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Research article

Genetic diversity and relationship of Indonesian swamp rice (*Oryza sativa* L.) germplasm based on agro-morphological markers

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Abstract

Importance of the work: Swamp rice (*Oryza sativa* L.) is essential germplasm for future rice breeding because of some agronomical characters or functional genes.

Objectives: The genetic diversity and relationship was determined of 108 cultivars of Indonesian swamp rice using 31 agro-morphological markers to identify the distinctiveness of the characters that contributed to the genetic diversity based on Pearson correlation analysis among these characters.

Materials & Methods: The standardized Shannon diversity index (*H*') was used to determine the genetic diversity of the germplasm. Principal components analysis (PCA) and the unweighted pair group method with arithmetic mean (UPGMA) were used to identify the distinctiveness of the characters that contributed to the genetic diversity and to reconstruct relationships.

Results: This germplasm was generally low in genetic diversity (Shannon index value of 0.31 for qualitative and 0.36 for quantitative traits). However, two agro-morphological characters, namely the flag leaf attitude and culm diameter of the basal internode, had the highest diversity (H' = 0.68 and 0.97, respectively). PCA confirmed that these two characters contributed significantly to the emerging phenomenon. The culm diameter of the basal internode had a moderate correlation with panicle length and the panicle number of the primary and the secondary basal branches (r = 0.44–0.67). The UPGMA revealed that this germplasm was grouped into nine clusters, with the eighth being the largest (71 cultivars). In addition, the UPGMA revealed that some cultivars had closest relationships, such as *Unyil* with *Karat Kaleng* and *Pelita Rampak* versus *Katimuri*. Conversely, the farthest relationships were for *Sawah Kanyut* versus *Siam Gumpal* and *Siam Salawi versus Siam Gumpal*.

Main finding: This information might be useful in future rice breeding programs, particularly in developing new rice cultivars for swamp areas.

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Introduction

Indonesia and several other Asian countries face severe food insecurity problems (Mursyidin et al., 2019) primarily due to the substantial population increases in the last few decades. In addition, the shrinking of productive agricultural land for various purposes has exacerbated this problem (Yagi and Garrod, 2018). Thus, utilizing marginal lands, such as swamps, is an alternative way to support the national food security program (Govindaprasad and Manikandan, 2014). While this land is generally fragile and lacks nutrients, hopefully, through careful and intensive management, it can become potential agricultural land in the future (Khairullah, 2020). In Asia, about 211.5–224.1 million ha of swamp land is still available for agriculture (Wang, 2020) of which around 34 million ha are in Indonesia, comprising 200.7 million ha of tidal swamp and 13.3 million ha of monotonous swamp (Mursyidin et al., 2019) that is spread over several large islands, mainly Sumatra and Kalimantan (Sulakhudin and Hatta, 2018).

Natural swamp is a unique ecosystem with diverse genetic resources of both plants and animals (Wang, 2020). However, local rice cultivars (also called swamp rice) are of interest (Mursyidin et al., 2021). While this germplasm has relatively low productivity (only 2 t/ha), it possesses some agronomic advantages, such as tolerance to submergence, acidity, salinity and heavy metal contamination (Mursyidin et al., 2017). In addition, this plant has adapted over hundreds of years to different types of stressful abiotic conditions, such as immersion, wave abrasion, water level fluctuation and low oxygen conditions (Wang, 2020). Consequently, swamp rice has some functional genes for future rice breeding (Das and Das, 2014). However, most of this germplasm is untapped, underutilized and uncharacterized optimally for this purpose.

The current study aimed: to determine the genetic diversity and relationship of Indonesian swamp rice germplasm using agro-morphological markers; to identify the distinctiveness of the characters that contribute to the genetic diversity; and to use Pearson correlation analysis among these characters. While these markers show limitations, such as time-consuming and multigenic inheritance with a strong influence from environmental conditions (Wu et al., 2021), they are commonly used in evaluating the genetic diversity of rice germplasm (Mursyidin et al., 2019). According to Wu et al. (2021), determining genetic diversity is essential for plant genetic resources conservation, selecting the genetically divergent parents for practice breeding and preventing the erosion of the genetic base of breeding populations. Furthermore, such studies facilitate understanding of the relationships between accessions and identifying redundancies or admixtures in the germplasm (Delfini et al., 2021).

On a local scale, determining the genetic diversity of this germplasm has been undertaken and revealed the complex interaction between the germplasm and the cultivation practices of farmers (Mursyidin et al., 2019; Mursyidin and Khairullah, 2020). On a global scale, such a study will provide an excellent overview of the population structure of germplasm (Roy et al., 2016). The results could be expected to provide essential information in supporting rice plant breeding programs, particularly the development of swamp rice in the future.

Materials and Methods

Plant materials

In total, 108 cultivars of Indonesian swamp rice were collected from eight provinces of Indonesia (Fig. 1), comprising 107 landraces and a single improved one (*Pelita Bogor*) as a comparative sample (Table S1).

Sample preparation and observation

All rice samples (10 replicates each) were planted and maintained in a Research Station of the Indonesian Swamp Agricultural Research Institute (ISARI), Indonesia, at Balandean, Barito Kuala, South Kalimantan, for 8 mth from September 2020 to May 2021. In total, 31 agro-morphological traits were used to characterize this germplasm comprising 11 qualitative (Table 1) and 20 quantitative (Table 2) traits, following standard rice descriptors (Biodiversity International, 2007).

Table 1 Genetic diversity (*H'* index) of Indonesian swamp rice germplasm based on qualitative characters

Character	Code	H' index
Culm attitude	A	0.22
Flag leaf attitude	B	0.68
Panicle exertion	C	0.14
Panicle shape	D	0.18
Panicle secondary branching	E	0.17
Culm color	F	0.23
Auricle color	G	0.30
Auricle shape	H	0.24
Grain shape	I	0.12
Endosperm type	J	0.22
Awn on grain tip	K	0.42
Average		0.25

H' > 0.60 = high; 0.40 – 0.60 = moderate; < 0.40 = low

Fig. 1 Map of Indonesia, showing sampling sites by province, with parenthetical numbers indicating numbers of swamp rice cultivars used

Table 2 Genetic diversity (*H'* index) of Indonesian swamp rice germplasm based on quantitative characters

Character	Code	H' index	Highest value	Cultivar	Lowest value	Cultivar
Plant height (cm)	L	0.49	151.33	*Ketan*	63.67	*Betek*
Tillering number (unit)	M	0.52	26.67	*Lakatan Hirang*	7.67	*Kuning Sore*
Leaf blade number (unit)	N	0.29	6.00	*Pandak Baru, Serai, Raanti, Semeru*	3.33	*Unus Organik*
Leaf blade length (cm)	O	0.44	72.33	*Menuh*	47.33	*Siam Mayang*
Leaf blade width (cm)	P	0.11	2.47	*Kapuas*	0.87	*Padi Merah*
Culm diameter at basal internodes (mm)	Q	0.97	21.23	*Kuning*	5.10	*Siam Panting*
Panicle length (cm)	R	0.23	49.33	*Senapi Super*	19.33	*Betek*
Panicle number of primary basal branches (unit)	S	0.42	14.33	*Ketan*	6.33	*Keromojoyo*
Panicle number of secondary basal branches (unit)	T	0.28	65.67	*Pandak Kembang*	18.67	*Keromojoyo*
Panicle number per plant (unit)	U	0.17	53.00	*Siam Ganal*	10.00	*Kamajaya Putih, Raden Rata, Siam Keriting*
Panicle stalk length (cm)	V	0.16	17.50	*Serai*	1.73	*Kamajaya Putih*
Flag leaf length (cm)	W	0.32	54.00	*Tumbara*	22.00	*Betek*
Flag leaf width (cm)	X	0.10	1.90	*Biduin*	0.93	*Siam Ganal*
Grain number per panicle (unit)	Y	0.24	348.00	*Badagai*	85.00	*Siam Super*
Fertile grain number per panicle (unit)	Z	0.13	315.00	*Badagai*	56.00	*Siam Salawi*
Sterile grain number per panicle (unit)	AA	0.18	126.00	*Siam Mayang*	3.00	*Serai Rampak*
Grain weight: 100-grain (g)	AB	0.39	3.54	*Kuning Sore*	1.74	*Lemo*
Grain length (mm)	AC	0.12	33.67	*Siam Tanggung*	5.77	*Ketan Serang*
Grain width (mm)	AD	0.50	3.00	*Menuh*	1.70	*Pulut Air*
Grain ratio	AE	0.25	5.25	*Pulut Air*	2.20	*Menuh*
Average		0.32				

H' > 0.60 = high; 0.40 – 0.60 = moderate; < 0.40 = low

Data analysis

All agro-morphological data were standardized and analyzed using a multivariate approach with the assistance of the MVSP ver. 3.1 software (Kovach, 2007). The standardized Shannon diversity index (*H'*) was used to determine the genetic diversity of this germplasm, based on Equation 1 (Mursyidin and Khairullah, 2020):

$$H = -\sum_{i=1}^{n} pi \ln pi \qquad (1)$$

where H is the diversity index, p_i is the proportion of the entries in the i^{th} class of an n-class character, n is the number of the phenotypic classes for a character, p_i is the relative frequency and ln p_i is the natural logarithm of this proportion. Each value of H was standardized by conversion to a relative phenotypic diversity index (H') by division by H_{max} = ln(n) to express the H' value in the range of 0–1. The level of this diversity was categorized as high ($H' > 0.60$), moderate ($0.40 \leq H' \leq 0.60$) or low ($H' < 0.40$) (Mursyidin and Khairullah, 2020). Pearson correlations (r) among agro-morphological characters were analyzed using the Excel ver. 2019 software (Microsoft Corp.; Redmond, WA, USA) following the criteria from Taylor (1990), namely weak ($r \leq 0.35$), moderate (r = 0.36–0.67) and strong ($r > 0.68$). Principal component analysis (PCA) and cluster analysis (CA) were conducted to identify the distinctiveness of the characters that contributed to the genetic diversity and to reconstruct their relationships, respectively. In the PCA, the proportion of a variance criterion was used to identify the different principal components that contributed to the total variation in the dataset. In CA, the distance matrix was generated using the Euclidean distance coefficients and the dendrogram was reconstructed based on the unweighted pair group method with arithmetic mean (UPGMA). Both analyses were carried out using the MVSP ver. 3.1 software (Kovach, 2007).

Results

Genetic diversity of Indonesian swamp rice

In general, Indonesian swamp rice has low genetic diversity based on agro-morphological characters, both qualitative (Table 1) and quantitative (Table 2), as indicated by the Shannon index values for each character (0.31 and 0.36, respectively). However, some characters showed high diversity, such as flag leaf attitude (H' = 0.68) for qualitative characters (Table 1) and culm diameter at basal internodes (H' = 0.97) for quantitative characters (Table 2). From Tables 1 and 2, six characters showed moderate diversity: awn on grain tip (H' = 0.42), plant height (H' = 0.49), tillering number (H' = 0.52), leaf blade length (H' = 0.44), panicle number of primary basal branches (H' = 0.42) and grain width (H' = 0.50).

Furthermore, based on Table 2, while most of the characters had low diversity, some cultivars had the highest values in each character observed. For example, *Ketan* was the cultivar with the highest plant architecture (151.33 cm) and the highest panicle number of primary basal branches (14.33 units). Similarly, *Serai* had the greatest panicle length (17.50 cm) and tillering number (26.67 units), while, *Badagai* had the highest grain number per panicle and fertile grain number per panicle (348 and 315 units, respectively), as shown in Table 2. In addition, *Kuning* had the highest culm diameter (21.23 mm).

The PCA analysis (Table S2) showed that two agro-morphological characters with high genetic diversity, namely flag leaf attitude and culm diameter at basal internodes, contributed significantly to the emerging phenomenon. In addition, most of the characters with moderate diversity, such as tillering number, leaf blade length, and grain weight, contributed significantly. Furthermore, several characters with low genetic diversity, like panicle length, flag leaf width, and grain number per panicle, made high contributions to the emergence of swamp rice genetic diversity (see Table 1 and Table S2).

The correlation analysis (Fig. 2) showed that the panicle number of primary basal branches versus the panicle number of secondary basal one, the grain number per panicle versus the fertile grain number per panicle and the grain length versus the grain ratio had the strongest correlations. Based on Fig. 2, some of the characters also showed moderate correlation, such as plant height with culm diameter at basal internodes, panicle length, panicle number of primary basal branches and panicle stalk length. Another example of moderate correlation was the panicle number of secondary basal one to the flag leaf length, grain number per panicle, and the fertile and sterile grain numbers per panicle.

Genetic relationship of Indonesian swamp rice

The UPGMA revealed that Indonesian swamp rice could be grouped into nine (I–IX) clusters, of which VIII was the largest with a total of 71 cultivars (Fig. 3, Table S3), while the groups with the smallest members (consisting of one cultivar only) were clusters I, II, IV and VII. The PCA analysis revealed that these germplasm groupings were closely related to their agro-morphological characters (Fig. 4). For example, in cluster IV, about 33 cultivars were close to each other and closely related to four agro-morphological characters, namely tillering number (M), panicle number per plant (U), grain length (AC) and grain ratio (AE).

Based on their similarity coefficients (Table S4), several closely related cultivars, such as *Unyil* with *Karat Kaleng*, *Pelita Rampak* versus *Katimuri*, and *Siam Unus Gampa* with *Ketan Bundel*, *Putih* and *Serai*, had a coefficient of 0.91. Conversely, the farthest related (similarity coefficient of 0.58) were represented by *Sawah Kanyut* versus *Siam Gumpal* and *Siam Salawi versus Siam Gumpal*. In this study, *Pelita Bogor* which was a superior cultivar, had the closest relation with *Kamajaya Hitam* (coefficient 0.90) and the farthest with *Pandak Kembang* (coefficient 0.66).

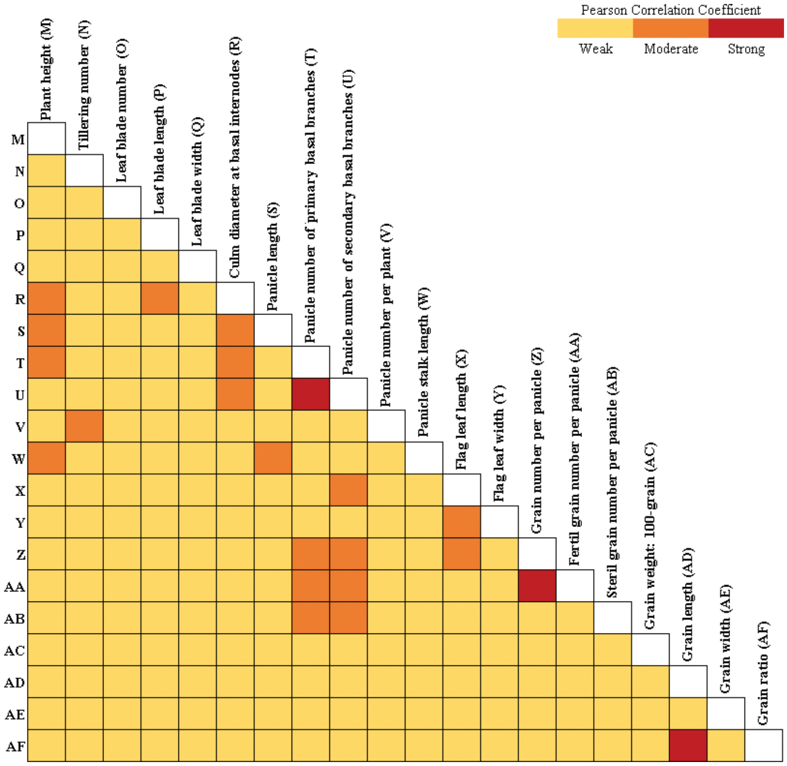

Fig. 2 Hit map showing Pearson correlation coefficients between characters of Indonesian tidal swamp rice cultivars

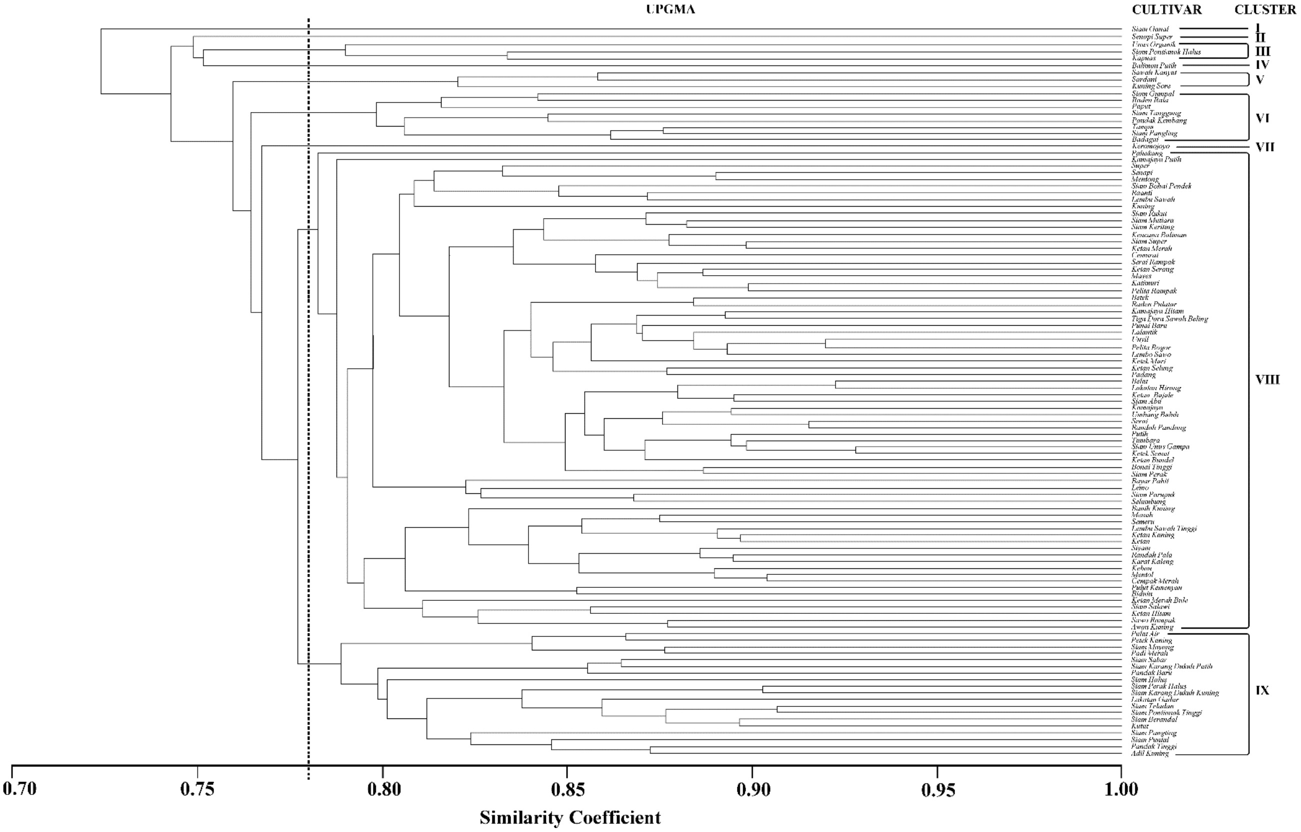

Fig. 3 Genetic relationship of Indonesian swamp rice based on unweighted pair group method with arithmetic mean, with germplasm grouped into nine main clusters (I–IX)

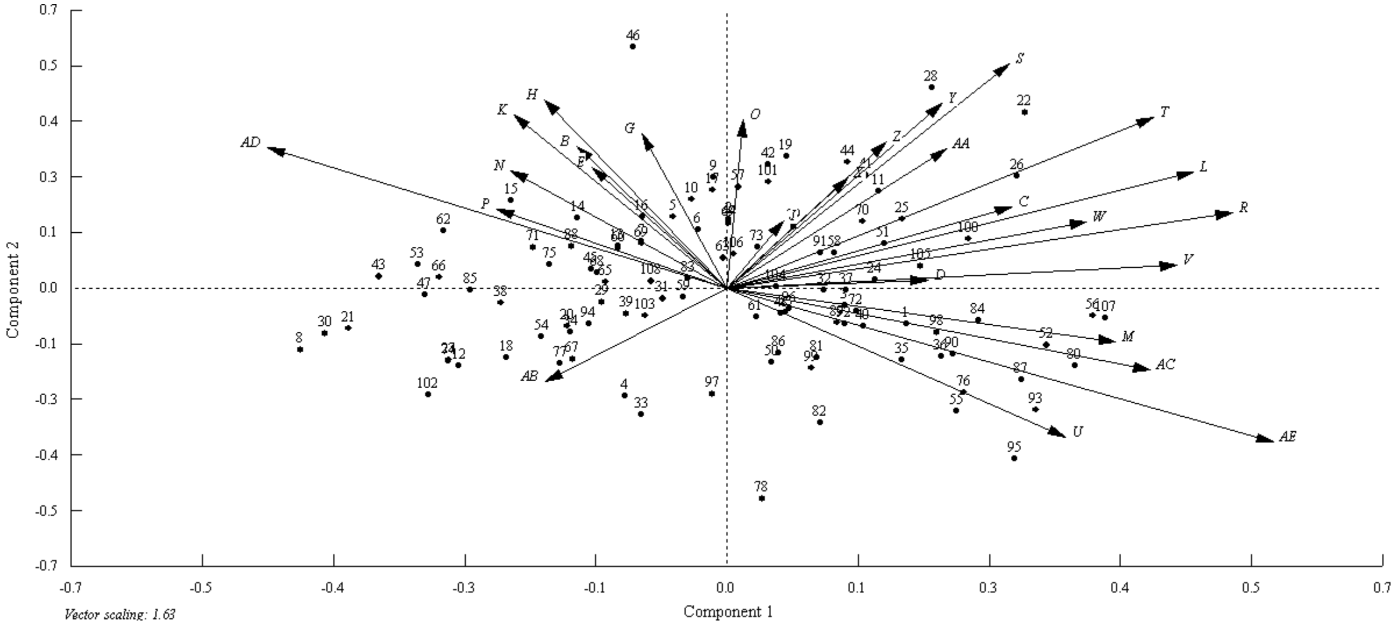

Fig. 4 Grouping of Indonesian swamp rice germplasm based on principal component analysis, where vectors indicate agro-morphological characters, with the names of each cultivar in Table 1 and the characters in Table 4

Discussion

Importance of genetic diversity and its related factors

Genetic diversity is indispensable in forming a baseline population for natural selection and the evolutionary process (Govindaraj et al., 2015). In other words, this parameter has an essential role in the future evolutionary direction or as a precondition for future adaptive changes. Hence, it has important implications for future conservation and breeding programs (Lloyd et al., 2016). Understanding genetic diversity is essential for conservation by increasing the effectiveness and efficiency of the program. Some aspects of the program, such as loss of genetic diversity, are only addressed by extensive population genetic studies (Luan et al., 2006). For plant breeding, genetic diversity becomes more important in the context of climate change (Govindaraj et al., 2015).

In this study, Indonesian swamp rice had low genetic diversity, for both qualitative (Table 1) and quantitative (Table 2) characters. This was consistent with Mursyidin and Khairullah (2020), particularly regarding the tidal swamp rice of South Kalimantan Indonesia. Compared to several other studies, such as Suriyagoda et al. (2011); Rabara et al. (2014) and Sinha et al. (2015), this germplasm showed lower diversity. According to Gao et al. (2017), low-level genetic diversity is affected by several factors, such as a founder effect, genetic isolation, population decline, natural selection or inbreeding. In this case, inbreeding was the most probable cause for the low level of diversity (Mursyidin et al., 2017).

In practice, local farmers generally select and cultivate their seeds from the previous harvest season based solely on the shape and color of the grain (Mursyidin et al., 2017). Consequently, the rice has a relatively similar (homogeneous) genetic background. Following historical perspectives, the low level of diversity is strongly related to the evolutionary pathway and distribution of this plant in this region (Chang, 2000). According to Chang (2000), the path of evolution and distribution of rice plants in Asia, especially Indonesia, is from Sumatra to Kalimantan and then to the Philippines. Li (2003) predicted that the distribution of cultivated rice to Indonesia occurred around 1599 before the current era. During this process, inbreeding would have been unavoidable and may have reduced genetic diversity (Gao et al., 2017). Furthermore, reduced genetic diversity may correlate with decreasing disease resistance and resilience to environmental disturbance and extreme conditions (Lloyd et al., 2016).

However, although this germplasm has typically low genetic diversity, two characters, namely flag leaf attitude (Table 1) and culm diameter at basal internode (Table 2), showed high diversity. According to Mursyidin and Khairullah (2020), those traits are the key to developing new superior rice cultivars. For example, flag leaf has played an essential role in the grain filling or yield potential of most cereals, such as wheat, barley, oats, triticale and rice (Al-Tahir, 2014). The culm diameter of the basal internode is also a crucial character for rice plants (Hirano et al., 2017) and is strongly correlated, especially with the level of lodging (Wu et al., 2021). In this case, once this phenomenon occurs, the photosynthetic rate decreases due to deterioration of the canopy architecture, translocation of nutrients and water are inhibited and pre-harvest sprouting leads to poor grain quality (Chigira et al., 2020).

Regardless of the importance of the two characters, the high genetic diversity of these two characters may be strongly correlated to genetic factors. For example, Zhang et al. (2013) reported the trend of erect and semi-erect flag leaf angles in various local rice cultivars from China. Several other studies also reported almost the same thing, such as Rabara et al. (2014) for local Filipino rice, Sharma et al. (2020) for local Nepalese rice and Umarani et al. (2017) for local Indian rice. Hence, this character is the main characteristic that distinguishes landrace rice from superior ones. Generally, the superior one has a relatively uniform direction of flag leaf growth, namely horizontal (Mursyidin and Khairullah, 2020).

The PCA analysis (Table S2) showed that flag leaf attitude and culm diameter at basal internodes significantly contributed to emerging diversity. In the current study, 15 cultivars of swamp rice, including *Ketek Muri*, *Padang*, *Puput*, *Unyil*, *Senapi Super* and *Siam Karang Dukuh Putih*, corresponded regarding flag leaf attitude, whereas only one cultivar (*Kuning)* was associated with the culm diameter of the basal internode. Hence, these cultivars are good candidates for the parental development of new rice cultivars, particularly for high grain yield potential. From an agronomic perspective, rice yield is determined by the integration of four yield components integration: number of panicles per unit area, number of grains per panicle, filled grain ratio and grain weight (Kim et al., 2014).

Besides the two characters of flag leaf attitude and culm diameter at basal internodes mentioned with high diversity, several characters with moderate one are also of interest, such as plant height, tillering number and panicle number of primary basal branches. According to Mursyidin and Khairullah (2020), plant height is the main trait of the target, specifically for swamp areas. Naturally, these areas have unique conditions, where water usually is present and there is constant flooding with highly variable levels. Thus, rice plants with high architecture (and thick culm diameter) are suitable for this region. From the current study, *Ketan*, with the highest plant height of 151 cm (Table 2), would be a good candidate for parental development of a new rice cultivar specifically for swamp areas.

The tillering number is one character that is strongly correlated to rice productivity (yield). In this context, the higher number of tillers, the higher the harvested grain (Constantino et al., 2015). Hence, cultivars with the highest tillering numbers traits have been the main target in rice breeding since the 18th century (Fukushima, 2019). In the current study, *Lakatan Hirang*, with the highest tillering number of 26.67 units (Table 2), would be a good candidate for developing cultivars with high yield production.

Finally, the panicle number of primary basal branches is a part of the panicle structure and is most important for rice yield (Das et al., 2018). Li et al. (2018) described this character as one of the main goal agronomical traits that determines branch number and grain number in rice (Fei et al., 2019). At the molecular level, this character is regulated by several genes, such as the *panicle rachis length5* (*Prl5*) and *primary branch length6* (*Pbl6*) genes (Agata et al., 2020) and *grain number1a* (*Gn1a*), *ideal plant architecture 1* (*IPA1*), *lax panicle1* (*LAX1*), *frizzy panicle* (*FZP*), *monoculm 1* (*MOC1*) and *tawawa 1* (*TAW1*) (Li et al., 2021). In the current study, the panicle number of primary basal branches was strongly correlated with the panicle number of secondary basal branches (Fig. 2). Furthermore, *Ketan* was the Indonesian swamp rice cultivar with the highest panicle number of primary basal branches (14.33 units), as shown in Table 2. Thus, it can also be used as a parental candidate in a rice breeding program or for developing novel cultivars for high yield production.

Nowadays, plant breeders utilize all aspects of plant genetic resources or genetic diversity to develop new and improved cultivars with desirable traits, associated with both biotic and abiotic stress tolerances and farmer-preferred (Swarup et al., 2021). Consequently, just as present-day populations need high genetic diversity to adapt rapidly, succeeding generations will need equally as much genetic diversity to adapt to future changes (Lloyd et al., 2016). In other words, efforts in broadening the genetic diversity of Indonesian swamp rice are urgent and can be developed using several methods, such as introgression, hybridization, mutagenesis or transgenically (Singh and Kumar, 2016; Laskar and Khan, 2017; Allier et al., 2020).

Genetic relationship and its implications

The UPGMA clustering (Fig. 3) revealed that geographical locations did not affect the germplasm grouping. According to Dwivedi et al. (2020), this parameter is not usually related to emerging genetic diversity, indicating that genotypes originating from the same region will not always be grouped within the same cluster. However, PCA showed a unique feature, where some of the germplasm was grouped by their agro-morphological characters.

However, information on the phylogenetic relationship is urgently needed and has implications for future conservation and breeding programs (Flint-Garcia, 2013). For the first (conservation) program, phylogenetic studies can be applied to infer species and their evolutionary history, including helping analyze species delimitation, gene flow and genetic differentiation (Fernández-García, 2017). Furthermore, the use of the phylogenetic relationship is the main focus of current attention, given its objective parameters for conservation in past evolutionary history, the genetic status of present species and the management of future species (Fernández-García, 2017).

This relationship is indispensable for the breeding program in predicting the genetic diversity of the offspring when individuals cross (Acquaah, 2017). Conceptually, when individuals with a distantly related cross out, their offspring may result in wide genetic diversity. In other words, when individuals from different groups or with an extant genetic distance cross, the chances of transgressive segregation are greater. Hence, there is a higher probability that unrelated genotypes from distant ones would provide unique, desirable alleles at different loci (Suriyagoda et al., 2011). Conversely, when closely related individuals cross, the genetic diversity of their offspring may be narrow (Turner-Hissong et al., 2020). To date, crossing individuals with a close relationship has been avoided by breeders or researchers because their offspring may well exhibit inbreeding. According to de los Reyes (2019), inbreeding may decrease yield potential and increase susceptibility to pests and diseases.

In conclusion, Indonesian swamp rice has a low genetic diversity based on the agro-morphological markers. However, two characters (flag leaf attitude and culm diameter at basal internode) showed high diversity. Furthermore, the UPGMA revealed that this germplasm has a complex relationship with several cultivars showing closest and farthest relationships, such as *Unyil* versus *Karat Kaleng* and *Siam Salawi* versus *Siam Gumpal*. *While* these findings provide novel information and could be used as a reference in supporting the rice breeding program in the future and in particular for the development of new rice cultivars for swamp areas, further studies are needed to ensure the genetic background of germplasm uses more powerful, molecular markers.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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References

Acquaah, G. 2017. Plant breeding, principles. In: Thomas, B., Murray, B.G., Murphy, D.J. (Eds.). Encyclopedia of Applied Plant Science, 2nd ed. Elsevier Inc. New York, NY, USA, pp. 236–242.

Agata, A., Ando, K., Ota, S., et al. 2020. Diverse panicle architecture results from various combinations of *Prl5*/*GA20ox4* and *Pbl6*/*APO1* alleles. Commun. Biol. 3: 302. doi.org/10.1038/s42003-020-1036-8

Allier, A., Teyssèdre, S., Lehermeier, C., Moreau, L., Charcosset, A. 2020. Optimized breeding strategies to harness genetic resources with different performance levels. BMC Genom. 21: 349. doi.org/10.1186/s12864-020-6756-0

Al-Tahir, F.M.M. 2014. Flag leaf characteristics and relationship with grain yield and grain protein percentage for three cereals. J. Med. Plants Stud. 2: 1–7.

Biodiversity International. 2007. Descriptors for Wild and Cultivated Rice (*Oryza* spp.). Biodiversity International. Rome, Italy.

Chang, T.T. 2000. Rice. In: Kiple, K.F., Ornelas, K.C. (Eds.). Cambridge World History of Food. Cambridge University Press. Cambridge, UK, pp. 132–149.

Chigira, K., Kojima, N., Yamasaki, M., et al. 2020. Landraces of temperate japonica rice have superior alleles for improving culm strength associated with lodging resistance. Sci. Rep. 10: 19855. doi.org/10.1038/s41598-020-76949-8

Constantino, K.P., Gonzales, E.J., Lazaro, L.M., Serrano, E.C., Samson, B.P. 2015. Plant height measurement and tiller segmentation of rice crops using image processing. In: Proceedings of DLSU Research Congress. Manila, Philippines, pp. 1–6.

Das, T., Das, A.K. 2014. Inventory of the traditional rice varieties in farming system of Southern Assam: A case study. Indian J. Tradit. Knowl. 13: 157–163.

Das, K., Panda, B.B., Shaw, B.P., Das, S.R., Dash, S.K., Kariali, E., Mohapatra, P.K. 2018. Grain density and its impact on grain filling characteristic of rice: Mechanistic testing of the concept in genetically related cultivars. Sci. Rep. 8: 4149. doi.org/10.1038/s41598-018-22256-2

de los Reyes, B.G. 2019. Genomic and epigenomic bases of transgressive segregation – New breeding paradigm for novel plant phenotypes. Plant Sci. 288: 110213. doi.org/10.1016/j.plantsci.2019.110213

Delfini, J., Moda-Cirino, V., dos Santos Neto, J., Ruas, P.M., Sant'Ana, G.C., Gepts, P., Gonçalves, L.S.A. 2021. Population structure, genetic diversity and genomic selection signatures among a Brazilian common bean germplasm. Sci. Rep. 11: 4964. doi.org/10.1038/s41598-021-82437-4

Dwivedi, S.L., Goldman, I., Ceccarelli, S., Ortiz, R. 2020. Chapter three– Advanced analytics, phenomics and biotechnology approaches to enhance genetic gains in plant breeding. Adv. Agron. 162: 89–142. doi.org/10.1016/bs.agron.2020.02.002

Fei, C., Yu, J., Xu, Z., Xu, Q. 2019. Erect panicle architecture contributes to increased rice production through the improvement of canopy structure. Mol. Breed. 39: 128. doi.org/10.1007/s11032-019-1037-9

Fernández-García, J.L. 2017. Phylogenetics for wildlife conservation. In: Abdurakhmonov, I.Y. (Ed.). Phylogenetics. IntechOpen. London, UK, pp. 27–46.

Flint-Garcia, S.A. 2013. Genetics and consequences of crop domestication. J. Agric. Food Chem. 61: 8267–8276. doi.org/10.1021/jf305511d

Fukushima, A. 2019. Varietal differences in tiller and panicle development determining the total number of spikelets per unit area in rice. Plant Prod. Sci. 22: 192–201. doi.org/10.1080/1343943X.2018.1562308

Gao, Y., Yin, S., Yang, H., Wu, L., Yan, Y. 2017. Genetic diversity and phylogenetic relationships of seven Amorphophallus species in southwestern China revealed by chloroplast DNA sequences. Mitochondrial DNA A: DNA Mapp. Seq. Anal. 29: 679–686. doi.org/10.1080/24701394.2017.1350855

Govindaprasad, P.K., Manikandan, K. 2014. Agricultural land conversion and food security: A thematic analysis. Int. Res. J. Agric. Rural Dev. 3: 1–19.

Govindaraj, M., Vetriventhan, M., Srinivasan, M. 2015. Importance of genetic diversity assessment in crop plants and its recent advances: An overview of its analytical perspectives. Genet. Res. Int. 2015: 431487. doi.org/10.1155/2015/431487

Hirano, K., Ordonio, R.L., Matsuoka, M. 2017. Engineering the lodging resistance mechanism of post-green revolution rice to meet future demands. P. Jpn. Acad. B-Phys. 93: 220–233. doi.org/10.2183/pjab.93.014

Khairullah, I. 2020. Indigenous knowledge cultivation of local rice varieties "Siam Mutiara" and "Siam Saba" at tidal swampland. Bio Web Conf. 20: 01007. doi.org/10.1051/bioconf/20202001007

Kim, B., Kim, D.G., Lee, G., et al. 2014. Defining the genome structure of 'Tongil' rice, an important cultivar in the Korean "Green Revolution". Rice 7: 22. doi.org/10.1186/s12284-014-0022-5

Kovach, W.L. 2007. MVSP 3.1: Multivariate Statistical Package. Kovach Computing Services. Pentraeth, Isle of Anglesey, UK.

Laskar, R.A., Khan, S. 2017. Assessment on induced genetic variability and divergence in the mutagenized lentil populations of microsperma and macrosperma cultivars developed using physical and chemical mutagenesis. PloS One 12: e0184598. doi.org/10.1371/journal.pone.0184598

Li, G., Zhang, H., Li, J., Zhang, Z., Li, Z. 2021. Genetic control of panicle architecture in rice. Crop J. 9: 590–597. doi.org/10.1016/j.cj.2021.02.004

Li, J. 2003. The natural history of rice. In: Katz, S.H. (Ed.). Encyclopedia of Food and Culture. Charles Scribner's Sons. New York, NY, USA, pp. 190–198.

Li, Y., Li, X., Fu, D., Wu, C. 2018. Panicle Morphology Mutant 1 (PMM1) determines the inflorescence architecture of rice by controlling brassinosteroid biosynthesis. BMC Plant Biol. 18: 348. doi.org/10.1186/s12870-018-1577-x

Lloyd, M.M., Makukhov, A.D., Pespeni, M.H. 2016. Loss of genetic diversity as a consequence of selection in response to high $p\mathrm{CO}_2$. Evol Appl. 9: 1124–1132. doi.org/10.1111/eva.12404

Luan, S., Chiang, T.Y., Gong, X. 2006. High genetic diversity vs. low genetic differentiation in *Nouelia insignis* (Asteraceae), a narrowly distributed and endemic species in China, revealed by ISSR fingerprinting. Ann Bot. 98: 583–589. doi.org/10.1093/aob/mcl129

Mursyidin, D.H., Khairullah, I. 2020. Genetic evaluation of tidal swamp rice from South Kalimantan, Indonesia based on the agro-morphological markers. Biodiversitas 21: 4795–4803. doi.org/10.13057/biodiv/d211045

Mursyidin, D.H., Nazari, Y.A., Badruzsaufari, Masmitra, M.R.D. 2021. DNA barcoding of the tidal swamp rice (*Oryza sativa*) landraces from South Kalimantan, Indonesia. Biodiversitas 22: 1593–1599. doi.org/10.13057/biodiv/d220401

Mursyidin, D.H., Nazari, Y.A., Daryono, B.S. 2017. Tidal swamp rice cultivars of South Kalimantan Province, Indonesia: A case study of diversity and local culture. Biodiversitas 18: 427-432. https://doi.org/10.13057/biodiv/d180155

Mursyidin, D.H., Purnomo, Sumardi, I., Daryono, B.S. 2019. Phenotypic diversity of the tidal swamp rice (*Oryza sativa* L.) germplasm from South Kalimantan, Indonesia. Aus. J. Crop Sci. 13: 386–394. doi.org/10.21475/ajcs.19.13.03.p1268

Rabara, R.C., Ferrer, M.C., Diaz, C.L., Newingham, M.C.V., Romero, G.O. 2014. Phenotypic diversity of farmers' traditional rice varieties in the Philippines. Agronomy 4: 217–241. doi.org/10.3390/agronomy4020217

Roy, S., Marndi, B.C., Mawkhlieng, B., Banerjee, A., Yadav, R.M., Misra, A.K., Bansal, K.C. 2016. Genetic diversity and structure in hill rice (*Oryza sativa* L.) landraces from the North-Eastern Himalayas of India. BMC Genet. 17: 107. doi.org/10.1186/s12863-016-0414-1

Sharma, S., Pokhrel, A., Dhakal, A., Poudel, A. 2020. Agro-morphological characterization of rice (*Oryza sativa* L.) landraces of Lamjung and Tanahun district, Nepal. Ann. Plant Sci. 9: 3731–3741.

Singh, M., Kumar, S. (Eds.). 2016. Broadening the Genetic Base of Grain Cereals. Springer. New Delhi, India.

Sinha, A.K., Mallick, G.K., Mishra, P.K. 2015. Diversity of grain morphology on traditional rice varieties (*Oryza sativa* L.) of lateritic region of West Bengal. World J. Agric. Sci. 11: 48–54. doi: 10.5829/idosi.wjas.2015.11.1.1843

Sulakhudin, S., Hatta, M. 2018. Increasing productivity of newly opened paddy field in tidal swampy areas using a local specific technology. Indones. J. Agric. Sci. 19: 9–16.

Suriyagoda, L.D.B., Thilakarathne, R.M.M.S. Nissanka, S.P., Samita, S. 2011. Morphological variation in selected rice (*Oryza sativa* L.) germplasm of Sri Lanka. J. Nat. Sci. Found. 39: 129–137. doi.org/10.4038/jnsfsr.v39i2.3173

Swarup, S., Cargill, E.J., Crosby, K., Flagel, L., Kniskern, J., Glenn, K.C. 2021. Genetic diversity is indispensable for plant breeding to improve crops. Crop Sci. 61: 839–852. doi.org/10.1002/csc2.20377

Taylor, R. 1990. Interpretation of the correlation coefficient: A basic review. J. Diagn. Med. Sonog. 6: 35–39. doi.org/10.1177/875647939000600106

Turner-Hissong, S.D., Mabry, M.E., Pires, J.C. 2020. Evolutionary insights into plant breeding. Curr. Opin. Plant Biol. 54: 93–100. doi.org/10.1016/j.pbi.2020.03.003

Umarani, E., Radhika, K., Padma, V., Subbarao, L.V. 2017. Agro-morphological characterization of rice (*Oryza sativa* L.) landraces based on DUS descriptors. Int. J. Pure App. Biosci. 5: 466–475. doi.org/10.18782/2320-7051.2624

Wang, Y. 2020. Wetlands and Habitats. CRC Press. Boca Raton, FL, USA.

Wu, F., Ma, S., Zhou, J., Han, C., Hu, R., Yang, X., Nie, G., Zhang, X. 2021. Genetic diversity and population structure analysis in a large collection of white clover (*Trifolium repens* L.) germplasm worldwide. Peer J. 9: e11325. doi.org/10.7717/peerj.11325

Yagi, H., Garrod, G. 2018. The future of agriculture in the shrinking suburbs: The impact of real estate income and housing costs. Land Use Policy 76: 812–822. doi.org/10.1016/j.landusepol.2018.03.013

Zhang, X.C., Lu, C.G., Hu, N., Yao, K.M, Zhang, Q.J, Dai, Q.G. 2013. Simulation of canopy leaf inclination angle in rice. Rice Sci. 20: 434–441. doi.org/10.1016/S1672-6308(13)60161-4