The shifting genetic diversity pattern of Indonesian rice improved varieties from 1943-2019 based on historical pedigree data

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Abstract. *Anas, Damayanti F, Kadapi M, Carsono N, Sari S. 2022. The shifting genetic diversity pattern of Indonesian rice improved varieties from 1943-2019 based on historical pedigree data. Biodiversitas 23: 4649-4656.* For rice plants in Indonesia, stagnation in increasing crop yields due to a reduction in genetic diversity is a significant issue. The issue of using the same parents in breeding programs and consumer preferences for a single main variety are among the causes of the narrowing of rice plants' genetic diversity. The purpose of this study is to figure out which ancestors are significant and how the genetic diversity of improved Indonesian rice cultivars has changed over time. Changes in the genetic background of the Indonesian rice gene pool were decided using pedigree analysis by calculating the coefficient of parentage (COP) among varieties. There are 280 ancestors in the rice gene pool. The pedigree map exemplifies the complexities of rice breeding in Indonesia. The four classical ancestors of DGWG, Taichung Native1, China, and Latisail had a noteworthy influence on all irrigated rice plant types (11.22%) and upland rice plant types (8.30%) in the gene pool. The dominance of the phenomenal variety IR64 has been continued by Inpari 32, which is a direct derivative of Ciherang. In the meantime, Inpago9, Luhur 2, and UPLRI ancestors set the foundation for the upland rice plant type. Inpara7 and Inpara9, along with their IRRI-introduced parents (IRRIpara4 and IRRIpara5), had a significant impact on Indonesian tidal rice plants. The A1, Hipa7, and Hipa3 varieties are heavily influenced by the hybrid rice plants of Indonesia.

Keywords: Genetic background, improved variety, pedigree analysis, rice

INTRODUCTION

Recently, the world has been confronted with serious problems in the restrictiveness of the food supply. The increase in food demand and the decrease in rice production have contributed to the food crisis in the world. Global climate change impacts prolonging the dry season in Indonesia, temperature increases, and decreases in plant productivity (Aragón et al. 2021; Malhi et al. 2021). The fourth-largest Indonesian population is expected to reach 306 million by 2035 (BPPN et al. 2013), necessitating an increase in rice production of more than 2 million tons of dry milled grain from base rice production in 2019 (BPS 2017, 2020).

The decline of genetic diversity has become a global issue, and high genetic diversity is most important for the sustainability of agriculture, ecosystems, and crop improvement (Hoban et al. 2021; Swarup et al. 2021). The national rice breeding program is closely related to the history of IRRI rice-released cultivars. A significant increase in rice productivity in Indonesia was achieved from 1981 to 1990 and has been associated with the introduction of the high-yielding Cisadane cultivar. Almost every modification of the pedigree selection method was applied by breeders to improve plant yield. However, the average rice productivity in the next decade decreased and was constant at a rate of 1.19%. If there isn't enough genetic diversity in the parents that are used to make

populations through hybridization, there may be less genetic variation for quantitative traits.

The Indonesian government has released more than ±328 superior rice varieties over the last 76 years, and during the period 2008-2019 has released ±110 superior rice varieties (10 varieties per year). However, the average contribution of this new variety to the increase in rice productivity is only two kg ha-1 annually. The increase in rice productivity in Indonesia for 76 years only ranges from 4.89 to 5.11 tons ha-1 (BPS 2020), and is slightly below Vietnamese and Japanese rice productivity, which on average is 5.53 tons ha-1 and 6.68 tons ha-1, respectively (FAOSTAT 2020).

Genetic background and the presence of genes are essential for success in rice breeding programs. Improvement of the character controlled by a polygene is constantly crucial in plant breeding programs. A molecular approach for improving the quantitative character of rice through QTL analysis has been investigated by several researchers (Bakti and Tanaka 2019; Baltazar et al. 2019; Jewel et al. 2019; Liu et al. 2020; Sandhu et al. 2021; Zhao et al. 2022). However, molecular techniques are expensive, labor-intensive, and difficult to apply in countries with limited resources. Pedigree analysis has been widely used in plant breeding programs (Egan et al. 2019).

The high selection pressure of rice breeding has been focused on high yield and tolerance to pests and diseases. It usually breeds without considering the proper selection of the parent's genetic background and might result in a

decline of the genetic diversity in the Indonesian rice gene pool. The goals of this study are to find out which ancestors are important and how the genetic diversity of improved Indonesian rice cultivars has changed over time; to make a relatedness map of Indonesian rice ancestors; and to find out which ancestor led to inbreeding and kinship.

MATERIALS AND METHODS

Plant materials for rice database
Development of rice database
The term "improved variety" refers to all rice cultivars released by the government, with an official document decree. The term "ancestor" refers to all rice genotypes that were at the top of the pedigree tree hierarchy and were considered ancestors. The recorded database of the improved rice varieties was from two sources: online and offline databases. A total of 675 improved variety databases were subjected to evaluation and validation of the improvement pedigree databases from the public database resources. The online databases were collected from: a) the Indonesian Centre for Rice Research (ICRR) database (http://bbpadi.litbang.pertanian.go.id/); b) the Indonesian Agency for Agricultural Research and Development (IAARD) database (http://www.litbang.pertanian.go.id/); c) International Rice Research Institute (IRRI)-Rice Release Improved Variety database (https://sites.google.com/a/irri.org/released-rice-varieties/released-varieties/2014); d) IRRI-Germplasm Resource Information Network-Global (GRIN-Global) (https://gringlobal.irri.org/gringlobal/accessiondetail.aspx?id=95905); e) IRRI-Books (http://books.irri.org/9712201228_content.pdf); f) Rice Research Station-TIRUR, Tamil Nadu Agricultural University India-Varieties Release (https://tnau.ac.in/rrs-tirur/varieties-released/ and https://drdpat.bih.nic.in//Rice%20Varieties%20-%2001.htm). The offline databases were from libraries and journals at the ICRR Sukamandi and books on collections of various rice varieties (Romdon et al. 2014).

Validation of pedigree data record
For data validation, the pedigree data records are traced back to their ancestors' parents or landraces using a pedigree tree. We generated the whole pedigree tree of each variety using the variety names obtained in the paddy germplasm bank's data. All pedigree data records for ancestors with incomplete pedigree trees were omitted and classified as broken pedigree data records. In addition, we validated the naming procedure for the rice variety. For all pedigree data records, the same variety was given a consistent name. The pedigree program will determine the relationship between varieties based on the occurrence of the same variety's name in multiple pedigree tree data records. According to their cultivar descriptions, rice varieties were divided into four categories.
A total of 333 improved rice varieties consisting of lowland rice, upland rice, tidal rice, and hybrid rice have been confirmed in this study (Figure 1). These improved rice varieties were developed over a timeframe of 77 years, from 1943 to 2020. The improved rice variety included cultivars from a different group of Indonesian rice, chosen either for their completeness of pedigree data, performance information, commercial potential, or as parents in the national rice breeding program.
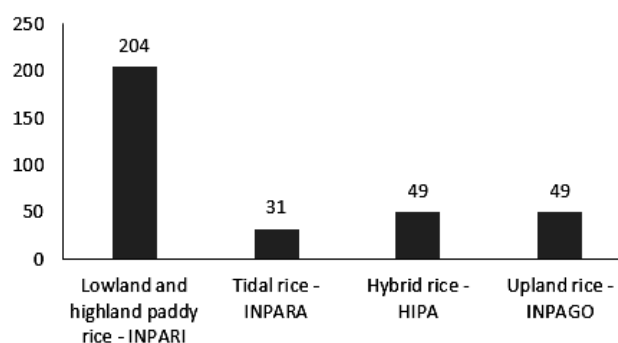
Pedigree analysis and population structure
The pedigree tree data records the name variety and serve as data sources for the AZ-Prolog program. Using Microsoft Excel 2010, all crossing histories of a variety, including parents and offspring, were entered as data. The coefficient of parentage (COP) was generated using the C programming language and the AZ-Prolog Interpreter software. The COP was calculated using equation $r_{xy} = (1/2)^{n1+n2} \cdot ((1+F_z)/2)$ where r_{xy}: COP between two individuals X and Y; Z: general parent of X and Y; F_z: *coefficient of inbreeding* of parent Z; n1 and n2: a number of *ancestors* to general parent Z (Kempthorne 1969). The parameters to be analyzed include the total number of common and unique ancestors, number of generations, and percentage contribution of variety to the gene pool.
Visualization of a large pedigree tree, the number of ancestors and the number of last progeny was performed by Helium software (Shaw et al. 2014). The kinship on the similarity of the parents (COP) was figured by the JMP 16 trial version (JMP 2021).

RESULTS AND DISCUSSION

Distribution of ancestors and progenies in Indonesian rice gene pool
Two hundred improved rice varieties were analyzed for genetic background studies in the Indonesian rice gene pool following the screening and validation of pedigree data. From 1943 to 2020, 331 ancestors or parents were evenly distributed throughout the Indonesian rice gene pool. During this period, 175 final progenies at the very end of the pedigree tree were released (Figure 2B). The IR64 variety demonstrated the highest contribution of genetic background to the Indonesian rice gene pool.

Figure 1. Total Improved varieties from 1943-2020 (77 years)

A

B

Figure 2. A distribution of ancestors and final progenies within the gene pool of Indonesian rice. Reading the pedigree map from the top to the bottom. The upper dots represent the pedigree map's origin (initial crossing), while the lower dots represent the final pedigree products (terminal progeny). The red and blue lines represent parental diversity as female and male, respectively. The solid black dot illustrates the distribution of ancestor (A) and offspring (B) in the rice gene pool. The size of the dot represents a variety's genetic contribution to the rice gene pool. The black arrow indicates the well-known IR64 variety

The use of various ancestors as parents in the gene pool is more concentrated in the top area before the domination of IR64 rice in Indonesia's breeding programs (Figure 2A-red arrow). On the other hand, more new varieties were produced after IR64 became the center of rice breeding programs in Indonesia (Figure 2B). However, the terminal progenies were also found at the top of the pedigree map. This suggests that there is an effort to produce new varieties that have no relationship to the common parents in the gene pool, such as IR64 (Figure 2B, red box).

Pedigree map of Indonesian rice germplasm

The pedigree map of Indonesia's improved rice varieties was overly complicated and showed the great contribution of the IR64 variety to the Indonesian rice varieties. There
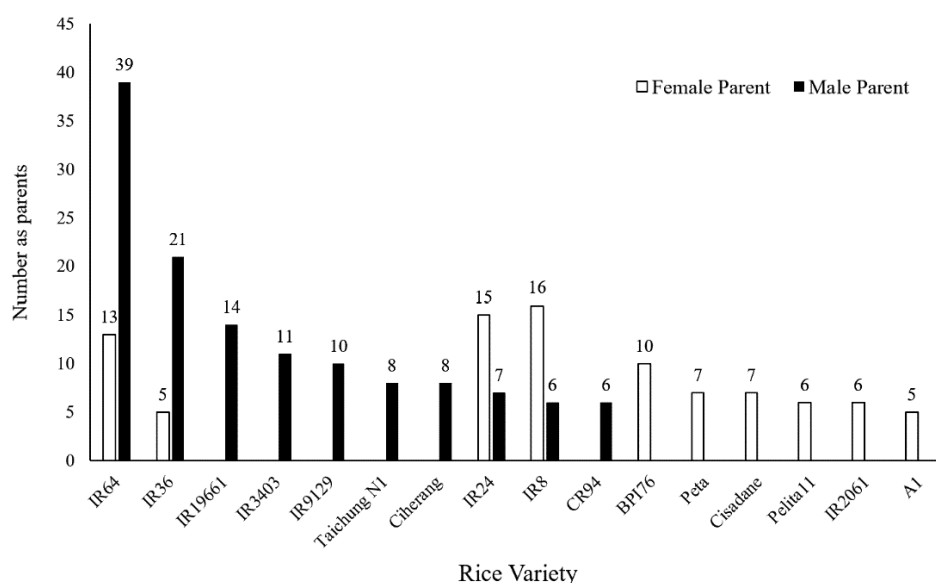
are essentially four major nodes as breeding cores in the Indonesian rice gene pool, namely IR64 (52 progenies), IR36 (26 progenies), IR24 (22 progenies) and IR8 (22 progenies) (Figure 4, red circle). All these varieties were originally introduced by IRRI Philippines, and IR64 and IR36 were released as eminent cultivars in 1986 and 1978, respectively.

IRRI varieties were the tenth most frequently used as female or male parents in the Indonesian rice breeding program (Figure 3). Eight IRRI varieties were ranked among the top 10 varieties utilized in rice breeding programs in Indonesia. Four of the eight IRRI types were utilized as both male and female parents (Figure 3). In the Indonesian rice gene pool, IR64 was the most frequently selected male parent. In contrast, IR8 is the most used
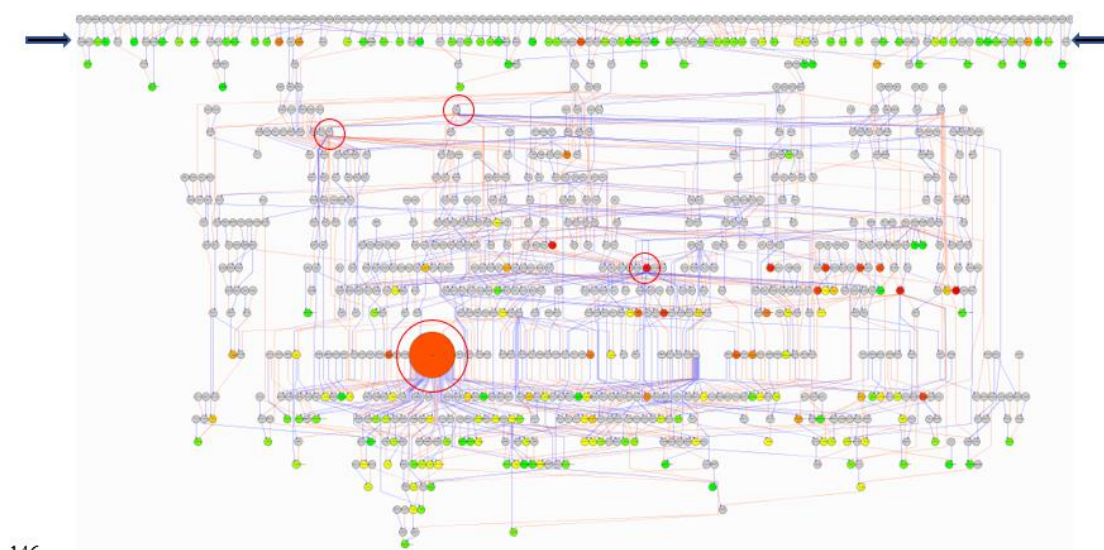
female parent in rice breeding programs in Indonesia. In the rice breeding program, three classical ancestors are among the top 10 varieties that are frequently employed. Cisadane, a direct descendant of the Pelita variety, was widely utilized as a female parent.

Six varieties have only one parent. These rice varieties are either direct introductions from IRRI or direct mutations from local varieties or landraces. Indonesia directly introduced Inpara 4 and Inpara 5 from IRRI in 2010. Meanwhile, Munawacita Agritan, Mustaban Agritan, and Inpari Sidenuk released after 2011 are mutation varieties from the local cultivars, and Cakrabuana Agritan
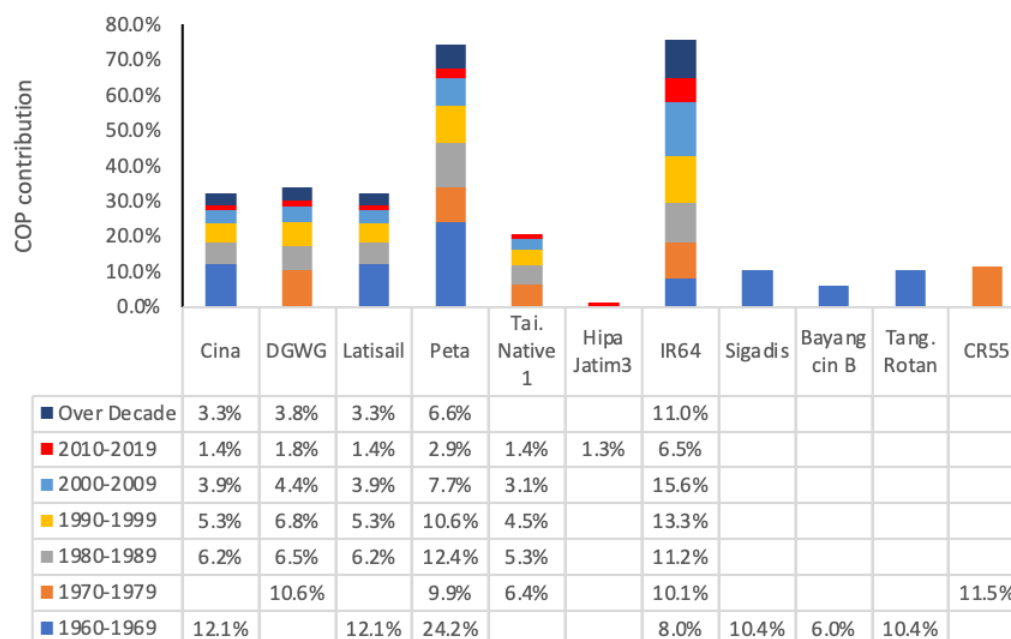
released in 2018 is a radiation product from the improved variety. There are rice varieties released in their early years, occupying the top row in the pedigree map (Figure 4). This suggested that there was an effort by rice breeders in Indonesia to increase the variety of crossing parents in a breeding program. Besides that, there were also efforts to develop hybrid rice. There were 19 hybrid rice releases after 2002 that used different rice parents from those in the Indonesian rice gene pool. The blue arrow shows the position of these varieties in the top row of the pedigree map (Figure 4).

Figure 3. Top ten varieties as the female and male parent in Indonesia rice gene pool during 1943-2020

Figure 4. Pedigree map visualization of all improved varieties released from 1943 to 2020 showed high complexity. Reading from the top of the pedigree map to the bottom. The upper dots represent the origin (first crossing) of the pedigree map, whereas the lower dots represent the final pedigree products (terminal progeny). The size of the dot represents the contribution of each variety's genes to the rice gene pool. The green dot indicates an improved variety released after 2011; yellow to light green dots indicate varieties released between 2000 and 2010; and orange to dark red dots indicate varieties released before 2000

	Cina	DGWG	Latisail	Peta	Tai. Native 1	Hipa Jatim3	IR64	Sigadis	Bayang cin B	Tang. Rotan	CR55
■ Over Decade	3.3%	3.8%	3.3%	6.6%			11.0%				
■ 2010-2019	1.4%	1.8%	1.4%	2.9%	1.4%	1.3%	6.5%				
■ 2000-2009	3.9%	4.4%	3.9%	7.7%	3.1%		15.6%				
■ 1990-1999	5.3%	6.8%	5.3%	10.6%	4.5%		13.3%				
■ 1980-1989	6.2%	6.5%	6.2%	12.4%	5.3%		11.2%				
■ 1970-1979		10.6%		9.9%	6.4%		10.1%				11.5%
■ 1960-1969	12.1%		12.1%	24.2%			8.0%	10.4%	6.0%	10.4%	

Figure 5. Shifting contribution of the most influential ancestors (highest five) to the Indonesian rice gene pool for each decade. COP: coefficient of parentage

Two ancestors, Peta and IR64, showed a considerable influence on rice varieties released over six decades (Figure 3 and 5). The IR64 variety could be considered an ancestor as well as an improved variety because of its high contribution to the pedigree map (Figure 2). In the early decades of rice breeding, four ancestors (Sigadis, Bayangcin B, Tangkai Rotan, and CR55) showed a noteworthy influence on the development of the Indonesian rice gene pool. Over time, the influence of these ancestors decreases. It might be that the progenies of these rice ancestors were undesirable and less favorable to Indonesian people. On the other hand, the IR64 variety and its progeny showed influence from the early decades to the last decade of Indonesian rice development.

Ancestor contribution to the Indonesian rice improved variety

There was a 9.1% decrease in the effect of IR64 in the 2010-2019 decade compared to the 2000-2009 decade (Figure 5). After 2010, the focus of Indonesian rice breeding was assembling rice with a specific location and purpose. In addition, the government has bred hybrid rice (HIPA code) and tidal rice (Inpara code) with more diverse parents in the last decade (Table 1).

INPARI, INPAGO, and INPARA rice plant types have a strong relatedness to the IR64 variety (Table 1). Only hybrid rice plant types have no relationship to the IR64 variety. The four classical ancestors of DGWG, Taichung Native1, China, and Latisail strongly affected all irrigated rice plant types (11.22%) and upland rice plant types (8.30%) in the gene pool. Meanwhile, Inpago9, Luhur 2, and UPLRI ancestors specifically set the background for upland rice plant type.

Among the types of rice plants, the tidal rice plant type had the most diverse ancestor. Twenty-one ancestors occupied the five highest contributions to the tidal rice plant background. Inpara7 and Inpara9 and the parents introduced from IRRI (IRRIpara4 and IRRIpara5) had a strong influence on tidal rice plants in Indonesia (Table 1). Meanwhile, the A1, Hipa7, and Hipa3 varieties heavily influenced the Indonesian hybrid rice plant. The ten rice varieties that showed strong relatedness to the Indonesian rice gene pool had a crossing history with IR64 or with their derivatives such as Ciherang, Cigeulis, and Cibogo (Table 2). The landraces of Pepe, Tukad Unda, and Wera contributed more than 1.5% to the Indonesian rice gene pool and were developed from the crossing between landrace and IR64.

Discussion

The coefficient of parentage (COP) that measures the chances of two genes in a child (progeny) is the same because the offspring could be estimated in advance of the high performance of a cross combination. In the current study, COP could estimate the genetic background of Indonesian rice and describe the contribution of ancestors over decades to the Indonesian rice gene pool (Table 1 and Figure 5). The breeding programs widely used pedigree analysis to trace the genetic background of a particular character and to know the ancestor or parent that contributed the most to one variety (Egan et al. 2019). Estimation of the diversity of rice and grasses can also be done using COP values (Setotaw et al. 2013; Brasileiro et al. 2014; Egan et al. 2020).

Table 1. The five highest contributions of ancestors according to rice plant type, released from 1967 to 2019

INPARI		INPAGO		INPARA		HIPA	
Ancestor/ genuine parent	Contri.	Ancestor/ genuine parent	Contri.	Ancestor/ genuine parent	Contri.	Ancestor/ genuine parent	Contri.
IR64	11.22%	IR64	8.30%	Inpara7, Inpara9Agritan, IRRIpara4, IRRIpara5	8.17%	A1	4.78%
Peta	4.53%	Inpago9	4.92%	IR64	4.67%	Hipa7, Hipa3	4.31%
DGWG	2.89%	Luhur2	4.43%	Batang Ombilin, Mesir, B10597FKN18, IR6008023, Bio12, Beras Merah, B10600FKN7, B117IU10	4.09%	Hipa8, Hipa5 Ceva, Hipa9	3.83%
Tai. Native 1	2.28%	Peta	4.18%	Peta	2.73%	Hipa11, Hipa Jatim3	3.35%
Cina. Lat sail	2.26%	UPLRI	3.94%	Cibodas, IR600803, IRBB21, Luhur2, Inpari 24 Gabusan	2.04%	Hipa Jatim2, Hipa10, A6, Hipa4	2.87%

Note: INPARI: lowland rice; INPAGO: upland rice; INPARA: tidal rice; HIPA: hybrid rice

Table 2. The ten most important rice varieties have contributed to the Indonesian rice gene pool

Variety name	Total COP	Contribution (%)	Release year	Pedigree
Pepe	34.39	1.562%	2003	Simariti3/ IR64
Tukad Unda	34.27	1.556%	2000	IR64/Balimun Putih
Wera	34.27	1.556%	2001	Hawara Bunar/IR64
Inpari1	33.56	1.524%	2008	IR64/1/IRBB-7//IR64
Ciherang	33.24	1.509%	2000	IR18349-53-1-3-1-3/IR19661-131-3-1//IR19661-131-3-1-///IR64/////IR64
Batang Gadis	32.27	1.465%	2001	IR 64/NDR 308//IR 64
Wayapo Buru	31.53	1.432%	1998	IR18349-53-1-3-1/IR19661-131-3-1//IR19661-13-1-3-1-3///IR64////IR64
Inpari 45 Dirgahayu	31.15	1.414%	2019	Cibogo / Ciherang
Singkil	30.03	1.364%	2001	IR35432-33-2/IR19661-131-3-1//Ciliwung///IR64
Inpari 16 Pasundan	29.72	1.350%	2011	Ciherang/ Cisadane// Ciherang
Cigeulis	29.06	1.320%	2002	Ciliwung/Cikapundung//IR64
Inpari 22	28.66	1.302%	2012	IR42/IRBB5// Ciherang///Towuti
Cibogo	28.55	1.297%	2001	S487B-75/2*IR19661-131-3-1//2*IR64

Genetic diversity is necessary for meaningful genetic advances in plant breeding programs. A broader genetic background will prevent the occurrence of genetic vulnerability in plants. Thomson et al. (2007) examined the diversity of 330 Indonesian rice accessions using 30 SSR markers and reported that Indonesian rice cultivars generally belong to the indica group (68%), with a low level of genetic diversity of 0.46 and 32% in the tropical japonica rice group. Narrow diversity was also reported among the 289 rice accessions for blast resistance and leaf blight (Vasudevan et al. 2014; Raboin et al. 2016; Li et al. 2022).

It has long been predicted that Indonesia's rice cultivars have reached a yield plateau and rice productivity tends to be sloping (Panuju et al. 2013). The main reasons for stagnant rice productivity are 1) the lack of controlling genes, which makes it difficult for plants to adapt to environmental changes; and 2) the repeated use of the same parents, which reduces genetic diversity and makes it difficult to create new gene combinations (Fehr 1987; Sleper and Poehlman 2006).

Yoshida et al. (2009) reported the total land area of the 10 most widely planted rice cultivars in Indonesia, and approximately 50.6% had an IR64 rice background. This current study confirmed that the contribution of IR64 to the Indonesian rice gene pool decreased slightly, although it still makes an enormous contribution compared to other ancestors from 2010 to 2019. This suggests the efforts of Indonesian rice breeders to extend the genetic background of the Indonesian rice gene pool by using different parents in crosses. This can be seen clearly after the release of hybrid rice and specific rice for certain environments (Figure 4). However, IR64 is still a big part of the genetic background of both irrigated (INPARI code) and upland (INPARA code) rice in Indonesia. Indonesia still needs to put in more work to increase the genetic variety of both lowland and upland rice.

The Ciherang variety, released in 2000, has replaced the dominance of IR64 since 2007 and occupied more than 40% of the planted area of paddy land in 2011. Unfortunately, the genetic background of Ciherang was strongly influenced by IR64 (67.5%) and IRRI parents. Ciherang's planted area decreased by around 29% in 2020

(Pertanian 2021). Currently, Inpari 32 is one of the top three most widely planted varieties after Ciherang and Mekongga (Pertanian 2021). The planting area of Inpari 32 reached approximately 800 thousand hectares (about 8% of the total planted area of rice in Indonesia). Inpari 32 was an improved variety of Ciherang released in 2013.

It seems that IR64 and its progenies can be well adapted to the Indonesian environment and have good eating qualities, thus dominating rice cultivation in Indonesia. Interestingly, all IR64 progenies with Indonesian local varieties (Pepe, Tukad Unda, Wera-Table 2) did not show their dominance in the area of cultivation. IR64 can work well with parents from IRRI to make rice plants that do well and have a good eating quality.

The breeding for the enrichment of the IR64 genetic background has been crossed with the wild-type *Oryza rufipogon* for improving crop yields and other important traits (Septiningsih et al. 2003). Knowledge of the recurrent genetic background and determination of quantitative trait loci (QTL) positions that are unrelated to the negative character of donor parents is essential for the success of rice breeding programs.

The acceleration of the breeding program for quantitative characters is not as fast as the improvement of simple genic characters. The strategy of using the molecular markers technique for quantitative characters is often summarized in a QTL map depicting the spread of markers on chromosomes. The establishment of a major QTL for the selection process requires validation research using plants' different genetic backgrounds (Swamy et al. 2013; Bakti and Tanaka 2019). The presence of genes and genetic background are critical for the success of rice breeding programs.

In Indonesia, stagnant crop yield growth among rice plants is a significant issue due to a decline in genetic diversity. The reduction in genetic diversity of rice plants is attributable, in part, to the use of the same parents in breeding programs and consumer preference for a single main variety. There are 280 ancestors within the rice gene pool. The pedigree map displays the complexity of rice breeding in Indonesia. The four classical ancestors of DGWG, Taichung Native1, China, and Latisail, had a significant influence on the irrigated rice plant types (11.22%) and upland rice plant types (8.3%) of the rice gene pool. Since 2009, the proportional effect of IR64 has decreased. Despite this, it continues to dominate the genetic background of irrigated rice in Indonesia. Meanwhile, Inpago9, Luhur 2, and UPLRI ancestors established the basis for the upland rice plant variety. In conjunction with their IRRI-introduced parents (IRRIpara4 and IRRIpara5), Inpara7 and Inpara9 had a substantial impact on Indonesian tidal rice plants. The A1, Hipa7, and Hipa3 varieties are significantly influenced by Indonesian hybrid rice plants.

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