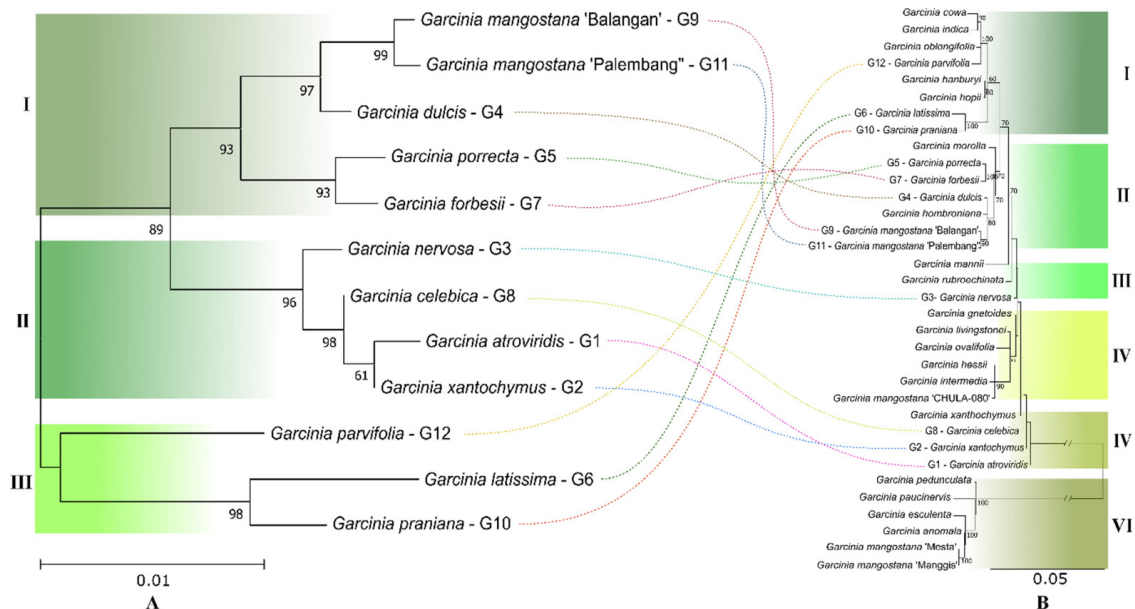


Fig. 2 Phylogenetic relationships of native *Garcinia* based on combined *matK* and *rbcL* markers, where A indicates local scale and B indicates global scale.

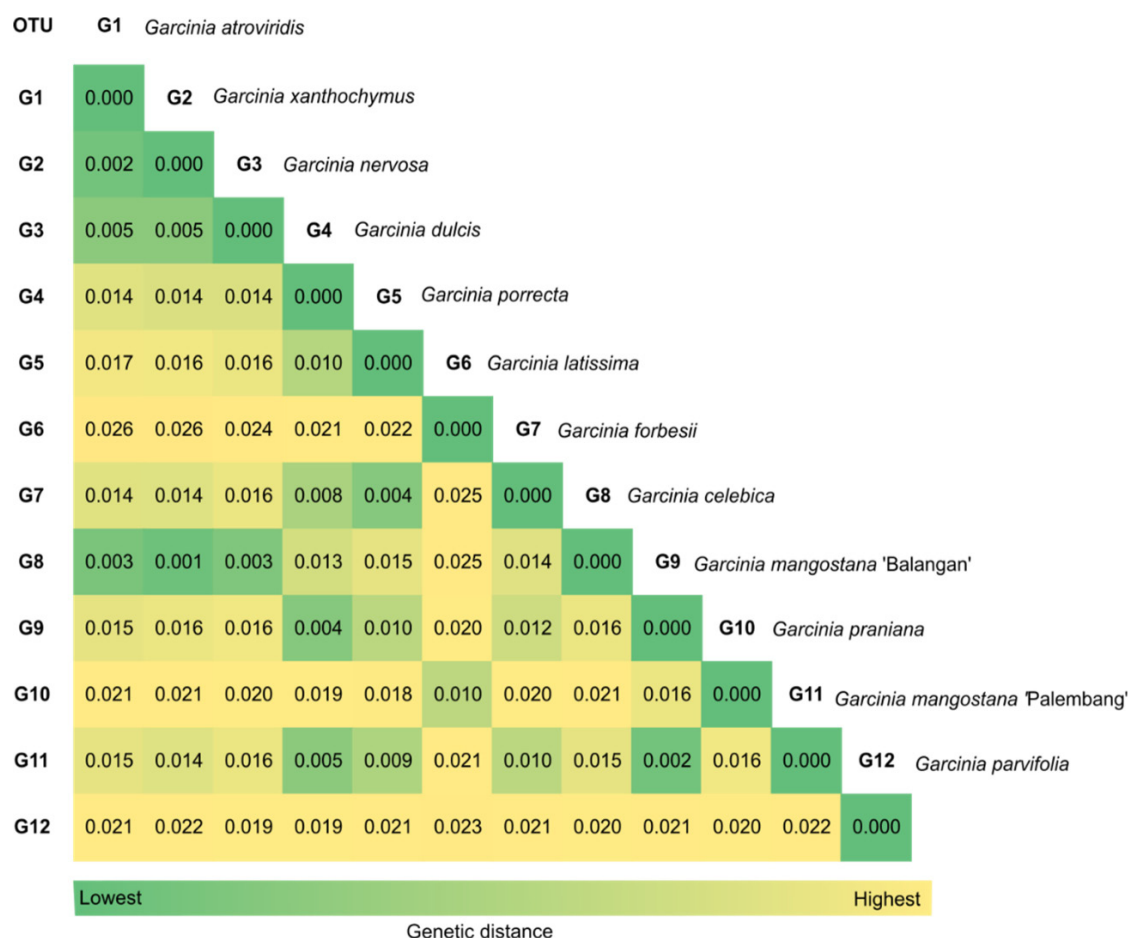


Fig. 3 Genetic distances of native *Garcinia* based on combined *matK* and *rbcL* markers, where OTU = operational taxonomic unit.

According to Mursyidin et al. (2024), information on molecular phylogeny or phylogenetic relationships can be used to improve the efficiency and effectiveness of plant breeding programs. In this context, cross-breeding between the samples studied can expand the existing genetic diversity and enhance the quality of the desired plant. For mangosteen, quality improvement is still oriented towards yield, in addition to improving the quality of fruits and plants to be resistant to pest and disease attacks, as well as adaptive to abiotic stresses, such as drought and salinity.

Because mangosteen has a weak reproductive barrier, self-improvement can be achieved through crossbreeding, where the parents at the interspecific level are crossed to produce the desirable hybrids. For example, 'Julu' is one of the commercial mangosteen cultivars from the Philippines that was developed by this method for the characteristics of larger fruits and seeds (Murthy et al., 2018). In contrast, the 'Mesta' cultivar from Malaysia has been developed with the characteristics of a smaller fruit size without a seed (Murthy et al., 2018).

Sutthinon et al. (2018) suggested using *G. celebica* as a donor for refining a male functionality gene in mangosteen

Furthermore, information on molecular phylogeny is helpful in supporting conservation tasks. Crossing parents with distant genetic relationships can produce offspring with high genetic diversity, while crossbreeding with close relatives generally results in offspring with low or narrow genetic diversity (Acquaah, 2015). Based on the current results, mangosteen was closely related to *G. parvifolia* and *G. latissima*, as well as to *G. dulcis* (Fig. 2C).

Nazre et al. (2018) used a variety of markers, from morphological to molecular, to reveal interesting results about the relationships between mangosteen and other *Garcinia* species. Based on morphological markers, namely petal color and pistil shape, they reported *G. mangostana* was closely related to *G. malaccensis*. The proximity of *G. mangostana* to *G. malaccensis* was also reported by Sobir et al. (2009), based on the AFLP molecular marker AFLP. Mursyidin and Maulana (2020) reported the closeness between *G. mangostana* and

G. wightii, based on biochemical markers (bioactive compounds and their bioactivities). Sinaga et al. (2010) used isozyme markers to reveal the proximity between *G. mangostana*, *G. hombroniana* and *G. malaccensis*.

Furthermore, Sobir et al. (2011) revealed the proximity of *G. malaccensis* to *G. mangostana*, an allopolyploid derivative ancestor, based on ISSR analysis. Using a similar ISSR marker, Sulassih et al. (2013) reported proximity between *G. mangostana*, *G. malaccensis* and *G. celebica*. Finally, in different studies, based on the internal transcribed spacer (ITS) marker, *G. mangostana* was reported to have the closest relationship with *G. intermedia* (Liu et al., 2016), *G. penangiana* (Nazre, 2014) and *G. xanthochymus* (Parthasarathy et al., 2016).

In conclusion, the native *Garcinia* from Kalimantan, Indonesia, had high molecular diversity, as indicated by π values of 0.062 for *matK* and 0.083 for *rbcL*. The phylogenetic analysis, using the combination of *matK* and *rbcL* markers, revealed that this germplasm was divided into three (local scale) and six groups (global scale), where *G. mangostana* was closely related to *G. parvifolia*, *G. latissima*, and *G. dulcis*. This information should support future breeding and conservation programs of mangosteen.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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