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Research Article

Genetic Diversity and Phylogenetic Position of Traditional Rice (*Oryza sativa* L.) Landraces: A Case Study of South Kalimantan in Indonesia

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Abstract: Traditional rice (*Oryza sativa* L.) landraces provide many essential genes for improving yield, disease resistance, abiotic stress tolerance, and other parameters for future rice breeding. This study aimed to analyze the genetic diversity and determine the phylogenetic position of the traditional rice landraces from the tidal swamp areas of South Kalimantan, Indonesia, compared to other rice germplasm, including wild relatives, obtained from the GenBank database, using a cpDNA-*rbc*L marker. In this case, six traditional rice landraces from this region were collected and analyzed molecularly using the *rbc*L marker and compared with 16 similar others and 25 wild relatives from the GenBank database. The genetic diversity of this germplasm was determined using the nucleotide diversity index (π), whereas the phylogenetic analysis by maximum likelihood with bootstrap for 1 000 replicates. The principal component analysis (PCA) was employed to confirm this grouping. Based on this marker, the traditional rice landraces have a genetic diversity of 0.38, lower than intra-species and inter-species levels, i.e., 0.44 and 0.83, respectively. The phylogenetic analysis shows that this germplasm has separated from most *O. sativa* rice cultivars and their wild relatives, except for the 'GBVN' and 'NARC' (comparison cultivars obtained from GenBank). This information has substantial implications for future rice breeding and conservation efforts, locally and globally.

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1. Introduction

Over the last 10 000 years, rice, an important staple crop for over half of the world's population, has been massively domesticated (Hu et al., 2018). As a result, it is unsurprising that this crop has been distributed far from the center of its diversity and cultivated in various ranges of environmental systems and conditions, i.e., from monoculture (single-crop) in temperate zones to the tropics with rainfed and irrigated polycultures (Reig-Valiente et al., 2016). Even rice is widely cultivated in more than 120 countries, from 35ºS to 53ºN geographic ordinate, and harvested from 163 million hectares per year, guided by China, India, Bangladesh, Thailand, and Indonesia (Wei and Huang, 2018). Domestication has also led to various cultivated rice with different traits. In national and international germplasm collections, over 400 thousand rice cultivars have been stored and recorded (Wei and Huang, 2018).

In general, two species of cultivated rice with a unique historical background of domestication, namely *Oryza sativa* (better known as Asian rice) and *Oryza glaberrima* (African rice), are known (Sweeney & McCouch, 2007). According to Hu et al. (2018), *O. sativa* and *O. glaberrima* have domesticated independently from the AA genome wild *Oryza* rice in Asia and Africa. By the cytological analysis, the genus *Oryza* comprises 22 wild relatives and separates into four species complexes, i.e., the *O. sativa*, *O. officinalis*, *O. ridleyi*, and *O. granulata* (Wei and Huang, 2018). *O. sativa* complex contains two domesticated species: *O. sativa* and *O. glaberrima*, and six wild species, including *O. barthii*, *O. glumaepatula*, *O. longistaminata*, *O. meridionalis*, *O. nivara*, and *O. rufipogon* (Wei and Huang, 2018; Xu and Sun, 2021).

According to Izawa (2008), all cultivated and wild rice have different distributions. *Oryza sativa*, for example, is distributed around the world with a concentration in Asia, while *O. glaberrima* is in Africa. Barth's rice (*O. barthii*) and long-stamen rice (*O. longistaminata*) are African ones, where the first is endemic to West Africa, whereas the second is to the entire of Africa. In contrast, *O. glumaepatula* is endemic in Central and South America, and *O. meridionalis* is native to Australia. So both are known as South American and Australian wild rice, respectively. Finally, *O. rufipogon* (usual wild rice) and *O. nivara* (annual wild rice) are present throughout Asia and Oceania (Sweeney and McCouch, 2007; Wei and Huang, 2018).

Besides the various rice germplasm, rice breeding is production or yield-oriented. On the other hand, domestication and contemporary rice breeding created a wide genetic bottleneck. Consequently, the superior genes or alleles that contribute to yield, and other variables, like disease resistance and abiotic stress tolerance, might be lost in the modern rice cultivars because of this effect. Meanwhile, these superior genes were present in the wild progenitors and traditional rice landraces (Reig-Valiente et al., 2016). However, due to human interference destroying their habitats, wild species are in danger of going extinct, and farmers' preference for high-yield commercial cultivars has resulted in the disappearance of traditional landraces (Mursyidin et al., 2017; Wei and Huang, 2018). Thus, collecting, documenting, analyzing, or characterizing wild and cultivated (traditional) rice cultivars are indispensable (He et al., 2021).

South Kalimantan in Indonesia is an urgent route for the domestication and distribution of traditional rice cultivars worldwide (Mursyidin et al., 2017). In this region, hundreds of traditional rice cultivars are found and still preserved, also maintained by the local farmers (Mursyidin et al., 2017). Previously, we have successfully characterized this germplasm by morphological markers, both at the macro (Mursyidin et al., 2018; Mursyidin and Khairullah, 2020) and micro-structure levels (Mursyidin et al., 2019, 2021). While these markers are essential in evaluating rice germplasm, they were strongly affected by environmental variables (Nadeem et al., 2018). Besides, these traits have certain disadvantages, such as time-consuming, low polymorphism, late expression, and low heritability (Anumalla et al., 2015).

Recently, the *rbc*L marker, part of the cpDNA genome, has been valuable and urgent in characterizing rice germplasm, including their domestication history. According to Izawa (2008), following this method, the order of most DNA changes, such as single nucleotide polymorphisms during domestication, can be inherited due to relatively low mutation rates. As a result, this study aimed to analyze the genetic diversity and determine the phylogenetic position of the existing traditional rice landraces from the tidal swamp areas of South Kalimantan in Indonesia and compared to other (*O. sativa*) cultivars and wild relatives (*Oryza* spp.) obtained from the GenBank database, using the *rbc*L marker. In this study, we hypothesized that traditional rice landraces from this region have low diversity. Thus, our results provide urgent guidance to support future rice breeding and conservation efforts, locally and globally.

2. Material and Methods

2.1. Plant materials

A total of 47 samples of rice (*Oryza* spp.) comprise six traditional rice (*O. sativa*) landraces from the tidal swamp areas of South Kalimantan in Indonesia, including 16 other commercial rice cultivars (*O. sativa*) and 25 wild relatives, obtained from GenBank, were used in the study (Table 1).

Table 1. Rice samples (*O. sativa*), including wild relatives, used in the study, their accession number and nucleotide length of *rbc*L

Rice samples	Origin	Accession Number	Nucleotide Length (bp)
Landrace (*O. sativa*)			
'Lakatan Gadur'	Sungai Tabuk, Banjar, South Kalimantan	MZ198245	608
'Raden Rata'	Tabunganen, Barito Kuala, South Kalimantan	MZ198246	606
'Lemo Putih'	Kertak Hanyar, Banjar, Kalimantan Selatan	MZ198247	605
'Pandak Kembang'	Barambai, Barito Kuala, South Kalimantan	MZ198248	605
'Siam Mutiara'	Aluh Aluh, Banjar, South Kalimantan	MZ198249	608
'Karang Dukuh'	Barambai, Barito Kuala, South Kalimantan	MZ198250	607
Commercial cultivar (*O. sativa*)[1]			
'Shuhui498'	Republic of China	CP018170.1	607
'RP Bio-266'	Republic of India	KU705873.1	607
'Basmati'	Republic of India	KT289403.1	607
'Anonymous-1'	Saudi Arabia	JN861110.1	607
'93-11'	Republic of China	AY522329.1	607
'Hassawi'	Kingdom of Saudi Arabia	JN861109.1	607
'Anonymous-2'	Japan	X15901.1	607
'Nipponbare'	Japan	AY522330.1	607
'Anonymous-3'	Republic of China	KT289404.1	607
'Anonymous-4'	Republic of China	MW001303.1	607
'TN1'	Republic of Korea	KM103369.1	607
'IR8'	Republic of Korea	KM103367.1	607
'NARC'	Islamic Republic of Pakistan	KP827660.1	601
'N22'	Republic of Korea	MG252500.1	607
'HSAGSDYD1802'	Republic of China	MT653617.1	607
'GBVN15800'	Socialist Republic of Vietnam	KR073275.1	592
Wild relatives[1]			
O. alta	Republic of China	MT726934.1	607
O. australiensis	Republic of China	MT726929.1	607
O. barthii	Republic of China	KF359904.1	607
O. brachyantha	Republic of China	MT726939.1	607
O. coarctata	Republic of China	MT726931.1	607
O. eichingeri	Republic of China	KX085496.1	607
O. glaberrima	Republic of China	KF359903.1	607
O. glumipatula	Republic of China	KF359905.1	607
O. grandiglumis	Republic of China	MT726928.1	607
O. granulata	Republic of China	KF359920.1	607
O. latifolia	Republic of China	KF359915.1	607
O. longiglumis	Republic of China	MT726933.1	607
O. longistaminata	Republic of China	KM881642.1	607
O. malampuzhaensis	Republic of China	MT726935.1	607
O. meridionalis	Republic of China	KF359906.1	607
O. meyeriana	Republic of China	KF359921.1	607
O. minuta	Republic of Korea	KU179220.1	607
O. neocaledonica	Republic of China	MT726926.1	606
O. nivara	Japan	AP006728.1	607
O. officinalis	Republic of China	MT726930.1	607
O. punctata	Republic of China	MT726932.1	607
O. rhizomatis	Republic of China	KX085497.1	607
O. ridleyi	Republic of China	MT726937.1	607
O. rufipogon	Republic of China	KF359902.1	607
O. schlechteri	Republic of China	MT726927.1	607

[1] Obtained from GenBank database.

2.2. DNA isolation and other molecular assays

DNA isolation was performed using a commercial kit from Geneaid Biotech, Taiwan (Plant genomic DNA mini kit, GP100) against the young leaves of each rice sample. DNA samples were then quantified using the spectrophotometric UV-Vis method and amplified using a pair of specific rbcL primers (Gholave et al., 2017), i.e., 5'-ATGTCACCACAAACAGAGACTAAAGC-3' (Forward) and 5'-GTAAAATCAAGTCCACCRCG-3' (Reverse). The amplification reaction follows the instructions of Gholave et al. (2017), using a PCR machine from Applied Biosystem, USA (SimpliAMP Thermocycler PCR), with a total volume of 25 μL. The volume reaction consists of PCR mix (22 μL, MyTaq HS Red Mix, Bioline, UK), forward and reverse primer (10 μM, 2.0 μL), and DNA template (10 ng, 1.0 μL). The formed target DNA (rbcL) was then separated by the electrophoresis method (2% gel agarose in 1xTBE Buffer and GelRed dye) and observed in a UV transilluminator. After that, it was isolated and re-purified for sequencing at 1st Base Ltd., Malaysia, using the Sanger (bidirectionally) method. The sequence results were deposited in Genbank with accession numbers MZ198245- MZ198250 (Table 1).

2.3. Data analysis

By the MEGA-X program, all *rbc*L sequences were examined, modified, and put together (Kumar et al., 2018). Utilizing the nucleotide diversity index (π) approach, the genetic diversity was determined and classified into three categories: low (0.1 to 0.4), medium (0.5 to 0.7), and high (0.8 to 2.0) (Nei & Li, 1979). Multiple sequence alignments of the sequences were carried out using Clustal-Omega for phylogenetic analysis (Sievers et al., 2020), and they were manually altered using a similar program to the one previously used to create an unbias sequence alignment. The Consortium for the Barcode of Life (CBOL) provided instructions for the use of Kimura 2-Parameter (K2) distances in MEGA-X to determine interspecific genetic divergences (Kumar et al., 2018). Maximum likelihood was used for the phylogenetic analysis (ML) (Lemey et al., 2009), followed by the bootstrap for 1000 replicates (Mursyidin et al., 2019) and the PCA (Kumar et al., 2022).

3. Results and Discussion

Information on genetic diversity is valuable in crop improvement and conservation efforts (Lloyd et al., 2016). Based on the *rbc*L marker, traditional rice landraces from the tidal swamp areas of South Kalimantan in Indonesia has lower genetic diversity (π% = 0.38) than at intra- and inter-species levels, i.e., 0.44 and 0.83, respectively (Table 2). However, compared to other studies with similar markers, this diversity is higher, such as *Durio zibethinus* and its wild relatives (Mursyidin et al., 2022). Teixeira and Huber (2021) contend that a high genetic diversity level is essential for population survival and ensuring natural populations' capacity for adaptation in the face of constantly shifting environmental stressors.

Table 2. Characteristics of the *rbc*L sequence of *Oryza* germplasm, including traditional rice landraces of South Kalimantan, Indonesia[1]

Parameter	**Traditional rice population (*O. sativa*)**	***O. sativa* population (intra-species)**	**Global rice population (inter-species)**
Sequence length (bp)	605-608	592-608	502-608
Polymorphic sites (*S*)	6	10	26
Akaike Information Criterion (AICc)	1823.853	1980.191	2400.480
Bayesian Information Criterion (BIC)	1885.781	2311.761	3178.071
Maximum Likelihood Value (ln*L*)	-901.896	-945.953	-1105.932
Transition/transversion bias value (*R*)	0.75	0.86	0.94
Guanine-Cytosine/GC content (%)	43.55	43.55	43.47
Nucleotide diversity (π%)	0.38	0.44	0.83
Tajima test of neutrality (D)	-0.64	-0.03	-0.44

[1]Following Kimura 2-parameter model.

Table 3. Polymorphic sites (mutations) are present in the *rbc*L region of traditional rice (*O. sativa*) landraces of South Kalimantan, Indonesia

Landraces	**Accession Number**	**Nucleotide Position**									
		2[a]	**3b[c]**	**4[c]**	**15[c]**	**19[b]**	**588[c]**	**600[c]**	**601[b]**	**610[bc]**	**611[a]**
'Lakatan Gadur'	MZ198245	-	T	T	.	.	.	.	.	C	.
'Raden Rata'	MZ198246	-	-	.	.	.	.	.	.	.	-
'Lemo Putih'	MZ198247	-	-	.	.	.	.	.	.	.	-
'Pandak Kembang'	MZ198248	-	-	.	.	.	C	.	.	.	-
'Siam Mutiara'	MZ198249	.	A	A	C	-	.	A	.	-	-
'Karang Dukuh'	MZ198250	-	T	.	C	.	C	A	-	.	-
Consensus		A	C	G	A	A	T	G	A	A	A

a = insertion, b = deletion, c = transversion.

According to Frankham et al. (2004), the low level of diversity strongly correlates to a mutation occurring in this region. In this study, the traditional rice landraces have six polymorphic or mutation events. In contrast, at the intra- and inter-species levels, the number of polymorphic sites was 10 and 26, respectively (Table 2). In this case, the mutations present in the *rbc*L of rice are substitution (transversion) and indels (insertion-deletion) (Table 3). Referring to Aloqalaa et al. (2019), the transition is more common in these sequences than in transversions. Furthermore, in the course of molecular evolution, there is frequently a pattern where nucleotide transitions repeatedly occur over transversions (Stoltzfus and Norris, 2016).

Further, several factors, such as the founder effect, natural selection, genetic isolation, population bottleneck, and inbreeding, can all contribute to a low level of diversity (Gao et al., 2017). In this case, inbreeding is the most likely cause of this condition (Mursyidin et al., 2017). Local farmers of this region usually select and replant their seeds from the previous crop season. Furthermore, they do both depending on the grain shape and color only. As a result, this rice is homogenous and has a relatively identical genetic background (Mursyidin et al., 2017). In other words, most rice is autogamous (self-pollinated), and inbreeding resulting from this type of reproduction also contributes to low genetic diversity (Jain and Kharwal, 2004).

The Tajima neutrality test (D) has also supported this condition, where this germplasm has an indicating the expansion of population size (for example, after a purifying selection or bottleneck) because all sequences have negative values ($D<0$) (Korneliussen et al., 2013). Consequently, future rice improvement must be oriented to outcrossing, as was employed by Niruntrayakul et al. (2009) and Bierschenk et al. (2020). According to Gaikward et al. (2021), most wild rice relatives have novel beneficial alleles for improving cultivated rice varieties, such as better adaptation to different ecological regimes and biotic and abiotic stresses. Allier et al. (2020) added that broadening the genetic diversity or gene pool of germplasm could be employed by hybridization, introgression, mutation, or genetic engineering.

According to historical records, the low level of rice diversity due to inbreeding is strongly related to the evolutionary pathway and distribution of this plant in this region. Kiple and Ornelas (1999) have predicted that rice plants evolved and spread from Sumatra Island to this region about 300 years before the century. During this period, inbreeding is unavoidable and may reduce genetic diversity (Gao et al., 2017). However, the last parameter is indispensable in generating a foundation population for natural selection or general evolutionary processes (Govindaraj et al., 2015). In other words, this parameter plays a significant role in the future evolutionary direction and adaptive changes. As a result, it has substantial consequences for future conservation and breeding efforts (Lloyd et al., 2016).

The phylogenetic analysis shows the unique relationship of rice germplasm globally. Following the maximum likelihood (ML), this germplasm was separated into three distinct clades (Figure 1). In this case, the traditional rice landraces of South Kalimantan, Indonesia, are separated from most *O. sativa* rice cultivars and their wild relatives. According to Gascuel et al. (2015), these grouping and separation may correlate with ecological factors and landscape dynamics, where each sample is obtained. Similarly, environmental factors and evolutionary history may shape this phylogenetic relationship (Saladin et al., 2019). From the global perspective, dispersal and niche evolution may jointly shape the geographic turnover of phylogenetic clades across continents (Eiserhardt et al., 2013).

The substantial variance in species richness or composition among distinct groupings at the broadest evolutionary scales is due to some intricate and interrelated causes. The most basic assumption behind this research is that clade age should be connected only with this occurrence in extant clades. In other words, older clades will have more time to develop variety than younger clades under the same conditions (Rabosky et al., 2012).

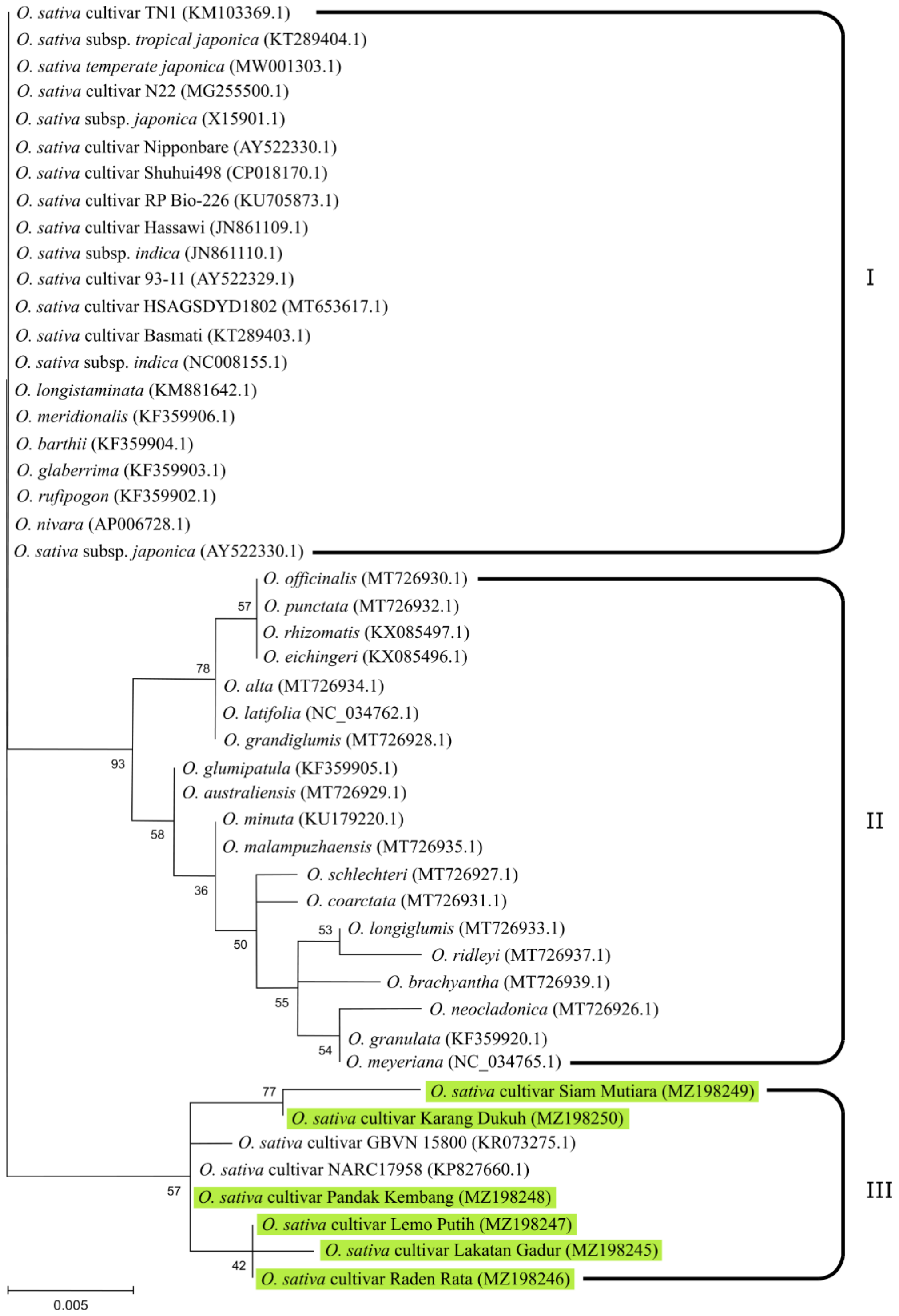

Figure 1. Phylogenetic relationship of tidal swamp rice (O. sativa) landraces of South Kalimantan, Indonesia (highlight), compared to others, including wild relatives (Oryza spp.), based on the ML. The numbers above branches are bootstrap values of 1000 replicates.

Interestingly, two comparison cultivars obtained from GenBank, namely 'GBVN' and 'NARC', are difficult to distinguish because they are joined or clustered together or have the closest related to this traditional rice germplasm (Figure 1), except for the PCA result (Figure 2). In the PCA (Figure 2), this germplasm was clustered into four groups, where the traditional rice landraces were separated into two different groups (i.e., II and III). Furthermore, the 'NARC' is still joined with most tidal swamp rice, whereas the 'GBVN' was formed as a new one (IV).

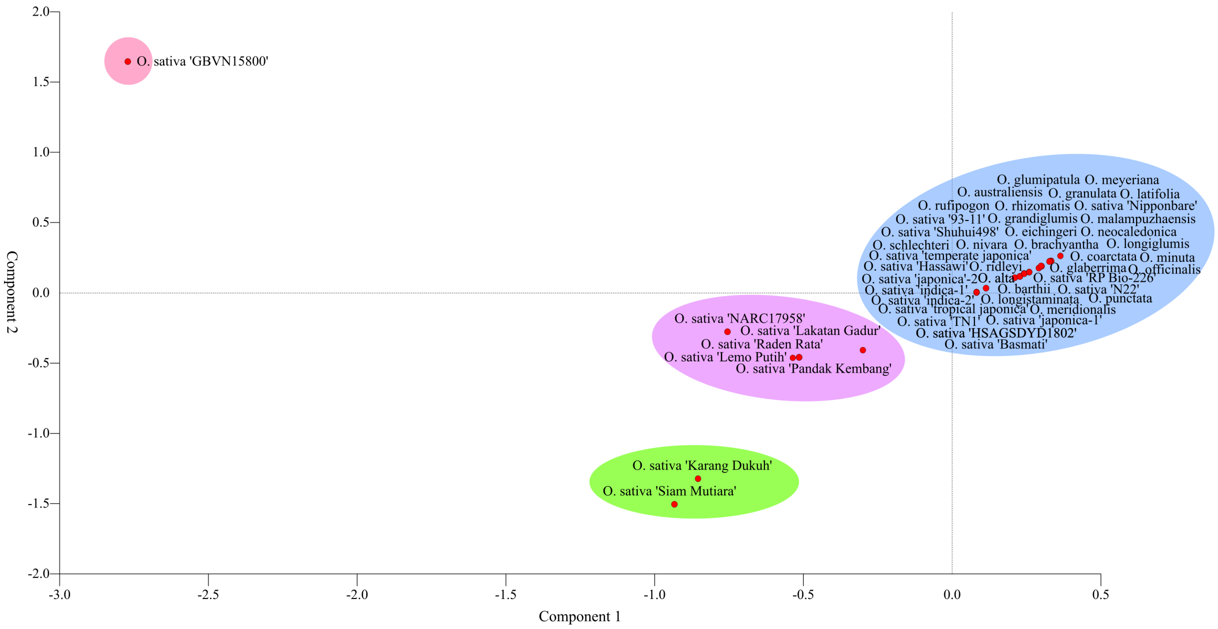

Figure 2. Grouping of traditional rice (*O. sativa*) landraces from South Kalimantan in Indonesia, compared to others, including wild relatives (*Oryza* spp.), based on the PCA.

Philippe et al. (2011) hypothesized that two factors significantly share this case. First, when speciation events occur at close intervals, the quantity of phylogenetic signals produced is generally limited, resulting in short internal tree branches that are difficult to resolve. Second, if the events of interest are old, the terminal nodes are likely to be lengthy and brimming with many substitutions at the same position, known as homoplasy (Philippe et al., 2011). However, the primary cause of this grouping may be an identical single-nucleotide polymorphism (SNP) on the sixth glutamic acid triplet (GAA/GAG). It suggests that the Southeast Asian region may have been the origin of the germplasm ancestors (Hernández-Soto et al., 2022).

As a result, information on this phylogenetic relationship has substantial implications for future rice breeding and conservation efforts, both locally and globally (Flint-Garcia, 2013). Concerning conservation, the phylogenetic study can help resolve species delimitation, gene flow, and genetic differentiation and infer species and their evolutionary history (Fernández-García, 2017). The use of the phylogenetic relationship is also the main focus of current research due to its objective parameters for conservation in previous evolutionary history, the genetic status of present species, and management for future species (Fernández-Garca, 2017).

Finally, the breeding program also depends on the phylogenetic relationship since it forecasts the genetic variety of progeny when individuals mate (Acquaah, 2015). In theory, when distantly related individuals cross out, their descendants may have a broad genetic diversity. In other words, the chances of transgressive segregation increase when individuals from different groups or with a known genetic distance cross. As a result, there is a better chance that distant genotypes will provide unique, desirable alleles at specific loci (Koide et al., 2019). However, crosses between rice subspecies usually have a high rate of infertility. Then, some limitations to this strategy emerge (Guo et al., 2016). In contrast, when closely related individuals cross, the genetic heterogeneity of their progeny may be limited (Turner-Hissong et al., 2020). Breeders and researchers have avoided crossing individuals with a close relationship since the progeny will most likely be inbred.

Briefly, our results complement our previous study that used morphological markers to characterize traditional rice cultivars in the swamp areas of South Kalimantan, Indonesia, as discussed in the introduction section (Mursyidin et al., 2018, 2019, 2021; Mursyidin and Khairullah, 2020). Thus, these findings have novel information and could be valuable as a reference in supporting the rice conservation and breeding program in the future, both locally and globally.

4. Conclusion

In conclusion, the traditional rice landraces naturally growing in tidal swamp areas of South Kalimantan, Indonesia, has lower genetic diversity than other *O. sativa* cultivars (intra-species) and their wild relatives (inter-species). However, it tends to increase along with the taxonomic level observed. Following the phylogenetic analyses used (ML and PCA), this germplasm has a unique relationship, shown by its composition and position where this germplasm is grouped. In this case, all were joined together in a similar clade and separated distinctively from other *O. sativa* cultivars and their wild relatives. Thus, these findings have novel information and could be valuable as a reference in supporting the rice conservation and breeding program in the future, both locally and globally.

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