Diallel analysis of length and shape of rice using Hayman and Griffing method

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Research Article

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Abstract: Length and shape of rice are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of length and shape of rice requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of length and shape of rice using full diallel analysis. The plant material used was a full diallel cross-population of six rice genotypes, namely, Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari, and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\text{reciprocal}}$, were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio were used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive gene action influencing the length and shape of rice. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high, revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape

1 Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food; therefore, it has an important role in global food security [1,2]. Indonesia is the world's third largest rice producer, and it is also one of the world's main rice consumers [3]. More than 80% of Indonesian people consume rice as a staple food, and it contributes 62.1% of the energy intake [4]. It is the main source of income of approximately 18 million household farmers [5]. It also has strategic value from economic, environmental, social, and political aspects [6,7]. Therefore, rice self-sufficiency in Indonesia is required to fulfill the needs.

The government's program for rice self-sufficiency has four main targets, that is, to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize imports [8]. Improving yield potential of rice varieties through plant breeding plays an important role to increase the national production. High yielding rice varieties contributed to 56% of the national rice production [6]. Thus, rice breeding in Indonesia aims to develop high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests [9].

Yield still is the main target of rice development; however, rice grain quality is now getting more attention due to increasing awareness of its importance [10]. Rice grain quality determines the market price, consumer acceptability of a variety, and consumer acceptability of a variety and becomes the second goal of rice plant breeding after yield [11,12]. High yielding varieties with high rice grain quality are easy for farmers to adopt [13].

Grain quality consists of rice length, rice shape, rice translucency, and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality, that is, rice appearance, length and shape of rice, which is followed by cooking quality and taste [14,15]. Hence, length and shape of rice determine the level of rice market demands and

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price [16]. Therefore, breeding rice varieties that encompass desirable length and shape of rice became a major concern for rice breeders in Indonesia.

A rice breeding program begins with increasing genetic diversity by crossing rice genotypes with wide genetic differences, followed by the traits selection of interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information [17]. An effective and efficient breeding program is determined by the genetic information that controls the inheritance of traits under study [18,19]. Sometimes selection in segregation populations results in low-quality progenies to fulfill breeding objectives [20]. Hence, it is necessary to know genetic information of traits before determining a breeding and selection method [21]. Diallel analysis is one of the manners to obtain genetic information for grain quality traits in rice such as length and shape of grain.

Diallel analysis is a mating design, which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny [22,23]. This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation [24,25]. It is also the quickest method for understanding the genetic control of the inheritance of quantitative traits [26].

Diallel analysis can be carried out using Hayman and Griffing methods. Hayman's method can be used to study gene action, genetic components, and heritability [27], whereas Griffing's method [28] is used to estimate general combining ability (GCA), specific combining ability (SCA), and reciprocal effects. Also, it can be used to calculate additive and non-additive effects. Hayman and Griffing methods are often used together for interpretation of complementary data [21]. Hayman and Griffing methods have been used (either one or both) to obtain genetic information of plant traits. It has been widely used to study genetic parameters of length and shape of rice [29–41]. The results of the study show various conclusions. Furthermore, this research is rarely performed in Indonesia [42]. The present research was conducted to study genetic components of F_1 population from a cross of six parents with various lengths and shapes of rice. The purpose of this study was to estimate the genetic parameters of length and shape of rice using the full diallel analysis.

2 Materials and methods

2.1 Location of the experiment

A field experiment was conducted at the experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at coordinates 7°24′28.7″LS and 109°15′13.3″N, and it is at an altitude of 112 m above the sea level. The experiment was carried out from June 2019 to December 2019.

2.2 Plant material

Six rice genotypes, i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari, and Tarabas rice, were used as the parents in this study. These parents have different origins and have various length and shape of rice (Table 1). The research material used consisted of 36 rice genotypes, which were developed from full diallel crosses among six parents. It consists of 6 parents, 15$F_{1,}$ and 15$F_{1\text{reciprocal}}$.

2.3 Experimental design

The experimental design was a randomized complete block design with three replications. Seeds of 36 genotypes were sown in a seed box for 2 weeks, followed by transplanting to 35 cm × 40 cm polybags containing 8 kg of inceptisol soil. Each polybag consisted of one plant per genotype. Recommendations for rice cultivation and plant protection were adopted. Fertilizer applications of 0.4 g N/polybag and 1.0 g N-P-K/polybag was applied twice i.e., 10 days and 20 days after transplanting.

2.4 Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of length and shape of rice. The shape of rice is determined by rice length-to-width ratio [43]. Therefore, the observed trait in this study is rice length, width, and

Table 1: Six rice genotypes used for diallel mating design

No.	Genotype	Length and shape of rice	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

length-to-width ratio measured with help of digital caliper. Data collected were used for diallel analysis to estimate the genetic parameters of length and shape of rice. Diallel analysis was perfomed according to Hayman and Griffing method-1 [44] and the results were calculated using the software Microsoft® Excel.

1. Analysis of variance for F_1 in full diallel crosses

   Analysis of variance for F_1 in full diallel crosses for length and shape of rice followed the statistical model

$$Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}, \tag{1}$$

where m is the general mean, T_{ij} is the effect of $i \times j$th genotype, b_k is the effect of kth block, $(bT)_{ijk}$ is the interaction effect, and e_{ijkl} is the error effect.

2. Genetic components of variation

Genetic components of variation were calculated using the following formulas:

$$\text{Regression coefficient of } b\ (W_r, V_r) = \frac{\text{Cov}(W_r, V_r)}{\text{Var}(V_r)}, \tag{2}$$

where W_r is the covariance between parents and their offspring, V_r is the variance of each array, $\text{Cov}(W_r, V_r)$ is the covariance of (W_r, V_r), and $\text{Var}(V_r)$ is the variance of V_r.

$$\text{Additive genetic variance } (D) = V_{0L0} - E, \tag{3}$$

where V_{0L0} is the variance of parents and E is the environmental variance.

$$\text{Dominance variance} \quad H_1 = V_{0L0} - 4W_{0L01} + 4V_{1L1} - (3n - 2)E/n, \tag{4}$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, V_{1L1} is the mean variance of the arrays, n is the number of parents, and E is the environmental variance.

$$\text{Proportions of positive or negative genes in the parent} \quad H_2 = 4V_{1L1} - 4V_{0L1} - 2E, \tag{5}$$

where V_{1L1} is the mean variance of the arrays, V_{0L1} is the variance of the mean of arrays, and E is the environmental variance.

$$\text{Mean covariance of additive and dominance} \quad F = 2V_{0L0} - 4W_{0L0} - 2(n - 2)E/n, \tag{6}$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, n is the number of parents, and E is the environmental variance.

$$\text{Dominance effect} \quad h^2 = 4(M_{L1} - M_{L0})^2 - 4(n - 1)E/n^2, \tag{7}$$

where $(M_{L1} - M_{L0})^2$ is the difference between the mean of the parents and the mean of their n^2 progeny, n is the number of parents, and E is the environmental variance.

$$\text{Environmental variance} \quad E = 1/r(\text{Error SS} + \text{Rep. SS})/[((r-1) + (c - 1)) \times (r - 1)], \tag{8}$$

where Error SS is the sum square of error, Rep. SS is the sum square of replication, r is the number of replications, and c is the number of errors.

$$\text{Average degree of dominance} = (H_1/D)^{1/2}, \tag{9}$$

where H_1 is the dominance variance and D is the additive genetic variance.

$$\text{The proportion of genes with positive and negative effects in the parent} = H_2/4H_1, \tag{10}$$

where H_1 is the dominance variance and H_2 is the proportion of positive or negative genes in the parent.

$$\text{The ratio dominant and recessive gene in the parent} = [(4DH_1)^{1/2} + F]/(4DH_1)^{1/2} - F, \tag{11}$$

where D is the additive genetic variance, H_1 is the dominance variance, and F is the mean covariance of additive and dominance.

$$\text{Number of gene groups} = h^2/H_2, \tag{12}$$

where h^2 is the dominance effect and H_2 is the proportion of positive or negative genes in the parent.

$$\text{The coefficient correlation between } (W_r + V_r) \text{ and } Y_r(r) = \frac{\text{Cov}\,(W_r + V_r),\, Y_r}{\sqrt{\text{Var}\,(W_r + Y_r) \cdot \text{Var}(Y_r)}}, \tag{13}$$

where $(W_r + V_r)$ is the parental order of dominance, Y_r is the parental measurement, $\text{Cov}(W_r + V_r)$ is the covariance of $(W_r + V_r)$, $\text{Var}(W_r + V_r)$ is the variance of $(W_r + V_r)$, and $\text{Var}(Y_r)$ is the variance of Y_r.

$$\text{Broad-sense heritability} \quad h^2_{bs} = (1/2D + 1/2H_1 - 1/4H_2 - 1/2F)/(1/2D + 1/2H_1 - 1/4H_2 - 1/2F + E), \tag{14}$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

$$\text{Narrow-sense heritability} \quad h^2_{ns} = (1/2D + 1/2H_1 - 1/2H_2 - 1/2F)/(1/2D + 1/2H_1 - 1/2H_2 - 1/2F + E), \tag{15}$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

2.5 Combining ability analysis

The statistical model for the analysis variance of combining ability that was used was as follows:

$$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl}, \tag{16}$$

where Y_{ij} is the mean of $i \times j$th genotype, m is the general mean, g_i is the general combing ability (gca) effect of ith parent, g_j is the general combing ability (gca) effect of jth parent, S_{ij} is the interaction, i.e., SCA effect, r_{ij} is the reciprocal effect, and $\frac{1}{bc}\sum\sum e_{ijkl}$ is the mean error effect.

$$\text{GCA variance } (g_i) = \frac{1}{2n}\sum(Y_{i.} + Y_{.j}) - \frac{1}{n^2}Y^2, \tag{17}$$

where $Y_{i.}$ is the total mean value of ith genotype cross, $Y_{.j}$ is the total mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\begin{aligned}\text{SCA variance } (s_{ij}) = {} & \frac{1}{2}(Y_{ij} + Y_{ij}) - \frac{1}{2n}(Y_{i.} + Y_{.i} + Y_{j.} \\ & + Y_{.j}) + \frac{1}{n^2}Y,\end{aligned} \tag{18}$$

where Y_{ij} is the mean of $i \times j$th genotype, Y_{ji} is the mean of $j \times i$th genotype, $Y_{i.}$ is the total of mean value of ith genotype cross, $Y_{.i}$ is the total of mean value of ith genotype selfing, $Y_{j.}$ is the total of mean value of jth genotype cross, $Y_{.j}$ is the total of mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\text{Reciprocal variance } (r_{ij}) = \frac{1}{2} = (Y_{ij} - Y_{ji}), \tag{19}$$

where Y_{ij} is the mean of $i \times j$th genotype and Y_{ji} is the mean of $j \times i$th genotype.

3 Results and discussion

3.1 Analysis of variance for genotypes

Analysis of variance showed significant difference among genotypes for length and shape of rice grain (Table 2). Similar findings were also reported by Bano and Singh [39] and Hijam et al. [37]. Significantly different in the analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis [44]. Thus, significant differences among the genotypes for length and shape of rice indicate that they are suitable for further genetic studies.

Table 2: Analysis of variance for F_1 in a full diallel cross for length and shape of rice

Source of variation	Degrees of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0.06	0.01
Genotype	35	3.16*	1.51*
Error	70	0.04	0.02

*Significantly different at the level of 5%.

3.2 Genetic components of variation

3.2.1 Gene interaction

The values of regression coefficient of $b(W_r, V_r)$ for length and shape of rice (1.20 and 1.15, respectively) were not significantly different from one (Table 3). Similar results reported by Bano and Singh [39] for kernel length before cooking (rice length) and kernel length/breadth ratio before cooking (rice length). The value of regression of coefficient of $b(W_r, V_r)$ may be used to determine the gene

Table 3: Estimates of genetic components of variation for length and shape of rice

Genetic components	Rice length (mm)	Rice shape
$b(W_r, V_r)$	1.20ns	1.15ns
D	2.72*	1.36*
H_1	0.26*	0.19*
H_2	0.25*	0.17*
F	0.44*	0.33*
h^2	−0.01ns	0.04ns
E	0.01ns	0.01ns
$(H_1/D)^{1/2}$	0.31	0.38
$H_2/4H_1$	0.23	0.22
Kd/Kr	1.71	1.95
h^2/H_2	−0.03	0.22
$r[(W_r + V_r), Y_r]$	0.69	0.89
h^2_{bs}	0.99	0.99
h^2_{ns}	0.94	0.91
Ratio of $h^2_{ns}:h^2_{bs}$	0.95	0.92

*Significantly different at the level of 5%, ns = not significantly different.

interaction of a trait. Based on t test, a significantly different value of $b(W_r, V_r)$ from one indicates gene interaction, while a non-significantly different value of $b(W_r, V_r)$ from one reflected no gene interaction [44]. It means that there is no interaction between genes controlling length and shape of rice in this study.

3.2.2 Additive (D) and dominance (H_1) variance

Additive (D) and dominance (H_1) variance were significantly different for length and shape of rice (Table 3). Significantly different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits [45], so that length and shape of rice are influenced by both additive and non-additive types of gene action. Similar findings were also observed by Kato [29], Fu et al. [31], Daradjat and Rumanti [42], Kumar et al. [32,33], Rafii et al. [30], and Senthil Kumar and Mudhalvan [38] for length and size of rice.

The results showed the value of additive variance (D) for length and shape of rice is 2.72 and 1.36, respectively, and the value of dominance variance (H_1) for length and shape of rice is 0.26 and 0.19, respectively (Table 3). These showed that the influence of additive variance is greater than dominance variance ($D > H_1$) for length and shape of rice. Higher magnitude of additive variance (D) indicated the greater role of additive gene action, while dominance variance indicated the greater importance of non-additive gene action *vice versa* [40,45]. The value of the additive variance, which is greater than the dominance variance, indicates the increasing importance of additive gene action [32,33]. This means that in this study, length and shape of rice are more influenced by additive gene action than non-additive gene action. These results are in accordance with the findings of Kato [29] and Thattil and Perera [46] for length and size of rice. However, Daradjat and Rumanti [42] and Senthil Kumar and Mudhalvan [38] reported that the non-additive gene action dominated over additive gene action for length and size of rice.

3.2.3 Gene distribution in the parents

Gene distribution in the parents can be determined by H_2 values. The results showed that the H_2 values for length and shape of rice were significantly different (Table 3). This indicates that the genes determining the inheritance of length and shape of rice are not evenly distributed among the parents. Genes controlling length and shape of rice that are not evenly distributed in parents have also been reported [38].

Proportion of positive genes to negative genes is indicated by the value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating the number of positive genes would be higher than negative genes. On contrary, the value of the H_1 is smaller than H_2 reflecting that the number of positive genes would be fewer than the negative genes [21,47]. Table 3 shows that the value of H_1 is 0.26 and 0.19, respectively, and the value of H_2 is 0.27 and 0.17, respectively, for length and shape of rice. It shows that the value of H_1 is greater than H_2 for length and shape of rice, meaning that positive genes are more involved in determining length and shape of rice than negative genes. The results were in agreement with those of Raju et al. [40].

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate that positive and negative genes are not present in unequal proportions in the parents [45,48]. The results showed the value of $H_2/4H_1$ for length and shape of rice is 0.23 and 0.22, respectively (Table 3). They were lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies [38–40].

3.2.4 Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3 shows the value $(H_1/D)^{1/2}$ of length and shape of rice is less than 1 (0.31 and 0.38, respectively), which indicated the existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato [29].

3.2.5 Dominance effect

Dominance effect is indicated by the h^2 value. Table 3 shows that h^2 values were not significantly different for length and shape of rice. This indicated no difference in average deviation of F_1 from most parents [47].

3.2.6 Environmental variance

Table 3 shows that environmental variance exhibited no significant influence on length and shape of rice. This reflected no influence of environmental factor on the expression of the traits studied [45]. Therefore, it is known that the expression of length and shape of rice is more influenced by genetic than environment effects.

3.2.7 Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent [47,49]. A ratio of Kd/Kr greater than one indicates more dominant genes in the parent; conversely, the ratio of Kd/Kr smaller than one indicated more recessive genes in the parent [44]. The results showed a positive value of F component, and a ratio of Kd/Kr of the length and shape of rice is greater than one (1.71 and 1.95, respectively) (Table 3), which indicated more dominant genes in the parent for length and shape of rice. The same finding was reported by Raju et al. [40].

3.2.8 Number of gene groups

Component of h^2/H_2 gives an indication of the number of gene groups that control a trait. The h_2/H_2 values of length and shape of rice are −0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes, which are responsible for their genetic control [45]. As a result, length and shape of rice are controlled by at least a single group of genes.

3.2.9 Direction and order of dominance

The positive value of the correlation between ($W_r + V_r$) and Y_r and close to unity indicates that dominant alleles have predominantly negative effects, i.e., acting in the direction of lower yields [50]. A positive value is obtained in the correlation ($W_r + V_r$) and Y_r for length and shape of rice (Table 3). That is, in length and shape of rice, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value ($W_r + V_r$) component. Based on the value ($W_r + V_r$) in Table 4, the dominance order of length and shape of rice was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9, and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (W_r) and variance (V_r) in Figures 1 and 2.

Table 4: Value ($W_r + V_r$) of length and shape of rice

Genotypes	Rice length	Rice shape
Basmati Delta 9	2.32	1.30
Basmati Pakistan	2.46	1.43
Inpari 31	1.99	0.93
Inpago Unsoed 1	1.00	0.37
Koshihikari	1.75	0.69
Tarabas	1.87	0.73

Distribution of parental array points along the regression line reflected genetic diversity of a trait [51]. The array point was scattered along the regression line for length and shape of rice, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (W_r) and variance (V_r) reflects the order of dominance. The position of parent which is closer to zero point indicating it is the most dominant genes [47,50]. Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for length and shape of rice. Mostly, Basmati Pakistan contains a recessive gene for length and shape of rice since it is the farthest from zero. Basmati, which has extra-long and slender rice, contains the most recessive gene, and this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result is in agreement with the findings of Kato [29], Murai and Kinoshita [41], and Ali et al. [52].

The straight line intercepted the vertical axis (W_r) above the origin for length and shape of rice (Figures 1 and 2). The straight line that intercepted the vertical axis (W_r) above the origin indicated partial dominance of the genes controlling a trait [21,50,51]. This reveals that length and shape of rice were controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid-parent value and not having overdominance, which exceeds the best parent [53]. This is reflected in the h^2 value of length and shape of rice, which is not significantly different, so that there is no difference between the F_1 average and the parents' average.

3.2.10 Heritability

Broad sense heritability (h^2_{bs}) estimates for length and shape of rice are similar to 0.99. Narrow sense heritability (h^2_{ns}) estimates for these traits are 0.94 and 0.91,

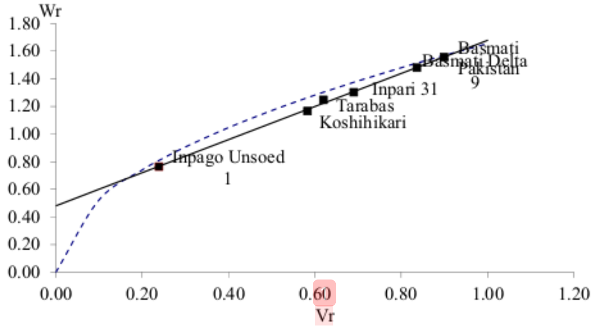

Figure 1: Covariance (W_r) and variance (V_r) graph of rice length.

respectively (Table 3). Values of heritability more than 0.5 are categorized as high (Stansfield, 1991); thus, broad-sense heritability (h^2_{bs}) for length and shape of rice is categorized as high heritability. Similar findings were reported by previous studies [54].

The estimated value of broad-sense heritability indicates the relative contribution of genetic factors to the variation of the observed trait [55]. A high broad-sense heritability value indicates that traits are more influenced by genetic than environmental factors [56]. In this study, broad-sense heritability estimate of length and shape of rice is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors was also reflected in the non-significant environmental variance observed in Table 3.

Narrow sense heritability estimates indicate the role of additive gene action in a trait. Estimates of narrow-sense heritability indicate more additive gene action than non-additive gene action [4,57–59]. In this study, the narrow sense heritability estimate of length and shape of rice was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow-sense heritability and broad-sense heritability reflects the role of additive and non-additive gene action in a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action [60]. Table 3 shows that the ratio of narrow-sense heritability and broad-sense heritability is 0.95 for rice length and 0.92 for rice shape, respectively. This indicates that additive gene action determines size and shape of rice more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population [21] so that the selection of length and shape of rice may be carried out using individual selection such as pedigree. This finding was in agreement with that of Raju et al. [40].

3.3 Combining ability estimation of length and shape of rice

Gene action and cytoplasm influence of the female parent for a trait can be predicted through combining ability. Variances of GCA, SCA, and reciprocals were obtained from diallel analysis of Griffing method-1. Variances of

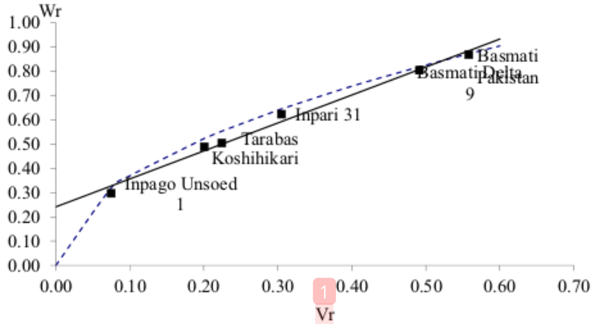

Figure 2: Covariance (W_r) and variance (V_r) graph of rice shape.

Table 5: Analysis of variance of combining ability and GCA:SCA ratio of length and shape of rice

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
GCA	5	6.909*	3.154*
SCA	15	0.138*	0.092*
Reciprocal	15	0.020^{ns}	0.006^{ns}
Error	70	0.015	0.007
GCA:SCA ratio		50.060	34.280

*Significantly different at the level of 5%, ns = not significantly different.

GCA and SCA are associated with non-additive and additive gene actions, respectively [61–63]. Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait [64].

GCA is endorsed to additive gene action, and SCA is mainly attributed to non-additive gene action [59,65]. This study shows significant effects of GCA and SCA on length and shape of rice (Table 5). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these traits. This finding was in agreement with that of Singh et al. and Soni et al. [66,67].

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio [68]. A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action [69]. Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait, and conversely, a GCA:SCA ratio less than one reflected that non-additive gene action has more influence on the expression of a trait [70]. In this study, ratio of GCA:SCA of length and shape of rice is greater than one (50.060 and 32.280, respectively) (Table 5), indicating that additive gene action is more influential than non-additive gene action on the expression of these traits. These results agree with the estimation of gene action using the Hayman method as described previously. Additive gene action in length and shape of grain has been previously reported [66,67]. Therefore, the selection of length and shape of grain will be effective using pedigree method [71].

Non-significant reciprocal effects were observed for both length and shape of rice (Table 5). This indicated that there was no influence of the female parent cytoplasm on the inheritance of these traits [64,72] so that the size and shape of the rice are not affected by the female parent cytoplasm.

4 Conclusion

The influence of additive and non-additive gene actions on length and shape of rice was confirmed. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high. This revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations might be combined into one population in the next selection generation.

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